INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

The concept of equilibrium in population ecology

by

Christian Haak

Submitted in partial fulfillment of the requirements for
the degree of Doctor of philosophy

at
Dalhousie University
Halifax, Nova Scotia, Canada
September 2000

0-612-57352-4

DALHOUSIE UNIVERSITY

FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "The Concept of Equilibrium in Population Ecology"

by Christian Haak

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Dated: September 8, 2000

External Examiner

Research Supervisor

Research Supervisor

Examining Committee

[redacted]

DALHOUSIE UNIVERSITY

DATE: September 12, 2000

AUTHOR: Christian Haak

TITLE: The concept of equilibrium in population ecology

DEPARTMENT OR SCHOOL: Interdisciplinary studies

DEGREE: Ph.D **CONVOCATION:** October **YEAR:** 2000

Permission is herewith granted to Dalhousie University to circulate and to have copied for non-commercial purposes, at its discretion, the above title upon the request of individuals or institutions.

[redacted]

Signature of Author

Table of contents

List of figures

List of tables

Abstract

This thesis investigates the equilibrium concept in population ecology. Equilibrium is a state in which something is in balance. What is in balance and why? This two-part question has concerned ecologists for decades and is still debated today. One influential account postulates density-dependent mechanisms in the population as leading to equilibrium densities. This account suggests a form of self-regulation of populations. However, the existence of density-dependence and even the importance of regulation are hotly contested issues in ecology.

Focusing on the debate about equilibrium, I follow a form of naturalized epistemology, in which knowledge is to be understood by looking into the workings of science itself. I examine, in particular, the scientists' reasons to hold on to the concept of equilibrium. I describe these reasons as justifying the use of the concept. To understand the debate about equilibrium we need to answer the question: "How is equilibrium justified?"

I show that during the debate the justification of equilibrium has changed due to a change in reference of 'equilibrium'. With 'equilibrium' being defined as the outcome of density-dependent processes, equilibrium has come to be understood as a statistical property of a data set. This change in how the application of the concept is justified is a change that has itself been negotiated by scientists in debating their claims about equilibrium. I investigate this negotiation process and argue that it cannot be explained away by referring to the use of models to understand equilibrium. On the contrary, thinking of theories as models makes the investigation of negotiations even more important.

The negotiation of equilibrium is a normal scientific process. What is negotiated is the relation between evidence and theory, and I maintain that this relation has to be understood in historical terms. The justification of the equilibrium concept is based on evidence, but also on interests, and scientific practice. Although this historical perspective does not explain all aspects of how the concept is justified, it offers an understanding of the concept that is critical to evaluating its use in population ecology.

Acknowledgements

I wish to thank my parents Gisela and Hans Werner Haak for their encouragement and support through the years of this journey; also my companion Sue Watson for doing her best to teach me the English language and for lots of advice. I am extremely grateful to my supervisors Eric Mills and Richmond Campbell from whom I learned so much and who had to be extremely patient with the slow moving progress in this adventure. I also want to express my gratitude to my supervisory committee who provided me with helpful comments, especially Gordon McOuat, for introducing me to inspiring literature. Last but not least my thanks goes to Dalhousie University and the former Dean of Graduate Studies Judith Fingard for offering me financial support and making it possible for me to come to Canada.

Chapter 1: Introduction

My object of study is the equilibrium concept in population ecology. The idea of an equilibrium in nature is part of several cosmologies and various scientific disciplines. Equilibrium generally means that something is in balance, but many definitions exist that differ in their assumptions of what exactly is in balance and which mechanisms lead to a balanced state.

In ecology the assumption of equilibrium is connected to fundamental questions of the discipline. Community ecology, for example, aims to discover mechanisms that lead to a stability of communities, and whether communities, if disturbed, bounce back to their original composition. Community ecologists often talk about the resilience of communities, which describes the ability of a community to return to a stable equilibrium state.

In population ecology the concept of balance is related to the regulation of animal populations. The basic question is how, for example, the rapid increase of a pest population can be predicted. The claim that a mechanism exists that is responsible for the regulation of populations was made by the Australian ecologist A. J. Nicholson. According to him, populations are regulated by their own density through intraspecific competition. With this claim Nicholson provided a causal mechanism for an equilibrium state, which was the outcome of the regulation. Nicholson's reasoning has been criticized ever since. For critics of the equilibrium concept, the assumption of regulating factors acting in a density dependent fashion is misguided. Critics admit that populations are stabilized, but according to them, this is due to environmental factors. They argue that density-dependence is too weak to be acting in a heterogeneous environment.

Changes in equilibrium

Although the discussion today is not all that different from the time Nicholson suggested the notion of density-dependence, ecologists today have shifted their focus and ultimately the object of their research. During the early 1970s, statistical analysis of long term population data was emphasized, and an important step in the statistical treatment of population data was the inclusion of time series analyses. Today time series models incorporating different assumptions about density-dependence are tested against each other to determine which model best predicts the data. Density-dependence is tested as part of these models.

What is tested (statistical equilibrium)

The relevance of models in modern science is discussed in detail by philosophers of science who subscribe to the 'semantic view of theories', according to which models are representations of idealizing scientific theories. The theories are tested against the real world by using these models. Several models can represent the same theory, and a number of models for density-dependence exist.

Ecologists use several definitions of "model", but mostly agree that models are idealizations. Population ecologists also use idealized models, which describe population dynamics with only a few parameters. This fits the account of equilibrium given by most interpretations of the semantic view. However, problems arise in understanding the changes in the equilibrium concept when solely using the semantic view. In its most common interpretations the semantic view does not include an adequate historical analysis of change in theories. A closer look at the debate about the concept of density-dependence reveals that the equilibrium models used in today's tests do not represent density-dependent regulation as Nicholson meant it. The time series models used indicate the existence of statistical equilibrium, which, as the critics warn, should not be confused with ecological equilibrium. Proponents of the equilibrium approach admit that the models represent statistical equilibrium, and that further tests are necessary to detect ecological density-dependence in the data. However, for these further tests it is essential to first know whether the data are in statistical equilibrium. In this context equilibrium is equated with a stationary probability distribution in the data set.

This development constitutes a change in the meaning of 'equilibrium' which indicates a shift in research aims. By a 'change in meaning' I speak of what scientists are referring to in their use of the term equilibrium. Equilibrium, according to Nicholson, was the result of density-dependent mechanisms. Equilibrium in its modern form is statistical equilibrium, also called a stationary probability distribution of the data series. From an effort of testing for density dependent mechanisms in nature, the focus of the scientists has moved to the construction and testing of abstract models with parameters that represent statistical density-dependence.

I agree with the semantic view that models are not related to the world via meaning relations. However, a change in reference of the term 'equilibrium' is relevant in scientists' justification of equilibrium. I argue that an analysis of the change can only be achieved in a historical context in which the semantic view plays an important role but for which it might not be sufficient.

Analysis

Justification

Equilibrium in nature has become equilibrium in the data. I claim that the changes in reference are the result of a process I call 'negotiation of equilibrium'. The important aspect of this negotiation is that scientists' justification of the equilibrium concept has changed. By 'justification', I mean the reasons scientists give to use the equilibrium concept. Nicholson had an ontological commitment to the concept, i.e. it gave a causal explanation of why populations stayed in existence. Density-dependence, leading to equilibrium, was a causal account of how nature worked. Present approaches at first sight use the same justification of the concept of equilibrium, i.e. it is believed that populations are regulated by density dependent mechanisms. However, the present justification of the concept of equilibrium is that it leads to a better modeling of populations. The ontological commitment is to a statistical property of the data, the stationary probability distribution, which cannot be equated with equilibrium in nature.

I argue that the change in the equilibrium concept is not an approximation to answering the question of whether density dependent factors are responsible for population regulation. This, however, is claimed by ecologists, who say that improved computer power now makes a better analysis of data sets possible, and will eventually lead to a decision about whether density-dependence in Nicholson's sense is indeed present in nature.

It cannot be denied that statistical methods are far more sophisticated than during Nicholson's time. The statistical analysis also has a unifying effect because the same data analysis can be applied to data sets from different origins. Based on these achievements it might be that, in the future, density dependent factors will be discovered. At this point in time, however, progress in the discovery of equilibrium can only be interpreted as progress in data analysis. The testing of density-dependence has not led to an understanding of the validity of the original hypothesis. It has served as a vehicle for the shift in justification. Equilibrium is now part of a justification for certain modeling strategies.

Reasons for shift in justification

I focus on the development of scientific methodology and the account of modeling as the reasons for the shift in justification of the concept of equilibrium. Different accounts of the change are, however, possible. A change in the priorities of society might lead us to focus on realistic modeling because we want to know, for example, when a pest species will appear in large numbers instead of what are the fundamental causal mechanisms in nature. We would not need to know why it appears but when it appears. Another reason for the shift of justification of the concept of equilibrium might be changing interests by participants in the discipline or their institutions. Reasons for a change in justification can be numerous. This has been highlighted by the last decades of science studies.

My explanation of the change in justification of the concept of equilibrium is partial. I regard the developments in modeling and the statistical approach in ecology as important, but these are not the exclusive causes for the change in justification of the concept; they are, however, relevant for an understanding of the equilibrium concept. In a larger context the development of the equilibrium concept tells us that history and philosophy of science are linked.

Thesis

The investigation of the equilibrium concept in population ecology has revealed that the concept is connected to the idea of density-dependent growth of populations. Density-dependent mechanisms have been highly debated from the time of their introduction in the early 20th century. Efforts to test the existence of density-dependence have led to a statistical justification of 'equilibrium'. Closer analysis of this justification shows that it is different from what was initially suggested. Tests for density-dependence detect statistical density-dependence, which is an important characteristic of a data set and is important for further modeling. However, statistical density-dependence cannot be equated with ecological density-dependence. This is a change in justification of the concept and it has an effect on what scientists focus on in the real world. The testing, the negotiation of evidence in relation to theory, and other factors all play a role in the change of justification ultimately leading to a change in research focus. These findings are relevant for the relationship between history and philosophy of science. A philosophy of science that ignores the historical changes might explain what equilibrium is today, but it will not detect why scientists use certain models and why, in an ultimate sense, the models fit the data.

Overview of chapters

By comparing arguments in favor of equilibrium from the early twentieth century with more recent arguments, I will first establish the point that the justification of the equilibrium concept has changed over time. My method consists of analyzing the history of the debate which has shaped the recent discussion about equilibrium. Secondly, I analyze the change and its relevance for the philosophy and history of science.

Throughout the thesis I rely on publications in scientific journals. I use traditional archival material only sporadically and limit my sources to published material because, for my purposes, the public debate is the most telling. I do not deny that further results about the history of equilibrium can be gained from the study of traditional archival material such as personal letters; however, my thesis focuses on the notion of equilibrium as it manifests itself in scientific publications.

Chapter 2 provides an introduction into the nature of the equilibrium concept in general. When referring to the assumption of equilibrium, ecologists often use notions of physics and chemistry. I investigate these and claim that equilibrium is connected to specific mechanisms, and I suggest that it plays a role in the explanation of these mechanisms. I conclude that equilibrium is an important theoretical construct in many scientific disciplines. This claim is vague, as the notion of theory and its relationship to evidence is still being discussed. For this reason I focus on the idea of justification, investigating how the equilibrium assumption is justified given the data at hand. 'Justification' means the reasons scientists give for using the equilibrium concept.

My investigation focuses on equilibrium in population ecology, where its associated mechanism is density-dependent population growth, an idea that originated in the work of the ecologist A. J. Nicholson. Chapter 3 focuses on Nicholson and his view of equilibrium, which I contrast with the one held by Charles Elton, who seemingly rejected the assumption of a balance in nature. Closer analysis however, will reveal that Elton saw balancing mechanisms as being present in nature on a community level, whereas Nicholson believed in the overall regulation of nature on the population level. The chapter emphasizes the diversity of equilibrium usages in ecology. Different levels of investigation and different assumptions about the structure of nature lead to disagreements about the location of equilibrium, about how it is justified, and to different approaches toward the problem of regulation in nature.

Early in his career Nicholson used mathematical methods to substantiate his claims about a balance in nature because he did not believe he could justify his claims experimentally. Independently of Nicholson, other mathematical descriptions of biological equilibrium were developed in the early 20th century. To investigate the mathematical justification of equilibrium and the criticism of it I focus in Chapter 4 on the debates about the logistic curve. Like Nicholson's equations, the logistic curve implied a certain relationship between population growth rate and population size. These postulations, and the resulting justification of equilibrium, were questioned.

I describe the present debate about the exact relationship between growth rate and population size in Chapter 5. Mathematical justifications are still in use. They, as well as their assessment, have changed, however. After Nicholson, ecologists increasingly have used statistical tests of long term data sets to detect density-dependence. Such testing is a data based decision about which models fit the data best. This procedure leads to a shift in focus of the ecologists. Instead of testing for density-dependence in nature, the tests detect statistical density-dependence.

The proponents of the equilibrium approach are aware of this shift; however, they justify it by an improved ability to model population dynamics. This is a shift in justification of the equilibrium concept. In Chapter 6 I discuss this shift and the approach to modeling and testing that underlies it. The testing of models results in a different approach to equilibrium. Contrary to some philosophers of science, I claim that the testing of models requires an understanding of the historical development of their genesis, which, in the case of equilibrium, includes a negotiation between evidence and theory. Outside of their historical context what is tested for in equilibrium models cannot be understood. More generally, I conclude that a philosophical account that describes the testing of theories as a testing of models has to be historical in that it includes the efforts of the scientists to connect the models to the data. These connections are constantly negotiated, possibly resulting in a change of justification of concepts. As I will argue in Chapter 7, a purely historical account that ignores the importance of the semantic view and its philosophical consequences would not be adequate. An analysis of the justification of scientific concepts offers the opportunity for both a historical and a philosophical approach.

Chapter 2: Equilibrium in the non-ecological sciences and the relevance to ecology

In the 19th century, modern notions of equilibrium in chemistry (for example the law of mass action) and physics (the thermodynamic equilibrium introduced by Rudolph Clausius (1822-1888)) provided an important impulse for the disciplines. At that time population ecology, a discipline gaining influence in the 20th century, had not explicitly formulated the notion. This temporal priority of the equilibrium concept in the non-ecological sciences made possible certain conceptual influences on ecology.

This can be seen in that ecologists often use notions that are related to physics and chemistry. Chemical equilibrium is a good example since the behavior of molecules in chemical reactions is often used as an analogy for the balanced state in predator-prey systems (see for example Lotka 1925). The discipline of thermodynamics had an impact on ecology observable in the work of Eugene Odum, an influential 20th century American ecologist. Odum (1983 p.87) wrote that any system that does not conform to the laws of thermodynamics is "indeed doomed" so that Odum's description of ecological processes was based on these laws. The main focus of Odum's ecology was energy input, energy flow through the ecosystem and its output and the establishment of steady states. His use of the notion of a system in ecology is also derived from thermodynamics.

The notions of feedback and control are also used in population ecology. Here, as in cybernetics, the description of oscillations and their connection to regulation was central. Despite the fact that cybernetics seems to have disappeared as a scientific discipline since the 1960s, its impact is still noticeable. In the recent discussion about the regulation of populations, cybernetic vocabulary is used frequently.

The conceptual influence of non-ecological notions of equilibrium is not limited to definitions. More important is how mechanisms used in those disciplines were regarded as relevant to ecology. These are connected to the notion of equilibrium, which will become clear after I discuss equilibrium in the non-ecological sciences. The most basic and perhaps most intuitive notion of equilibrium often associated with ecological balance comes from the physical disciplines of statics and dynamics.

Statics and Dynamics

Definition

In physics the discipline of statics deals with the study of forces in equilibrium (Giancoli 1985). A body that is at rest is in static equilibrium and the sum of all forces on the body is zero. Because the forces of gravity are always acting on a body these forces have to be countered if a body is supposed to remain at rest. An architect, for example, has to know what the forces on a building are to keep the building in static equilibrium.

A body at constant motion is in dynamic equilibrium. Dynamic and static equilibrium are interchangeable if the observer moves with the body in tandem and thus changes the frame of reference (Thom and Welford 1994). The definition of dynamic and static equilibrium states that a body in equilibrium will not undergo any acceleration on its own. This definition leaves out an important property of an equilibrium state, namely a body's propensity to return to a previous position after a disturbance. I will call this propensity *rebounding behavior*.

Rebounding behavior

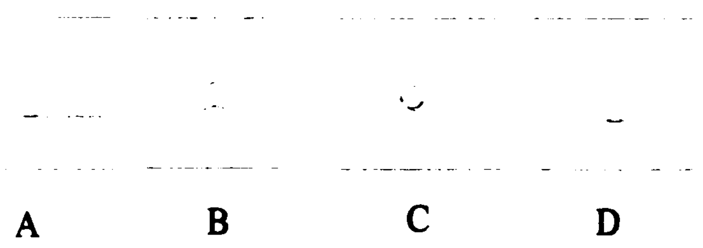


Figure 1: Forms of equilibria: neutral (A), unstable (B), metastable (C), stable (D)

Physicists describe equilibrium states according to their ability or propensity to rebound from disturbances. They distinguish four different kinds of equilibria: neutral, unstable, metastable, and stable (see Figure 1 adapted from Thom and Welford 1994).

Displacement from neutral equilibrium does not result in any rebounding behavior. An object in neutral equilibrium has zero propensity to rebound from a displacement. A ball on a horizontal table top will not regain its position but stays in its new position (Fig. 1A). The displacement from an unstable equilibrium results in a complete change of position in the direction of the displacement. The ball in Figure 1B, if pushed, will fall down the incline. Displacement from the metastable equilibrium can result in either a change in position or in a rebounding behavior. Slight disturbances will not move the ball very far but a strong disturbance will make it impossible for the ball to return to its original position (Fig. 1 C).

A body that is displaced from a stable equilibrium returns to the equilibrium point by undergoing a series of oscillations (Fig. 1 D). This is illustrated in physics by a spring which is pulled and then returns to its initial length. The initial length is not reached right away because the spring contracts further, undergoing oscillations described by Hooke's law. This says that the restoring force, the force which brings the spring back to its equilibrium, is directly proportional to the distance it has been compressed or stretched (Giancoli 1985 p. 295). A behavior like this is called simple harmonic motion. As long as the initial displacement is not too large this law is said to apply not only to springs but also to most solid materials (Giancoli 1985 p. 29). An ideal system with a stable equilibrium performs endless simple harmonic motion, whereas in real life the oscillations are damped due to friction and other forces so that the spring or pendulum eventually reaches a stable equilibrium again (damped harmonic motion).

Thermodynamics

The concept of systems

The discipline of thermodynamics deals with the behavior of systems, an important concept in ecology because ecologists do not deal with isolated bodies, as described by the laws of mechanics, but with systems composed of subsystems in interaction with each other.

A system can be defined as "any object or set of objects that we wish to consider. Everything else in the universe is the environment" (Giancoli 1985 p. 271).

The concept of an ecosystem was introduced by Alfred George Tansley (1871-1955) in 1935. The system concept enabled ecologists to focus their research on parts of nature that they deemed worthy of investigation. They did not have to study the entire biota of an area but could focus on smaller subsections of it. In these, however, biotic and abiotic elements could be considered. The work of Raymond Lindeman (1915-1942), for example, focused on the trophic-dynamic aspects of lakes. Lindeman's famous paper summarizing parts of his work started out by defining a system, in this case a lake, as a "primary ecological unit in its own right" (Lindeman 1942). The ecosystem concept was introduced as a means to make ecology a reputable scientific discipline and defend it against the holistic tendencies in the work of Frederic E. Clements (1874-1945) (Hagen 1992; Golley 1993).

Entropy and equilibrium

Ecologists described the exchange of energy between systems based on the laws of thermodynamics and how the exchange of energy led to equilibrium states. According to the first law, the sum of the different forms of energy in a closed system is constant. One form of energy cannot be destroyed without another form being created. The first law would allow that heat can be transferred into mechanical energy without any loss. We could imagine processes that transform heat into mechanical work, for example the motor of a car or a steam engine, and then use the heat produced from the mechanical work to keep running the motor. This would be what physicists call a reversible process, in which a system can be reversed to its initial state without any loss of energy.

However, it is not possible to convert the mechanical energy back into heat energy without any loss. Heat flows only from a hot body to a cold one. The reverse process is only possible by using outside energy. This fact is captured by the second law of thermodynamics, which describes the direction of energy processes. To describe the "downhill flow" of energy, the physicist Clausius coined the term 'entropy' in 1859.

The downhill flow of energy and how entropy was reached interested ecologists, as it described what happened in ecosystems. Entropy in its traditional formulation was a measure of the amount of energy exchanged, for example the amount of heat traveling from a hot body to a cool one. For reversible processes the increase of entropy in a system would be zero, that is, the amount of entropy would stay constant. But natural processes are irreversible. Because some energy is always lost in the transfer, the downhill flow of energy causes entropy to increase. An organism, for example, will decompose unless energy is used to keep it alive. Although the total amount of energy in the universe stays constant, the result of natural processes is heat energy which can not be transferred back into work. Heat energy is degraded and has a higher entropy than work energy (Giancoli 1985 p.283). Energy that can be transferred into work energy is called "free energy". This is at minimum when entropy reaches its maximum. The second law of thermodynamics says that in all systems entropy either stays the same, which holds for reversible processes, or entropy increases (which is the case for all natural systems). Based on these interpretations of the second law of thermodynamics ecologists, such as Odum, investigated the energy transfer between different organisms in an ecosystem and calculated the energy input into an ecosystem and the transfer of it between organisms.

A more encompassing definition of entropy was given by the Austrian physicist Ludwig Boltzmann (1844-1906) using probability theory: the increase in entropy is an approximation to the most probable state of a system. This state is the most random or disordered, so that Boltzmann's interpretation of the second law of thermodynamics is that all natural processes result in the most disordered or random distribution of energy and particles.

According to both approaches to entropy, the final state of the system with maximum entropy is the equilibrium state. In natural systems thermodynamic equilibrium is rarely reached because there is a constant influx of energy and matter into the systems, for example organisms ingesting food. Physicists call natural systems open systems. In these, the tendency towards maximum entropy prevails (Thom and Welford 1994). The equilibrium state acts as an attractor in the sense that all natural processes will inevitably arrive at the equilibrium state.

The state which is the closest to maximum entropy in open systems is called the steady state, the nature of which depends on the system itself and its surroundings. It is necessary to know how much energy is imported from outside or exported into the surrounding environment to determine the steady state of an open system. The system tends towards the steady state, and in this sense the behavior towards maximum entropy can be predicted given the situation of the system.

Even open systems cannot avoid the fate of maximum entropy. It can be predicted that the final state of the universe is heat death because all matter will be mixed and all heat will be exchanged so that a constant temperature can be observed in the whole universe. Physicists still argue about the possibility of heat death (meaning that all energy has reached the most random distribution in the universe) but it follows from the laws of thermodynamics.

In probabilistic terms the equilibrium state is characterized by the most random distribution of the parts of the system. Boltzmann distinguished between the micro and the macro states of a group of particles. The first refers to the position of every single particle, whereas the second describes the macroscopic properties of a system, for example temperature or pressure (Giancoli 1985 p. 284). Although each micro state is equally probable, not all macro states are. For example, if a fair coin is tossed, two micro states are equally probable, head or tail. If four coins are tossed at once the combination of two heads and two tails is the most probable. This is illustrated in Table 1 in which all possible combinations of heads and tails of four coins are listed. The combinations of heads and tails are called the macro states. It is obvious that different micro states can form the same macro state.

According to Boltzmann, the equilibrium state of four coins is two heads and two tails because it is the most probable one. This is also the state of highest disorder. The orderly, or more homogeneous, states of four heads or four tails are the least likely. Translated into the behavior of gas molecules this means that there are certain macro properties of a gas that are most likely. These are the states of highest disorder: for example, the even distribution of a gas in a container is more probable than all the molecules sitting

Table 1: Macro states of 4 coins and the possible Micro states (from Giancoli 1985 p. 284)

Macro states	Possible Micro states (H = heads, T = tails)	Number of Micro states
4 heads	HHHH	1
3 heads, 1 tail	HHHT, HHTH, HTHH, THHH	4
2 heads, 2 tails	HHTT, HTHT, THHT, HTTH, THTH, TTHH	6
1 head, 3 tails	TTTH, TTHT, THTT, HTTT	4
4 tails	TTTT	1

in one corner. Thus, it is not necessary to know the micro properties, meaning velocity and speed of every single molecule, to calculate the macro properties, meaning the probability distribution of all speeds. The equilibrium distribution, however, depends on the specifications of the thermodynamic probability. For example, the Maxwell-Boltzmann distribution is valid for gases with low interactions between the molecules at high temperature, whereas the Fermi-Dirac distribution is valid for particles like electrons in metals (Considine 1995 p.1172). The probability of an equilibrium depends on the matter that is analyzed. Information about the equilibrium state can not be given without prior information about the structure of the material.

The statistical interpretation of equilibrium predicts that a system tends to achieve its most probable steady state. This tendency exists even if the most probable state cannot be observed. Using the coin example above, we could imagine turning all coins to tails so that the equilibrium state of maximum entropy would never occur. The statistical interpretation, though, would predict that, if we keep on flipping coins and stop interfering with the outcome the system would return to the state of maximum likelihood, in our example to the state of two heads and two tails. Even if the equilibrium state is not realized, the important point is that a tendency towards equilibrium prevails.

Both interpretations of entropy agree on equilibrium being a final state in the process of energy exchanges. Equilibrium functions in both as an attractor, in that the system tends towards this state even if it is not realized. Entropy is the measure of the energy exchanges.

It can never decrease, although in an ideal reversible system it can stay constant, but in natural processes entropy always increases unless energy is imported into the system from outside.

All spontaneous reactions lead to an increase of entropy. The spontaneity however, does not mean that the reactions happen without any initial input of energy. In some cases spontaneous processes have to overcome some energy threshold to get started. For example, the oxidization of carbohydrates, which is performed by all living organisms, would take much longer without enzymes that lower the threshold of the reaction.

Because of the second law of thermodynamics and the downhill flow of energy, organisms have to create boundaries to their open systems (e.g. cells) to hold their equilibrium at a steady state necessary for survival. A different version of equilibrium, which is also relevant for survival and tries to capture the idea of a regulated system, is often called homeostasis. This notion and its associated mechanism of feedback have a strong influence on the debate about equilibrium in populations.

Homeostasis and Feedback mechanisms

In homeostatic systems, mechanisms exist that control the internal environment (Langley 1965 p.12). The control function works as a feedback mechanism as, for example, in a thermostat. The concepts of homeostasis and feedback were very popular in the 1950s and 1960s, when they formed the basis of the discipline of cybernetics, in which systems that possess such a control feature were investigated. In biology, systems that maintain a certain body temperature or a certain blood sugar level are examples of cybernetic systems. According to cybernetics, control systems in machines and animals are alike because they all function based on the principle that feedback processes cause a system to maintain a stable state. Disturbances in any direction are counteracted, for example the central nervous system "telling" the body to sweat when it is too hot, or to shiver when it is too cold. The control system always steers in the opposite direction of the disturbance, which is called negative feedback. Positive feedback control mechanisms are not often found in nature because they would lead to a breakdown of the system. Strictly speaking, all growth processes can be understood as being positive feedback, although it is debated whether these are regulated or not. Other cases of positive feedback can be imagined as a thermostat that is not working properly, in which case the temperature oscillates wildly (this behavior is called "hunting" Wiener 1961 p.7) and the amplitudes of the oscillations increase until the entire system breaks down. Negative feedback, on the contrary, is a stabilizing force, acting in machine and animal to maintain a constant inner environment.

The result of feedback mechanisms serving a control function is the equilibrium state. Although it can be expressed in thermodynamic terms, the emphasis in homeostatic equilibrium lies in regulation. To know the regulatory mechanisms in a system is important if changes in the system are to be explained or predicted or if the system is to be manipulated. This applies to engineering as well as to processes in nature. The notion of regulation is prominent in cybernetics, a discipline that has mostly vanished.

Chemistry

Reversible Reactions

Chemistry often deals with reversible reactions such as the reaction between hemoglobin and oxygen in which hemoglobin becomes oxyhemoglobin and after releasing oxygen turns back into hemoglobin. The partial pressure of oxygen determines which is present. A certain pressure of oxygen could be imagined at which both forms, oxyhemoglobin and hemoglobin, are present at once. In this case the reaction would have reached equilibrium.

It often happens in chemical reactions that the reactants are not completely converted into products (Brown and LeMay 1981 p.415) because the process that converts the reactants into products goes on with the same speed as the reverse. This means that the ratio of reactants to products does not change after a certain time and an equilibrium state is achieved.

For example, the reaction of reactant A that becomes product B is symbolized:

$$A \rightleftharpoons B$$

When substance B has reached a certain concentration it will be converted back into substance A. The ratio of concentrations at which A and B are in equilibrium is called the equilibrium constant, described by the equation:

$$K=[B]/[A]$$

where K is the equilibrium constant and the brackets symbolize the relative concentrations of the substances. K expresses the relative proportions of the substances at equilibrium, which is defined as the state in which two reactions happen at the same speed so that the net change is zero. The equilibrium state, as seen in the hemoglobin example, depends on factors like pressure and temperature, implying that the location of the equilibrium point can be altered by changing the pressure or temperature of a reaction. This application of the equilibrium concept in chemistry is important when substances are to be synthesized. The work of the French chemist Henry Louis LeChâtelier (1850-1931) aimed at understanding how it is possible to push the equilibrium of a reaction towards the right side of the equation, towards the products, as in the synthesis of ammonia where the equilibrium is pushed towards ammonia by an increase in pressure (Brown and LeMay 1981).

Underlying the equation for the equilibrium constant K is the law of mass action, introduced by the Norwegian mathematician Cato Guldberg (1836-1902) and the chemist Peter Waage (1833-1900) in 1867 (Bensaude-Vincent and Stengers 1996, p. 221). This described the forces governing a chemical equilibrium and had great significance for the development of quantitative chemistry because it allowed the calculation of the quantities involved in chemical reactions. The law of mass action in a more general form, $dm/dt=F(m_1 m_2 m_3 VT)$, says that the rate of change of mass in a chemical reaction is determined by the masses 1, 2, and 3 which are part of the reaction, as well as by the volume V and the temperature T. It not only applies to chemical reactions but can be used for "fundamental particle relations" (Waldram 1985, p. 135). If predator and prey organisms are seen as particles, the law of mass action can be used to develop equations that describe predator-prey interactions (see Lotka 1925, p. 58ff).

The law of mass action and LeChâtelier's principle assume an equilibrium state in chemical reactions that is not static but dynamic. Two reactions are going on at the same time, but the net change is zero. The importance of the equilibrium assumption in chemistry is that it makes quantitative measurement possible. It also provides opportunity to manipulate the equilibrium state, as seen in the production of ammonia and other chemical syntheses.

What is equilibrium?

Diversity of Definitions

The definitions of equilibrium discussed so far all share the feature that something is in balance. The balanced state, however, takes on different forms in the various scientific disciplines. In statics, dynamics, chemistry, and thermodynamics the term equilibrium is applied to closed systems. The elements that form the balanced state are part of the closed system, and input of other elements can be regulated and their effects calculated. The forces governing the equilibrium state are important because they determine whether an equilibrium can be manipulated or achieved. The focus in statics, dynamics and chemistry is on the equilibrium state itself.

In thermodynamics a balance of nature is seen as more or less inevitable. Systems exchange energy until all differences between the systems are evened out. In open systems a constant influx of energy occurs. This requires a more dynamic notion of balance, the steady state. The thermodynamic concept emphasizes the mechanisms that lead to the steady states and the focus is on the exchange processes between systems. The equilibrium state is not a starting point with which to measure the influence on equilibria, but an end point to which the system tends, an attractor state of the system. This means the equilibrium state just happens and, according to the statistical interpretation, it is the most probable result of an energy exchanging process. Because in natural processes energy is exchanged, all of nature follows the path of statistical equilibrium.

Equilibrium and associated mechanisms

Despite the difficulties of finding a definition of 'equilibrium' more telling than 'something is in balance', in all definitions so far a similarity can be found: all are connected to a mechanism that leads to equilibrium. I claim further that equilibrium plays an important role in explanations of the nature of these mechanisms. This explanatory feature of equilibrium I call 'epistemic value' because it helps in explanations of mechanisms of the system under study.

The mechanisms and epistemic values differ according to the discipline that utilizes the notion of balance. In thermodynamics the epistemic value of equilibrium is easiest to see because the steady state is an attractor state of the system. Equilibrium explains where the system is tending. The mechanism that is explained is the direction of energy exchanges. One could ask why a room gets colder, and the answer would be there is a downhill flow of energy from warm to cold and it is warmer inside than outside. The probabilistic interpretation uses equilibrium as an explanatory notion as well, where the equilibrium state is the most probable (which is why the frequency distribution of the coin tosses is normal).

In statics and dynamics different sorts of equilibria are classified according to their rebounding behavior. Equilibrium in these disciplines means that a body is at rest. The explanatory notion of the balanced state seems less obvious. A closer look, however, shows that the equilibria shown in Figure 1 are characterized by their rebounding behavior, which is the associated mechanism. In itself the stable equilibrium is not distinguishable from the unstable one. However, the rebounding behavior, which characterizes balance in dynamics, is different in all four states. The notion of an unstable equilibrium explains the mechanisms that lead to it, in that the displacement from equilibrium results in a loss of the equilibrium state. By referring to the unstable equilibrium, for example, one can explain why a displaced ball does not return to its original position.

In chemistry the mechanism associated with equilibrium is the net zero change in concentrations, which can be manipulated by the chemist. The equilibrium state of a reaction is useful to explain the quantitative relations of products and reactants. If this state is known, predictions about the results of manipulations can be made.

Finally, in cybernetics the associated mechanism is control via negative feedback. If we ask, for example, why insulin levels are more or less regulated in the human body we refer to feedback processes in the liver. Control processes explain equilibrium. Using an ultimate explanation one could also say that equilibrium explains control processes because, for evolutionary reasons, equilibrium states are desirable, which explains the feedback processes.

Equilibrium is a description of a special state of a system under investigation, which, in some cases, has something to do with manipulation of systems, or with the aims of the investigators. More generally, the special state of the system is used to explain the mechanisms that lead to it, the rebounding behavior in dynamics for example being a mechanism that is explained by the equilibrium assumption. Table 2 provides a summary of the disciplines discussed and the mechanism explained by equilibrium.

The explanatory role of equilibrium will be discussed in more detail in regard to population ecology. So far I want to indicate that equilibrium has an epistemic value, meaning first that equilibrium can not be seen in isolation but is embedded in the discipline. Secondly, equilibrium is connected to mechanisms that lead to it, and it also plays a role in the explanatory strategy that is used by scientists in the discipline.

Table 2: Epistemic values connected to equilibrium in different disciplines

Discipline	**Mechanism**
Statics/dynamics	Rebounding behavior
Thermodynamics	Direction of entropy
Chemistry	Ratio between reactant and product
Cybernetics	Control of homeostasis

Relationship to ecology

Figure 2 provides a summary of the different influences of the equilibrium concept on ecology. The epistemic value of equilibrium connected to rebounding behavior is used in community ecology, where the ability of communities to recover (rebound) from environmental stress is investigated (for example Underwood 1989; Dayton, Tegner et al. 1992), and in population ecology. For populations the return to equilibrium after a disturbance is sometimes compared with damped oscillations, as described by Hooke's law. Gotelli (1995, p. 35) describes the damped oscillations populations undergo before reaching their carrying capacity.

As will be shown in the next chapter, the description of oscillations and the explanatory value of equilibrium for these oscillations, played an important role in the

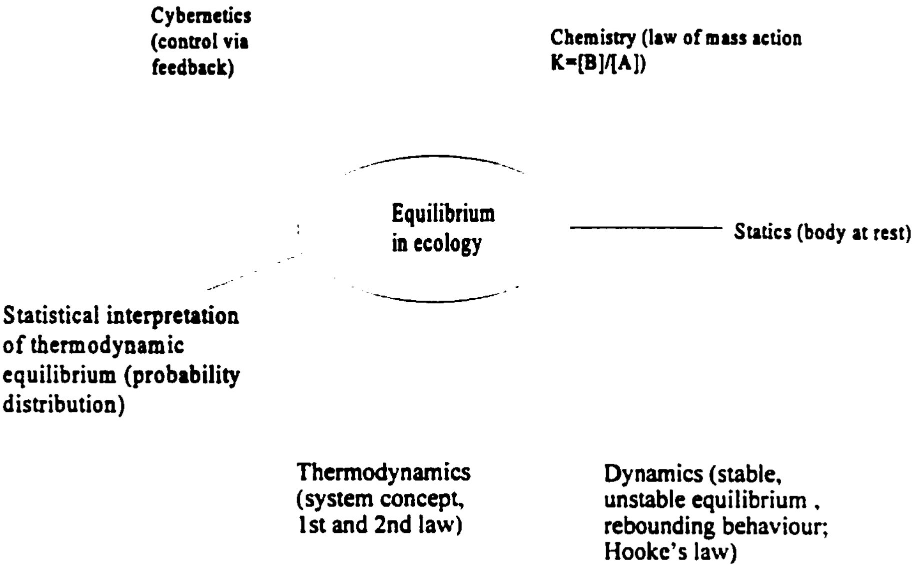


Figure 2: Influence of different scientific disciplines on the equilibrium concept in ecology

establishment of the equilibrium concept in ecology. Different interpretations of oscillations resulted in conflicting views about equilibrium. I will demonstrate this by discussing the treatment of the equilibrium concept by two influential ecologists.

Summary

Mechanisms which lead to equilibrium form an important part in the conceptual understanding of scientists. I use the notion of 'epistemic value' to describe their use of equilibrium in explanations or predictions. It can be said that equilibrium plays an important theoretical role; however, the notion of theory in the sciences is vague. What does it mean if we say that equilibrium is a theoretical construct? In the following chapters I choose a historical approach to this question, beginning by asking how equilibrium was used in the early stages of ecology. The historical approach will lead to an appreciation of changes in the equilibrium concept and to its role in theory.

Chapter 3: Equilibrium in population ecology

My claim in the preceding chapter was that the definition of 'equilibrium' in a discipline is always associated with a mechanism that is investigated. Thus, the concept has to be investigated as part of the larger context formed by the discipline. I also claimed that certain epistemic values are connected with equilibrium. I will substantiate this further in this chapter, which discusses the equilibrium concept in population ecology, and I will show that the notion of epistemic values is not sufficient to understand the concept. I will investigate the ontological commitments to the balance of nature by two influential ecologists of the early 20th century, Alexander John Nicholson and Charles Sutherland Elton, and describe how their understanding of the equilibrium concept was influenced by their views of the structure of nature. Elton and Nicholson were interested in different levels of ecological analysis, Elton as a community ecologist (though not without interests in populations), and Nicholson as a population ecologist. Both were pioneers in their fields, and Nicholson especially was an important figure for mathematical ecology.

Regulation but no balance, Charles Elton

Charles Elton was born on March 29th 1900 in Manchester, England. Early in his life he became interested in natural history, stimulated by his older brother Geoffrey (Cox 1979, p. 8). Elton studied at the University of Oxford where he graduated in 1922 and where Julian S. Huxley (1887-1967) became his mentor. Huxley made it possible for Elton to join three expeditions to Spitsbergen in 1921, 1923, and 1924, organized by George Binney for the University of Oxford. Binney later became an officer for the Hudson's Bay Company for which Elton was a biological consultant from 1925 until 1930. In 1929 Elton became a part-time zoology demonstrator at Oxford and held this position until 1945.

Elton had a strong influence on the scientific community through the Bureau of Animal Population (BAP), an independent research laboratory at the University of Oxford which he founded in 1932. In 1967 upon his retirement the BAP became part of the Zoology Department at Oxford. Elton was also influential through writing the first ecological textbook. *Animal Ecology*, published in 1927, summarizing all observations that had been gathered in ecology up to this time and placing them under several general principles. This allowed the new discipline, ecology, to gain independence from other biological sciences (McIntosh 1985, p.89). Charles Elton died in 1991.

Early influences: the ecological survey

To understand Elton's approach to the equilibrium concept it is important to note that his work is characterized by two elements, the ecological survey and the investigation of fluctuations of populations. Terrestrial animal ecology in the 1920s was still in its early stages, lagging aquatic ecology and plant ecology (McIntosh 1985, p. 61) because interactions between organism and the environment were more easily observable in plant ecology or in the confines of a lake. Terrestrial ecology was hindered too by problems of identification and capture (McIntosh 1985, p. 63).

In his approach to ecology Elton was influenced by Victor E. Shelford (1877- 1968) (Cox 1979, p. 10: Crowcroft 1991, p. 3). Shelford, a graduate of the University of Chicago, regarded ecology as a physiology of nature, an attitude similar to Ernst Haeckel's (Haeckel coined the term 'ecology' in 1866). As an example of the physiological approach to ecology the work of Frederick Clements is often cited (Hagen 1992, p. 20 ff.). Clements likened the plant community to an organism and tried to find out how this organism reacted to its environment and how it formed it. His idea of succession describes how a plant community develops from a pioneer into a mature climax state.

Shelford used the physiological approach to find an explanation for the distribution of animals (Mitman 1992, p.38). According to him, it was important to know the physiological constraints of the animal in isolation, a sub discipline called autecology, often based on laboratory studies. From there the distribution of members of the same species in nature could be analyzed "based on environmental stimuli" (Mitman 1992, p.42). Shelford hoped to find similarities in physiology between different species that occupied the same habitat, for example different species in a community developing the same response to arid conditions. These studies of the composition of animal communities were called "synecology" (Mitman 1992, p. 43), using, for example, the concept of a food chain to describe interactions between organisms. Besides showing how species fit into a specific environment Shelford was interested in explaining how communities developed in time. Here Shelford used the concept of succession developed by Clements and both worked together on uniting plant and animal ecology in describing the interaction among animals and between animals and plants.

Elton used Shelford's classification of different communities according to their habitats in his survey of Bear Island during the expeditions to Spitsbergen. He divided the fauna into different habitats according to dominating plant community or dominating geographical features (Summerhayes and Elton 1923). The method of the ecological survey and the observation of food relations was used by Elton throughout his career (see for example Elton 1966) but he physiological approach had its limits. Elton thought organisms not only chose their habitats according to physiological constraints but had other preferences as well, for example breeding or protection against predators (Elton 1927, p. 40). The geographical distribution of animals was more complex than what their physiological limits could tell ecologists. Another weakness of Shelford's physiological approach, according to Elton, was that it did not account for species which were not confined to one sort of habitat, for example, sea birds that breed and nest on land but feed and live on the ocean. These "interlocking species" which moved between habitats were of special interest to him (Cox 1979, p. 24). According to Elton, an ecologist is interested in what animals do (Elton 1927, p. 34) and physiology played an important but not sufficient role in finding out about this.

The structure of communities

The composition of animal communities, according to Elton, was based on several principles, one of them the principle of the food chain (Elton 1927, p. 55). The results of a survey of Bear Island near Spitsbergen by Victor Summerhayes and Elton shows how they conceived of food relations structuring a community. As can be seen in Figure 3, all food chains together in the animal community form a food cycle within which every animal has a certain place. Feeding relations, described in food cycles, form the ground plan of every animal community. Elton noticed similarities in food chains in different habitats. Although species differ in different habitats, their roles in the food cycle are roughly the same. Elton gives the example of aphids (leaf sucking insects): "in every kind of wood in England we should find some species of aphid, preyed upon by some species of ladybird" (Elton 1927, p. 63). The terms "food chain" and "food cycle", though adapted from Shelford, were coined by Elton (Cox 1979, p. 88) and they had significant influence on ecology.

From the principle of food chains and cycles Elton arrived at his principle of the pyramid of numbers. Going up the food chain, the animals become bigger and can also handle bigger sized food. Being dependent on a certain size of food is the underlying cause of the existence of food chains: "[e]ach stage in an ordinary food chain has the effect of making a smaller food into a larger one, and so making it available to a larger animal" (Elton 1927, p. 61). He admitted that exceptions to the food chain principle exist; however, the principle holds true most of the time.

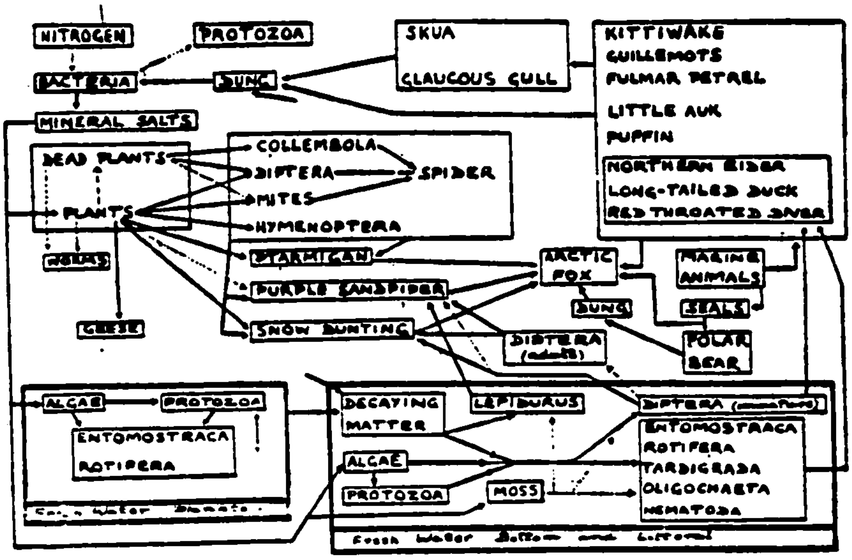


Figure 3: Elton's food cycle among animals on Bear Island. The dotted lines represent food relations not yet proved (from Elton 1927, p. 58).

According to Elton, the size of the animals in the chain is connected to their abundance. Smaller animals, lower in the food chain, are more numerous than larger animals higher up. The herbivorous animals are most abundant and also have the highest capacity to increase, forming "key industries" in the community. The larger the animal, the less it is capable of increase in numbers. The largest carnivores form the final link in the food chain and cannot support any higher levels. They also have the largest area to cover in pursuit of food and are not confined to the limits of habitats.

To describe the status of animals in a community, Elton uses the term "niche". The niche of an animal, according to Elton, describes its place in the community and its "relation to food and enemies" (Elton 1927, p. 64). The niche describes what the animal is doing and it is another important theoretical principle that Elton made popular, although the priority of the niche concept in its modern form and complexity is not clear. Griesemer (1992) claims that Elton modified the definition of niche originally proposed by the American ecologist Joseph Grinnell (Griesemer 1992). Elton himself writes that Grinnell and he "independently started using the term" (Elton and Miller 1954). According to Griesemer, Elton's niche concept focused mainly on the community, whereas Grinnell's version emphasized the role of the environment. Like the food chain, the niche principle made it possible to compare different habitats in their "essential structures" (Elton 1927, p. 64). In addition, the same niches may be occupied by different species in different habitats.

Fluctuations and their relevance for regulation

The principles of the food chain and the pyramid of numbers allow us to understand Elton's concept of regulation and control of animal numbers. At first sight it seems as if Elton rejected any notion of a controlling factor that could act as a feedback mechanism. In his studies, especially in his work for the Hudson's Bay Company, and in the literature, Elton saw evidence for strong increases and crashes of populations. Population numbers of a species, for example a rodent, increased rapidly and would crash soon after. This made Elton reject the idea of an equilibrium in nature: "the balance of nature does not exist and perhaps never has existed" (Elton 1930, p. 17).

Elton gives several examples of instabilities in nature, mostly from his studies in the

Canadian Arctic. He had read about the fluctuations in the book *The Arctic Prairies* by Ernest Thompson Seton (1860 -1946) who was the first to publish graphs about fur-returns of the Hudson's Bay Company. The fluctuations were also documented in the book *The Conservation of the Wild Life in Canada* by Gordon Hewitt, which Elton had read as preparation for the Spitsbergen expeditions (Cox 1979, p. 11). The graphs in these books show strong fluctuations in numbers of lynx and hare and other fur-bearing species. Elton concluded that "there is hardly a fur-bearing animal in Canada that does not fluctuate in numbers from year to year in a most striking way" (Elton 1930, p. 19), and he found additional evidence of rapidly rising and crashing populations from accounts by natives of Labrador transmitted by explorers, missionaries, and doctors. He valued these accounts of population imbalance because they gave an illustration of nature in its pure and unmodified form and because the data were collected in an unprejudiced way, not by some "biologist hard-set in some particular theory of animal life" (Elton 1930, p. 19).

To gather data from lemmings and foxes in the arctic Elton relied on reports in the Hudson's Bay Company's archives. His own field work took place in the woods around Oxford where he studied voles, which were also known to fluctuate in numbers (Crowcroft 1991, p. 6). Fluctuations of populations were Elton's focus of research that later led to the foundation of the BAP, the aims of the which were the monitoring of populations, establishing census methods, the study of the effects of diseases, and the "control of breeding seasons" (Elton quoted in Crowcroft 1991, p. 14).

In his paper *Periodic fluctuations in the numbers of animals their cause and effects* from 1924, Elton described the cyclic behavior of populations of the lemming and the arctic fox which displayed a peak every 3.5 years. He also observed cycles in sunspot numbers with a phase of 11 years coinciding with the rhythm of populations of animals that live further south than the arctic fox, for example rabbits, and suggested that the population dynamics of rabbits in more southern regions are influenced by sunspot activity. Foxes preying on rabbits also showed an 11 year period in their population dynamics. Elton then found that the 3.5 year cycle of the arctic fox had an underlying 11 year period, this period however not being as pronounced as the 3.5 year one. From this he gathered that animals in southern areas are more influenced by sunspot activity than the northern animals because the influence of the sun is less in higher latitudes. However, he assumed that some climatic factor must be responsible for the increase and decrease of northern populations as well (Elton 1924). In a later paper Elton rejected the sunspot theory but he still assumed that populations were controlled by climatic factors (Elton and Nicholson 1942). He provided further evidence for this theory by citing data from muskrat catches by the Hudson's Bay Company in which patterns could be observed spanning large geographical areas. Elton could not believe that anything other than climatic factors could have such a wide ranging effect.

As we know today, the example of lemming populations shows that matters are more complex than Elton suggested. The population cycles of the lemmings have been of interest for many centuries because apparent mass migrations of the small rodent have been observed. It could not be determined, however, why these migrations happened and where they led to, because large numbers of dead lemmings were never found. Sometimes they were seen on ice flows or their tracks were seen close to the shore so it was assumed they regulate their population size by jumping off cliffs or committing other forms of suicide. The belief was so strong that even the makers of the nature movie *White Wilderness* by Disney re-enacted a mass suicide by throwing lemmings off some cliffs after the captured rodents refused to "commit suicide on cue" (Chitty 1996, p. 210). Dennis Chitty presents evidence that the suicide of lemmings neither can be proven nor that the migration is a form of population regulation (Chitty 1996, p. 179). His own hypothesis is that natural selection favors certain genotypes during crowding of the populations and other genotypes during less crowded periods causing the cycle. Chitty's hypothesis is still debated and an agreement on the causes of cycles has not been reached yet but it is unlikely that an environmental factor alone is responsible for it.

Although Elton saw the fluctuations as evidence against the view that some controlling mechanism existed he still postulated some ordering mechanism in nature. He saw, however, that this order was constantly upset. A clue to Elton's belief in some form of balance is that he posited an optimal population level for every species. He wrote: "...it becomes clear that every animal tends to have a certain suitable optimum which is determined mainly by the habits and other characteristics of the species in question" (Elton 1927, p.114). This density was variable because the conditions were constantly changing (Elton 1930, p..26 ff.), making it hard to believe that regulation exists. Another indication of a certain form of balance was the constancy of species composition: "The fact remains... that the species composition of most communities remains very much the same over long periods, and that each community can be treated as a biological unit of a pretty constant nature" (Elton 1930, p. 25).

According to Elton, even regulation of numbers could be achieved. The regulatory elements were the food cycles. Every species in the food chain controlled the level beneath it. The species on top of the food chain "have evolved rather curious methods of regulating their numbers...The Emperor Penguin... seems to depend chiefly on climatic factors to bring [regulation] about or rather should we say that the only checks against which it has to produce extra numbers are climatic ones" (Elton 1927, p. 123). The chief cause of fluctuations, as Elton thought in 1927, was instability in the environment. A favorable summer, for example, could result in a fast increase of herbivores which could not be limited by the controlling carnivore because of the smaller rate of increase of the latter following from the "pyramid of numbers" principle. Another important factor that could lead to regulation was the migratory behavior of animals. (This strategy will be discussed in the treatment of Elton's view of natural selection).

Because Elton equated 'balance' with constant numbers of organisms, he rejected the notion. However, he was convinced that some regulation took place in nature and he devoted most of his work to finding out about it. Research that took place in the BAP focused on what caused fluctuations in populations. The group at Oxford worked on the cyclic fluctuations of vole populations which they thought might display a similar behavior to the extreme fluctuations of lemmings in the arctic, attributing the cause of the cycles to the environment. The animal community in itself had mechanisms of regulation and here Elton mainly named food relations.

The later Elton

Later in his career Elton modified his approach to ecology; for example, he switched his nomenclature from food chain to "species network" (Elton and Miller 1954). Elton and Miller also emphasized the importance of energy flow through the ecosystem. This approach had already been suggested by Alftred Lotka in his book *Elements of physical biology* (Lotka 1925). For Lotka the program of biology was to describe the mechanisms of energy transformations in the organic world. The "mill wheel of life" was fed by sunlight and it dissipated heat. Ecology thus was concerned with the energetic pathways through ecosystems.

Through Lotka's, Volterra's, and Nicholson's work, Elton was also confronted with the concept of "self-regulating" populations. Although he still believed that regulation occurred at the community level which was disturbed by environmental disruptions, he saw that the food chains could not explain regulation in nature: "...there does not seem much doubt that theories that use food-chain for an explanation of the regulation of numbers are oversimplified, and often just untrue for certain species. There are other factors at work, not omitting disasters and - perhaps more commonly than we have formerly believed - various methods of regulation operating through the population of the species itself" (Elton 1958, p.131). He eventually, but reluctantly, accepted that regulation at the population level was possible. The impact of this insight on his approach to population regulation is difficult to assess, but it seems that it did not completely turn around Elton's thinking regarding regulation, i.e., he continued to focus on communities rather than on populations. The relationship between a parasitic insect and its host, and the regulatory function of the parasite with respect to the host was still interpreted by Elton as the unleashing of the "power of the food chain" (Elton 1958, p. 131).

The fragile relationships among members of the animal community also guided Elton's attitude towards environmental ethics. The concept of biological pest control and the introduction of species that could control pests led Elton to the problem of manipulation of natural systems. According to Elton, this could lead to a disruption of the whole community, for example, with the introduction of one pest-controlling agent leading to depletion of another resource that other species depended upon. Elton seemed throughout all his work to be more concerned with the effects of population fluctuations on the community level than with its causes on the population level. Although Elton's own practical research focused much on populations, in his theoretical work the communities took center stage. This becomes even more apparent if Elton's approach to natural selection is investigated.

Elton and natural selection

In his 1927 book *Animal Ecology*, Elton summarized his observations that coloration in animals is not necessarily adaptive. He had observed two different forms of arctic foxes differing in coat coloration, one colored white in winter and grey or blackish in summer, (seen as adaptation to the prevailing colors of the environment), the other grey or even black in winter and brown in summer. Elton wondered: if the former case - white coat in winter, brown in summer - could be seen as an adaptation, then how did the latter case evolve? These and similar observations of seemingly non-beneficial traits made him question the overall power of natural selection. He denied that "all animals are simply masses of adaptations" (Elton 1927, p. 181), arguing against adaptationism, the view that sees every trait of an organism as a result of natural selection processes and thus a contribution to the survival of the species. It is an interesting alternative Elton offered: "it seems probable that the process of evolution may take place along these lines: genotypic variations arise in one or a few individuals in the population of any species and spread by some means that is not natural selection" (Elton 1927, p. 185). In a 1938 article he approached the problem of natural selection as an ecologist who is aware of the patchiness of populations due to the heterogeneity of habitats, as a result of which populations often undergo local reductions in numbers so that the chance of random drift increases. The idea of random events fixing traits and its implication that the existence of some traits cannot be explained by referring to natural selection, makes Elton's view resemble the theory of neutralism, whose advocates believe that "most changes at the molecular (DNA) level do not result from Darwinian natural selection, rather, from random fixation of selectively neutral or very nearly neutral mutants through random drift " (Kimura 1992, p. 225).

What happens after a mutation is fixed by random drift? In his 1927 book Elton states that after a mutation is fixed, natural selection is "ultimately effective, probably acting rather on populations than on individuals" (Elton 1927, p.185). In 1930 he wrote that "we must admit that the whole of an animal community can act as a biological unit, operated upon by natural selection so as to bring about the best compromise in the way of optimum populations for all"(Elton 1930, p. 31). These are statements in favor of group selection, and (Kimler 1986) wrote that Elton himself was "perplexed at later criticism of group selection and community evolution". However, Elton dismissed the idea that whole ecosystems could be in competition with each other and he claimed that the "animal community, considered as a biologically efficient unit, cannot have been evolved solely by natural selection in the ordinary sense, as it has no competitors" (Elton 1930, p. 39). In a later article he wrote that after a mutation is fixed in the population the density in the population increases and "then another factor that does not discriminate between the old and new adaptation reduces the whole population, perhaps somewhat catastrophically (though not necessarily so) to a lower level" (Elton 1938, p. 136).

In his study of natural selection, Elton put emphasis on migratory behavior, stating that animals "do not sit about waiting for the environment mindlessly to select the fittest to survive, as plants must", a claim ascribed to him by Crowcroft (1991, p.2). According to Crowcroft, Elton believed in "natural selection of the environment by the animals": migration of animals would have an important impact upon natural selection. Migratory behavior occurs when a habitat becomes unfavorable for animals. As examples he mentioned saw flies which destroy currant and gooseberry leaves, until, when a bush is completely destroyed the caterpillars leave it in search of another. Similar migratory behavior can be observed in other animals (Elton 1930, p. 61). He believed that "adaptation is not only produced by the elimination of the unfit from a stationary population of animals". Migration, according to Elton, provided a means of "adaptive radiation" (Elton 1930, p. 71).

The study of animal fluctuations was the main goal of the BAP but Elton always focused on the functioning of the whole system, which, though regulated through feeding relations and other mechanisms, was fragile, so that climatic change as well as man made interference could upset the balance. It seems that Elton's research on populations had to serve the aim of discovering the balance of whole communities. To this end, he did not shy away from association with businesses that were interested more in an increase of the return of fox pelts than in an investigation of the balance of nature. He was certainly aware of their intentions but saw the funding by, for example, the Hudson's Bay Company, as a means to an end. On the final page of *Voles, Mice and Lemmings* (1924), Elton used an exploration analogy to describe the state of population biology, which so far had only discovered a "few islands rising out of the mist". He goes on:

> Let us hope that wise governments will train navigators and equip them to explore more closely the Islands of Vole, Mouse and Lemming; and that they will do so not only in order to round Cape Fox and cross Dog Deep, but with some idea of understanding, not for power alone, but on account of its own wilderness and interest and beauty, the unstable fabric of the living cosmos (Elton 1942, p. 482).

The balance of competition - A. J. Nicholson

A contemporary of Charles Elton, the Australian ecologist, Alexander John Nicholson (1895-1969), also worked on regulation in nature but started with different premises and had a different scope than Elton. Nicholson was born on March 25th 1895 in Biackall, Co. Meath, Ireland, but grew up mostly in England. In 1912 he started his studies at the University of Birmingham, where he graduated in 1915. He began post-graduate research in Birmingham but then was hired by the University of Sydney in 1921, from which he received a Doctor of Science in 1929. The same year he became Deputy Chief of the Division of Economic Entomology of the Commonwealth Council for Scientific and Industrial Research (CSIR) in Canberra until he resigned from that position in 1960. Nicholson died in 1969.

Nicholson's main contribution to ecology was the concept of density-dependent population growth and a causal explanation for it. He also was one of the first biologists to use mathematics to present and clarify his ideas. The equations Nicholson developed with the help of his physicist colleague Victor Albert Bailey (1895-1964) are still relevant for population biology today.

Mimicry and balance

Nicholson arrived at the problem of regulation in nature in several ways. One was through thinking about mimicry in insects, the topic of a presidential address to the Zoological Society of New South Wales in 1927. In his talk Nicholson presented the idea that "the abundance maintained by a species is not determined by the perfection of its adaptation, but rather by density-induced reactions in environment" (Nicholson in a letter to Kenneth Watt, December 1965, Adolph Besser Library, Australian Academy of Science, Canberra, Australia).

Nicholson, like Elton, believed that regulating forces in nature existed. His reasoning, however, differed from Elton's in that he postulated regulating forces on the population level rather than on the community level. Nicholson believed in the regulation of populations because he saw population levels fluctuating between observed limits. What caused the population to stay within limits? He had assumed that insects, for example, were limited by several factors, for example food supply. A student criticized this claim by stating that even the worst pests never completely eliminate their prey, even if all other control mechanisms fail. Nicholson had to admit that populations never grew indefinitely and rarely went completely extinct, persisting for a long time and varying according to environmental conditions (Kingsland 1995). He wrote in 1933: "The observed facts that there is a relation between the population densities of animals and environmental conditions can be explained only in terms of balance, just as the relation between the weight carried and the height reached by a balloon can be explained only in this way". But how was regulation achieved? "For the production of balance, it is essential that a controlling factor should act more severely when the density is high... In other words, the action of the controlling factor must be governed by the density of the population controlled" (Nicholson 1933, p. 135). Nicholson then concluded that the controlling factor was competition, or "some form of competition", occurring when a population of animals randomly searched for food. The more animals there were, the lower the success rate of every individual animal. This he called the "diminution of success with increasing density", through which the success rate of each individual reaches a limit (Nicholson and Bailey 1935). This assumption sounds realistic, but the way Nicholson justified it is puzzling. Because all of his further analysis was based on his assumption of diminution of success, it is necessary to take a closer look at the argument.

The competition curve

Nicholson's work focused on the dynamics of parasitic insects and their hosts, which were insects as well, a relationship analogous to that of predator and prey because the hosts are considered prey organisms (the larval stages of the parasites eat their hosts). Contrary to non-parasitic predators, however, the reproductive rate of the parasites is directly connected to the number of hosts. This direct connection makes the parasite-host relationship less complex to investigate than predator-prey relations (Nicholson 1933).

The activity of finding hosts was modeled by Nicholson as a random search. Although individuals might efficiently search an area, other members of the population search independently. Thus, in a group it often occurs that one part of the area is searched twice, leading him to the assumption that populations search randomly, a behavior analyzed theoretically in a form reminiscent of Zeno's paradox. He claimed that a population of

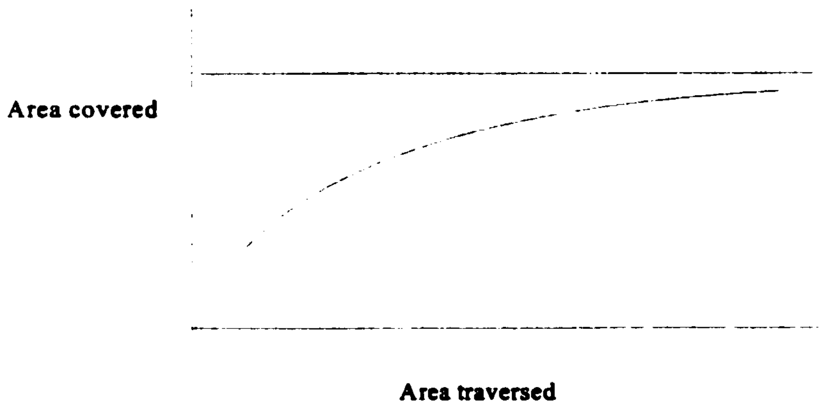


Figure 4: The competition curve. Adapted from Nicholson (1933) The horizontal line represents the limit of successful searching

parasites can never completely search a whole area and called the area being searched in total "area traversed". The area that was newly searched was termed "area covered". Nicholson then claimed: "thus the area traversed represents the total amount of searching carried out by the animals. while the area covered represents their successful searching" (Nicholson 1933, p. 141). He made the argument that when the population started searching the first tenth of an area it would completely search that tenth. Subsequently, however, the area covered would become increasingly smaller because other individuals of the population would have already been there. Nicholson's argument was that "...after traversing three-tenths of the total area the animals have covered only 2.71 tenths. The calculation may be continued in this way indefinitely, and it is clear from the nature of the problem that, at each step of one tenth traversed, the animals cover a smaller fraction of area than in the preceding step. Also, because at each step the animals cover only one tenth of the previously unsearched area, the whole area can never be completely searched " (Nicholson 1933). He claimed that the area covered reached a limit asymptotically, represented by a curve he called the "competition curve" (Figure 4), which shows approximation to a limit. The mathematical treatment of the competition curve was done by his university colleague Victor A. Bailey who was consulted by Nicholson. Bailey considered the search by parasites as analogous to the movements of particles in a gas (1995, p.117) implying that a parasite moves through space in the same way a gas particle moves through the gas cloud. Bailey treated the encounters between parasite and host like collisions between gas particles. He (1931) modeled the speed of parasites as constant and referred to the theory of the mean free path by Maxwell in a footnote. Nicholson claimed that, besides illustrating searching behavior of prey organisms, "the competition curve has a general application to all problems of random sampling" (Nicholson 1933).

How Nicholson arrived at the competition curve is difficult to understand. He can be interpreted as saying that the crowding of a population results in a lower success rate of the parasites in finding hosts and in a lower reproductive rate, his curve describing the "approximate character of the diminution of success" (Nicholson and Bailey 1935). This seems to be what he had in mind, given his translation of 'area covered' as success rate of the individual's searching effort. Nicholson wanted to show how increasing intraspecific competition leads to a diminishing success rate of predators. In this sense the competition curve is the result of a "thought experiment". However, stated in the terms of an area that is searched, it is not clear why the curve only approximates the total area covered and never actually reaches it. Why would predators not be able to completely search a specified area?

Oscillations between parasite and host

The competition curve shows that there is a specific relation between the "reduction of success of the searching animals and the increase of the intensity of competition" (Nicholson 1933). How much a population of parasitic insects is able to grow depends on the efficiency of the parasites and their reproductive rate. At a certain size parasites and hosts are theoretically in balance because a certain number of hosts sustains a certain number of parasites. This was called the steady state by Nicholson. Given his assumption that populations are regulated by competition, it was possible, using the equations, to calculate the size of a population at the steady state given the values for efficiency of the predator and its reproductive rate.

It has to be noted here that Nicholson looked at the parasite-host relationship in two ways. In his paper with Bailey in 1935, the search for a host by a parasite was investigated first as intraspecific competition in the parasite population. The host acts as food and space for reproduction because the parasite lays eggs into the eggs of the host and the larvae then feed on the host larvae. Nicholson and Bailey modeled the searching behavior of a group of parasites as intraspecific competition. In a later section of their paper they described parasite-host interactions as interspecific because parasite and host were members of different species.

Turning to interspecific competition, Nicholson and Bailey claimed that the controlling power of competition is not limited to intraspecific competition but includes other species. However, according to Nicholson intraspecific competition has priority as a regulatory mechanism. This can be seen in Nicholson's definition of 'control factor' as "one which responds to increase in the density of a given species either (1) by increasing the severity of its action against the species (as do natural enemies), or (2) by causing intraspecific competition to decrease the chance of survival of individuals (as do limited supplies of food or of suitable places to live). It should be noted that (1) is a special case of (2)" (Nicholson 1933, p. 147).

Although Nicholson's arguments were based on the idea of control and steady states, he failed to show how two populations in competition can reach equilibrium when their initial population sizes are not at equilibrium. In modeling predator-prey populations according to his equations, he observed that populations tend to the steady state density and initially oscillate around a steady state. He also found that the parasite populations lag the host oscillations by about a quarter of a period. Nicholson wrote: "...any displacement of a species from its steady density sets up a reaction tending to cause a return to this density, [and] there is always a delay in the occurrence of the reaction" (Nicholson and Bailey 1935). The problem was that, according to Nicholson's and Bailey's equations, the oscillations of the parasite and host populations increased with time, leading to the crash of the populations (Figure 5).

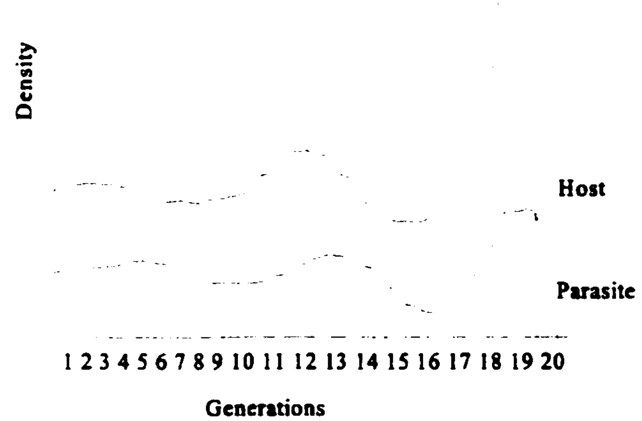


Figure 5: Oscillations between parasite and host according to the Nicholson Bailey equations. (Adapted from Nicholson 1935)

The increasing oscillations were contrary to what was observed in nature and they undermined Nicholson's argument of a steady state and a balance of nature. Although the equations were based on the assumption that populations are regulated, taken together it looked as if parasite and host could not coexist. Nicholson was not overly concerned about his theoretical predictions arguing that "it is inconceivable that such perpetual increase [of oscillations] takes place in nature, for this is certainly not compatible with what we observe to happen. When considering large fluctuations, however, account must be taken of other factors besides those already used in this investigation" (Nicholson and Bailey 1935, p. 590). One of these other factors was migration. Nicholson and Bailey saw the crash of the host and parasite populations predicted by their models as evidence for the formation of smaller host sub-populations that could escape from the parasites temporarily by migrating. They also suggested that other factors beside predation could limit the host population so that the fluctuations might be smoother than those illustrated in Figure 5. This could mean that oscillations would be "perpetually maintained at a large constant amplitude in a constant environment"(Nicholson and Bailey 1935, p. 590).

Nicholson's use of mathematical equilibrium displayed a certain degree of pragmatism. The balance of nature was one of his premises because he believed that balance-producing factors occur in nature. Because of his work on parasites he started to model the dynamics of the populations by using an important aspect of the parasites' feeding behavior, the search for prey. This, on a population level, was considered random. From there Nicholson developed his competition curve (Figure 4) and received help from the physicist Bailey to describe the curve mathematically. Applying the curve to interspecific competition, however, was unsuccessful because the equations predicted the crash of populations, which was the opposite of what Nicholson wanted to illustrate. The assumption of a balance of nature turned against its creator. However, he knew that the mathematical equations were simplifications, so he did not question his basic assumption of a balance of nature but continued using Bailey's equations to render his assumptions more realistic. The mathematical rigor that was used to describe the effect of competition was abandoned when the modeling did not predict the actual phenomena in nature. This can be seen by Nicholson and Bailey's discussion of Figure 5 (Nicholson and Bailey 1935), in which the crash of model populations was regarded as unrealistic. According to the two, oscillations in nature could not increase and an explanation why this was avoided was, for example, migration. The balance-producing mechanisms that induced the oscillations were not questioned; in a constant environment the oscillations would be smoother because additional factors limited the prey population.

The later Nicholson

Nicholson, as did Elton, modified his approach slightly in later years but remained faithful to the idea of balance and equilibrium. In a paper published in 1954 he begins by describing ecology as being concerned with the redistribution of matter and energy. He then returned to his main topic, the balance of populations, leaving energetics topics aside: "it is sufficient for the purposes of the present discourse to accept the fact that organisms have the properties we know them to possess, without specifically considering how these came into being, or the details of the metabolic processes which govern matter and energy exchange between individual organisms and their environment" (Nicholson 1954 b, p. 11). In this article a clarification of nomenclature can be observed, as was the case with Elton. In 1954 Nicholson, who had been criticized for claiming that density-dependent factors were the only regulating mechanisms in populations, distinguished *density-governing* from *density-legislating* forces. Density-governing forces modified their influences on population growth and were density-dependent in the traditional sense. Nicholson, however, reacted to criticism that these were not the only factors determining population size in saying that legislative factors, like climate, for example, could determine the size of a population but were not acting in a density-dependent fashion: "... climatic conditions are unaffected by any changes in the densities of the animals subject to them: and so, being unable to react to density change, they cannot govern populations, although they may have a profound legislative influence upon population densities" (Nicholson 1954 b, p. 44). The legislative factors set the level of population densities which the governing factors then regulated.

The self-governance of populations was the focus of Nicholson's work. He concentrated on intraspecific competition because that was the only way self-governance could be achieved. Nicholson's view of interspecific competition was also affected by this approach. To compete successfully, a species had to be in control of at least one essential resource. Species could only coexist if they controlled two different essential resources: "..each species must govern the density of at least one [essential resource] in order to govern itself, so excluding the possibility of any other species governing the reaction of the same [essential resource]" (Nicholson 1954 b, p. 48).

Despite criticisms of his approach, for the later Nicholson the production of balance was still a necessary and sufficient condition for the persistence of populations. This, however, did not imply that population densities stayed constant. Nicholson gave emphasis to the occurrence of oscillations because they were evidence for the existence of equilibrium. They were driven by population-internal mechanisms, such as competition for essential resources, which reacted to changing densities.

Nicholson and natural selection

Nicholson's view concerning natural selection emphasizes the important role balance plays in his conception of nature. Nicholson started thinking about the role of natural selection in ecology as early as 1927, when he published an article about mimicry in insects in which he claimed that mimicry itself did not constitute a selective advantage. This claim can only be understood given the background of Nicholson's view of natural selection, for he did not think that mimicry did not provide an advantage for the insects; rather, he questioned if the selective advantage would result in an increase in density of the population. The important point is that Nicholson equated increased fitness with increased abundance and argued against a teleological understanding of natural selection. To him, mimicry did not serve the purpose of increasing a species' population. He wrote that the terms "purpose and advantage...can have no place in a true explanation of mimetic resemblance" (Nicholson 1927, p. 99).

To account for the fact that populations did not increase indefinitely after acquiring a beneficial trait, Nicholson postulated a "compensating mechanism" that brought the population back to its steady state. In the case of mimetic insects, for example, he thought that increased protection of the adults led to increased predation on larval stages of the insect (Nicholson 1927,). Thus, he suggested two mechanisms acting on a population. Density-dependent or, in Nicholson's later words, *density-governing* factors, kept a population in balance with its environment. Natural selection then disrupted the balance, but the density governing factors compensated for density changes due to selective advantages. Advantageous traits, for example a similarity with the surrounding environment, were beneficial because they "fit an insect more perfectly to its normal environment" (Nicholson 1927, p. 98). He thought that natural selection should be seen more as a mechanism that perfects organisms rather than a mechanism that threatens a species' survival. It is not about destruction of the less fit; this would exhibit "a crudity such as one would not expect to find in nature" (Nicholson 1927, p. 99). The benefit of a trait was not an increase in numbers but a better fit into nature. He claimed that some traits brought about by natural selection might be advantageous to the organism but still lower the density of its population (Nicholson 1954 a, p.8).

The existence of balance was not evidence for group selection. An argument of this kind was made by V.C. Wynne-Edwards (1962, p.9) who claimed that it must be "highly advantageous to survival and thus strongly favored by selection for animal species ... to control their own population densities", citing Nicholson in support of this claim. Nicholson's view on this issue is more complex. Kimler (1986) claims that Nicholson was skeptical about the issue of group selection in the sense propagated by Wynne-Edwards, and Nicholson specifically wrote that "..selection operates upon individual differences without any reference to the success of the species" (Nicholson 1954 a, p. 8). This statement supports Kimler's (1986) claim that Nicholson rejected group selection. He does this, however, at the cost of separating natural selection from the balance-producing factors. He saw the latter as a "counterpart of selection in evolutionary progress"(Nicholson 1954 a, p. 1). In this, Nicholson had a different approach than Wynne-Edwards, who used the notion of a super-organism to account for natural selection producing balance in a population. How, in Nicholson's view, did balance-producing mechanisms come about? The answer he gives is that the balancing mechanisms are density-induced, writing in 1960: "thus density induced compensatory reactions to changes in the properties of organisms hold populations in a state of stability that permits the progressive improvement of adaptation by both environmental and competitive selection, even when there is no environmental change" (Nicholson 1960, p.513).

Density-governing and balance-producing factors cause an adjustment in population density which compensates for the balance-disturbing influence brought about by changes in the properties of organisms. Competitive selection, according to Nicholson, does not necessarily lead to higher population densities but can raise the equilibrium density of a population. Density-dependence plays a major part in Nicholson's ecology and his theory of evolution. High densities of populations cause competitive selection to be most severe. Compensating forces then bring the numbers in the population back to its equilibrium level.

The theoretical value of equilibrium for Elton and Nicholson

In the previous chapter I introduced the idea that equilibrium plays an important role in explaining mechanisms that are associated with it. I called this the epistemic value of equilibrium, which means that equilibrium is an important theoretical construct. This is the case for the ecologies of Nicholson and Elton. Although both connected the epistemic value of control with equilibrium, they put different emphasis on equilibrium and they associated different mechanisms with it.

Elton acknowledged Nicholson's work, and population phenomena entered into his research. He commented on Nicholson's work by saying: "Nicholson has perhaps unfortunately continued in his studies to use this word 'balance' for the mutual pressure between two populations, whether they are stationary or not. It is probably clearer, while the older conception still hangs in the air, to use Lotka's phrase 'moving equilibrium' for the fluctuation of two interrelated organisms" (Elton 1938, p.131). Balance, according to Elton, meant "constant numbers at a steady point"(Elton 1938, p.131), a notion he rejected. The differences though were not just about the meaning of the term 'equilibrium' or 'balance' but were about the justification of the assumption of balance. Each scientist justified this assumption in a different way.

For Elton equilibrium was not the focus of his work but it played a role because he assumed balancing mechanisms in nature and he justified his assumptions by the principles of the food cycle and the pyramid of numbers which suggested a certain order in nature. Later he included other mechanisms such as density-dependent population growth as regulating mechanisms. The balance, however, is constantly upset by the environment and equilibrium in the real world in terms of constant numbers does not exist. In Nicholson's ecology the balance of nature was central because it explained the persistence of populations, and he used mathematical models to justify his assumptions about the behavior of populations.

Fluctuations in nature

The different theoretical value that Nicholson and Elton associated with equilibrium can best be shown by their interpretations of fluctuations in nature. However, different aspects of the fluctuations were considered important. Nicholson used his competition curve to describe the behavior of parasite and host populations. The mathematical treatment of these equations by Bailey then illustrated the assumption of oscillating populations. Later, Nicholson experimentally showed that oscillations also appeared if larvae of insects competed for food because a time delay occurred between the laying of the eggs and maturity. Larvae produced by a small number of adults found enough food and could metamorphose resulting in a large number of adults. The adults, however, will be crowded and diminish until the population is again small enough and the cycle starts anew (Nicholson 1950). Although Nicholson's and Bailey's models suggested otherwise, Nicholson assumed that in a constant environment populations would oscillate around a steady state; the oscillations thus being an expression of equilibrium.

Elton interpreted fluctuations in organism density from the opposite viewpoint, namely as indication that the balance of nature was not achieved despite the balance-producing mechanisms he described. It can be inferred from Elton's writings that, according to him, in a constant environment fluctuations would be absent (because Elton kept assuming that climatic factors were responsible for the periodic cycles in lemmings). The effects of the fluctuations, however, were important because they disrupted the harmony of nature. To understand the consequences of fluctuations it was necessary to investigate communities as a whole.

Nicholson was interested in the equilibrium state between the fluctuations, whereas Elton was more concerned with the effect of these fluctuations on the whole system and, for Elton, the equilibria between abundance peaks were ephemeral states that were not significant. Thus Elton and Nicholson looked at the same phenomenon from different sides. Fluctuations, for Nicholson, were evidence of the existence of the stable states (much as in today's Chaos Theory). For Elton, fluctuations in nature were evidence of the opposite: they were signs of disruptions of stability implying that a balance would exist if it were not for the disruptions.

Research agendas

A reason that fluctuations and the theoretical value of equilibrium were judged differently by Elton and Nicholson could be different research agendas. Nicholson focused on populations and on two-species predator-prey systems because they made it possible to model the dynamics of parasite-host interactions. These were useful for him in several ways. First they were the organisms he was most interested in. As a director of the Entomology Division of the Council for Scientific and Industrial Research, Nicholson worked on biological pest control, making the dynamics of insects that controlled pests of considerable practical importance. Second, parasite-host interactions were important because they could be used to model intraspecific and interspecific competition. Nicholson and Bailey modeled the search behavior of parasites as intraspecific and the fluctuations of parasites and hosts as interspecific competition. The abundance of the host was closely connected to the abundance of the parasite and vice versa, since the host served as an egg depository, thus affecting the reproductive success of the parasite, and the host served as the only food source for the larvae of the parasite. On the other hand, Elton's concept of equilibrium made sense for a community ecologist because it helped him to find out more about the regulation of communities. The food cycles and pyramid of number principles were useful to understand how species interacted and how they kept each other in check.

Even if the different attitudes toward equilibrium can be attributed to different research agendas, it is not immediately clear why Elton and Nicholson chose different levels of analysis. In ecology both community ecology and population ecology have coexisted for a long time but in Elton's and Nicholson's cases the separation of the different levels is not easy to make. Elton did not merely look at communities: the phenomenon of population fluctuations had priority in Elton's research and in the BAP. Nicholson, seemingly a population ecologist, was also working on food relations between different species, as his and Bailey's models described relationships similar to the ones between predators and prey. Thus, Elton and Nicholson did not investigate different phenomena but interpreted the same phenomenon from different viewpoints.

What caused these different viewpoints? One possible interpretation is that the differences in Elton's and Nicholson's work were the levels on which they located the explanations for equilibrium. Here it could be said that Elton regarded the community as the equilibrium producing level and Nicholson the population, and what makes Nicholson a population and Elton a community ecologist is the level of explanation for fluctuations: the two ecologists differed in their assumption about equilibrium for epistemological reasons. One could then argue that both levels can coexist because they offer "autonomous levels of explanation". Neither explanation can be reduced to the other.

This possible interpretation could be supported by an argument made by Phillip Kitcher (1984), who emphasizes the epistemological autonomy of different levels of analysis in genetics, giving as an example the relationship between molecular and classical genetics. It is often assumed that classical genetics can be reduced to molecular genetics in the sense that all phenomena in classical genetics can be explained by referring to the molecular level. The notion of reduction often incorporates the idea that higher levels of analysis can be deduced from the lower levels in a logical argument. The more fundamental theory serves as a premise from which the less fundamental one can be derived. For example, Galileo's laws of free fall can be deduced from Newton's laws of gravitation. Galileo's theory is thus 'reduced' to Newtonian mechanics. For formal reasons this deduction requires "bridge principles" linking the two levels, and these seem impossible to specify. However, this is not the main reason why Kitcher rejects the reduction of classical genetics to molecular genetics. His main argument is mostly epistemological; he argues that the different levels of organization should be kept separate for reasons that have to do with our knowing about them. He denies that higher levels of organization have anything "more" to them in a metaphysical sense and thus subscribes to metaphysical reductionism denying the possibility of epistemological reductionism.

Looking at the equilibrium concept, however, I believe that ontological arguments play a role in choosing the level of explanation. I do not argue for reductionism but rather claim that Kitcher's epistemological holism is not sufficient for an analysis of equilibrium. Epistemological reasons and research agendas certainly played a role but do not show sufficiently why Elton and Nicholson interpreted fluctuations differently and arrived at different ontological commitments to the equilibrium concept. They also had different assumptions about nature, different metaphysical frameworks.

Nicholson's ontological commitment to the assumption equilibrium was much stronger than Elton's. The importance he ascribed to balance in nature and balance-producing mechanisms is underlined by his claim that: "'balance' refers to such a condition of corrective reaction to change which holds a system in being"(Nicholson 1958, p. 115). Populations, according to Nicholson, "accommodated themselves to changed conditions and so maintain themselves in being" (Nicholson 1957, p.155). The balance of populations was part of the explanation of their existence.

Elton always included the whole ecosystem in his analysis. Although he made modifications in later years he stuck to his early insight that food chains regulate communities and that the ecological survey is the correct method to investigate nature. Elton later acknowledged the existence of density-dependent mechanisms and endorsed the work done by Nicholson. He supported Nicholson's idea of populations splitting up and forming subgroups, which Nicholson had used to explain the crash of local populations. Elton thought that this point needed "wider recognition" (Elton 1949). He, however, did not share Nicholson's conviction that processes at the population level were to be considered primary. As Elton and Miller wrote:

> It is that whatever problem in natural population control or dynamics is being studied, one has to consider the working of density dependent situations and therefore of biotic relations both within ... the same population and between populations of different species. From this it follows that one needs to know about community ecology, in other words to undertake ecological surveys...(Elton and Miller 1954, p. 461).

We could ask why it follows that ecological surveys had to be done and not laboratory experiments. It seems that Elton accepted Nicholson's and Lotka's concepts but transferred them into his own metaphysical framework. Because the whole system was regulated and not just the populations, the Nicholsonian concept of self-regulation did not have the impact on Elton that it had on others. Elton's metaphysical framework was the harmony of nature in general. The whole ecosystem worked in a regulated fashion, explaining perhaps why he was influenced by Lotka's machine analogy for ecosystems (Nicholson used the machine analogy as well, albeit with a different meaning and applied it to the balanced state of populations - see Kingsland 1995, p. 119). Elton referred to the participating species as energy transformers. His system approach can be found also in his attitude towards environmental ethics: he warned against the overexploitation of the land and criticized the establishment of monocultures because they made ecosystems too simple and thus prone to invasions by foreign species because he held the view that simple ecosystems were less stable than complex ones (Elton 1958, p.145).

The different metaphysical frameworks of Elton's and Nicholson's work can also be detected in their treatment of natural selection. Referring to natural selection is useful because in Nicholson's and Elton's times the theory was not as well accepted and developed as it is now. Different views about the units of selection and the work of natural selection in ecology existed (Collins 1986), and it is not surprising that Elton and Nicholson offered explanations of natural selection that sound odd today. Kimler (1986) claims that Nicholson's view of natural selection received much less attention than his work in population ecology, and the same applies to Elton whose book about ecology and evolution published in 1930 received much less credit than his other work (Crowcroft 1991, p. 2). Their reasoning was guided primarily by their ecological insight rather than by interpreting ecology through the lense of natural selection. Both ecologists gave ecological explanations for natural selection and not natural selection explanations for ecology, the latter a common strategy today when the theory of natural selection is seen as the unifying theory of life (Pianka 1978, p.9). Both Elton and Nicholson interpreted the theory of evolution with caution. Both were careful about the principle of the survival of the fittest. However, in their accounts of how natural selection works, elements of their assumptions about nature can be found. Elton described the importance of migration for natural selection, arrived at from his description of food cycles. He also suggested that natural selection could act on whole communities and he believed that natural selection worked on higher levels than the individual.

In Nicholson's case the concept of natural selection was even more closely tied to this views about the structure of nature and the level of population control. The balance of nature took precedence over natural selection. Balance was disrupted by natural selection and could be reestablished by intraspecific competition.

My aim here is not to describe the whole metaphysical framework of the two ecologists. I only describe as metaphysical the ontological assumptions made by Elton and Nicholson as far as they are expressed in their scientific papers and some secondary sources. I also limit myself to an analysis of the metaphysical framework concerning equilibrium. I think that here Elton and Nicholson did indeed make different assumptions about the structure of nature. Similarities in their metaphysical frameworks certainly can be found; for example, both ecologists seemed to assume a certain harmony of nature and they also share some views about natural selection. Regarding equilibrium, however, their different assumptions about its location and its explanatory value were partly the result of different metaphysical views, that is, different assumptions about the structure of nature.

I have used the notion of explanatory value that is connected to equilibrium to describe its use in the non-ecological sciences. The notion, vague as it is, points to a feature of equilibrium that I analyzed in the writings of Elton and Nicholson. Although at first sight both ecologists attach explanatory value to equilibrium, a closer look shows that Elton does not really use equilibrium as an explanation for regulation. I claim that this can be detected in the different interpretation of fluctuations by the two ecologists, which can be only partly attributed to different research agendas and different research fields. The influence of ontological assumptions which are part of a metaphysical framework cannot be denied. My analysis of the metaphysical framework leads to my claim that epistemological factors are not solely responsible for different conceptions of the assumption of equilibrium.

Conclusion. What is equilibrium?

The notions used in this and the previous chapter such as 'epistemic values' or 'metaphysical framework' are admittedly vague. My main purpose, however, was to show that a definition of equilibrium is relative to a certain discipline and even within a discipline one has to investigate what scientists intend to use the equilibrium concept for. Then one has to enquire in what kind of metaphysical framework equilibrium is embedded.

A definition of 'equilibrium' without these considerations seems vacuous. Searching for this definition led me to the idea of epistemic values and then to an investigation of ontological commitments by scientists. A definition of 'equilibrium' in isolation is possible for every discipline. However, it is only part of the whole story about equilibrium. The ambiguities of the equilibrium concept and scientific constructs like it have been investigated by scientists and philosophers for a long time. The equilibrium concept is partly based on observations of nature and partly in the minds and practices of the members of a scientific community. Other important sources of influence on the equilibrium concept are also possible.

For example, a topic not mentioned is the social development around ecology in the early 20th century. Why were ecological questions brought up in the first place? What is the cultural significance of equilibrium, a concept used in so many disciplines? Another aspect is the institutional background of ecologists at the time and its influences on the notion of equilibrium, especially the notion of population control, a highly political subject.

It hardly seems possible to understand the development of the equilibrium concept without investigating these aspects. This claim, however, is problematic because it assumes the existence of the great "meta narrative" which would mean that all the different perspectives could be added up and a complete true story of equilibrium would emerge. Postmodernists and others have questioned this assumption profoundly and I find it questionable that all perspectives on the equilibrium concept would tell the true story. Given that there are already so many disciplines in science studies that do not communicate well with each other, it is difficult to imagine who would tell or write the great meta-narrative, even if it were possible.

The approach I am suggesting is to understand the justification of the concept of equilibrium, by analyzing why ecologists use the concept. I have begun with the early justifications by Elton and Nicholson. Concentrating on the justification of the equilibrium assumption by scientists I will not aim to arrive at a definition of equilibrium which stands above the usage in ecology but will look into ecology and how the justification of equilibrium has developed. Mine is a naturalistic approach to equilibrium as a theoretical concept and requires both a historical and a philosophical perspective.

Chapter 4: Mathematical justification and the logistic curve

In the previous chapter I showed that the assumption of equilibrium in nature took various forms within the discipline of ecology, and I analyzed some elements that play a role in these assumptions. For Nicholson the balance of nature was established through density-dependent growth which was the result of intraspecific competition. For Elton the interactions within a community provided some sort of balance which was constantly interrupted, mostly by climatic factors.

Symptomatic of the divergent views of equilibrium were the analyses of fluctuations by the two ecologists. In Elton's metaphysical framework fluctuations were evidence that balance did not exist, whereas Nicholson interpreted fluctuations as oscillations around an equilibrium state. This view resulted in a deeper ontological commitment to equilibrium by Nicholson.

The equations developed by Nicholson and Bailey were used to justify the assumption that populations oscillate around an equilibrium state. Although Nicholson was assisted by the more mathematically experienced physicist the initial motivation for a mathematical justification of the equilibrium assumption was Nicholson's own (letter to Kenneth E.F. Watt from December 15, 1965, Adolph Besser Library, Australian Academy of Science, Canberra Australia). He used mathematics because he did not think that experimental justification of his claims could be presented. In a letter to Frank E. Egerton of May 25th 1961 (Besser Library) Nicholson described his belief that the size of the populations needed and the space required prohibited testing his hypotheses in the laboratory. Later, he saw that experiments were possible and he used the sheep blowfly *Lucilia cuprina* for experiments on intraspecific competition. (Nicholson 1954 a).

Although the lack of experimental opportunity is one reason Nicholson turned to mathematical justification, one could still wonder why he trusted it. According to Nicholson, he had approached Bailey around 1929 for help with the predator-prey equations (letter to Watt, December 15, 1965). At this time other scientists were working independently on mathematical justification of ecological statements. Scudo and Ziegler (1978), for example, called the time between 1923 and 1940 "the golden age of theoretical ecology" because of the rapid development of mathematical methods in the discipline. The assumption of equilibrium, the illustration of oscillations, and mathematical representation, were connected in the history of the concept of equilibrium.

Before I investigate this statement further I have to clarify my use of the term 'justification'. In the last chapter I described how Nicholson justified the use of equilibrium. Then I showed that he relied on a mathematical representation of predator prey models which leads to my discussion of the justification of the equilibrium concept through mathematics in this chapter. One could argue that I have confused two distinct levels of justification. According to positivist philosophy of science the discovery of equilibrium and its justification belonged to different contexts, the discovery or the invention of the equilibrium concept being part of the context of discovery. Only here would Nicholson's ontological commitments matter. According to the positivists, the context of discovery is highly contingent and historical because many intangibles are involved. Justification, on the other hand, is ahistorical, based on the rules of logic, which provide the rules for the deduction of hypotheses and the proper testing of a theory. These rules are independent of the context of discovery.

This assumption of separate contexts is still entrenched in the thinking of many scientists and philosophers. For example, the context of discovery is often credited to the genius of the individual scientist and justification to analytical rigor. I do not consider this separation of contexts as helpful for an analysis of the concept of equilibrium. The point is not to deny that hypotheses are often developed in ingenious ways or that analytical skills play a role in science. However, the positivists' account is a mystification of the justification that took place for the equilibrium concept. I claim that justification cannot be seen separately from the discovery, or, more cautiously, what caused the justification of the equilibrium concept cannot be decided independently of the debate about it. It is not the case that general ahistorical rules of inference were followed and provided an a priori justification for the equilibrium concept. For this reason I understand 'justification' as including the context of discovery, by investigating the scientists' motivations to use the equilibrium concept.

The golden age of theoretical ecology

Although the 1920s saw an increase in mathematical representations of nature, national differences seemed to have existed in their acceptance. In a letter to the Italian mathematician Vito Volterra (1860-1940) the Canadian entomologist W.R. Thompson (1887-1972) wrote that he published his work in French journals because he was afraid "American journals would not accept the mathematics" (quoted after Milán Gasca 1996, p. 356). As will be shown shortly, besides France Italy apparently provided a fertile atmosphere for mathematical justification. In Britain, on the other hand, Nicholson and Bailey had difficulties finding an editor for their book. In a rejection letter from Clarendon Press, Nicholson's original approach was appreciated. However, the reviewers "came to the conclusion that they were not yet satisfied with the marriage of mathematics and biology" (letter from Clarendon Press to Nicholson, March 30th 1932, Besser Library). After more letters of this kind, Nicholson and Bailey resigned their efforts to publish their theories in book form. Nicholson, however, was granted extra space to publish his work about the balance of nature in the *Journal of Animal Ecology* whose "physical and spiritual home" was the Bureau of Animal Population and whose editor was Charles Elton (Crowcroft 1991, p. 14).

Nicholson's approaches to parasite-host relationships were influential and were used especially by entomologists who were interested in biological population control of pests, such as the researchers at the Division of Biological Control of the Citrus Experiment Station in Riverside, California (Palladino 1996, p. 11). Bailey visited Riverside in 1937 and had heard to his delight that the entomologists there were "most enthusiastic" about Nicholson's and Bailey's work (Bailey in a letter to Nicholson July 1937, Besser Library). The Riverside scientists found Nicholson's and Bailey's models useful because of the difference equations used and the inclusion of time lags that occurred between predator and prey interactions. Another approach to predator-prey dynamics and equilibrium, perhaps as influential as

Nicholson's, was developed by Volterra and the Austrian - now Ukraine - born American Alfred James Lotka (1880-1949).

Lotka and Volterra

A.J. Lotka was educated in chemistry and physics in Germany and France and influenced by a thermodynamic approach to those disciplines (Kingsland 1995, p. 28). When he moved to the United States in 1902 he began working for the General Chemical Company in New York until 1908, when he took a master's degree in physics from Cornell. He then had several non academic jobs as chemist and physicist and worked at General Chemical Company again during the war. In 1920 the influential biologist Raymond Pearl (1879-1940) brought Lotka to Johns Hopkins University in Baltimore. Pearl saw potential in Lotka's work on the connection between mathematical and physical methods in biology which he had published in his spare time while working as a chemist. In 1922 Lotka received a fellowship from Pearl's department at Johns Hopkins and began working on his book *Elements of physical biology*, which was published in 1925. Shortly after, Lotka took a position as mathematician and later statistician at the Metropolitan Life Insurance Company in New York where he stayed until his retirement in 1947.

Volterra studied natural sciences at the University of Florence and physics at the Scuola Normale in Pisa. As a young man he already had published many papers on mathematical topics. After receiving his degree in physics at the age of 22 he became full professor at the University of Pisa one year later. In 1900 Volterra was offered a position at the University of Rome and his acceptance speech was titled: "*On the attempts to apply mathematics to biological and social sciences*" (Borsellino 1979, p. 410 ff). Volterra made many contributions to the field of mathematics, especially in the analysis of differential equations, which he used to describe-predator prey relations. He regarded these deterministic equations as superior to a probabilistic approach to biology as it was being propagated for genetics in the early 20th century by Ronald A. Fisher (1890- 1962), John B.S Haldane (1892-1964), and Sewall Wright (1889-1988) (Milán Gasca 1996, p. 348). According to Volterra, his equations provided mathematical form to Darwin's theory of natural selection because they described what Darwin had suggested about predator-prey relationships in the *Origin of Species* (Milán Gasca 1996, p. 353). In addition to becoming a Senator of the Italian Kingdom in 1905, Volterra was an influential member of the Italian scientific community, for example as president of the Accademia dei Lincei, until the rise of fascism in his homeland. He then resigned from all public and academic activities and worked at home or abroad until his death in 1940 (Scudo 1971).

These two authors differed in their approaches, which they developed independently, but many similarities can be found so that the predator-prey equations are today called Lotka-Volterra equations. Both used differential equations focusing on the rate of change in populations rather than on change in actual numbers and both based their approach on analogies to physics and chemistry. The mathematical description of oscillations between predator and prey formed one part of the equilibrium discussion in the 1920s and it was relevant for community and population ecology.

Oscillations

Mathematical methods in ecology were often inspired by the observation of cyclic fluctuations of predator and prey populations, the investigation of which were at the core of Elton's and Nicholson's work. Thompson, for example, was encouraged to use a mathematical approach by cyclic population dynamics in insects: "for he who says periodicity, regularity, rhythm, says the possibility of a mathematical representation" (Thompson 1923 quoted in Kingsland 1995, p. 100).

Lotka and Volterra were interested in oscillation for different reasons. Lotka first approached the subject in his paper *Contribution to the Theory of Periodic Reactions*, published in 1910. In his 1925 book Lotka gave a broad treatment of oscillatory behavior of predator and prey populations. His starting point was an investigation into the redistribution of matter in general, because he saw equations that described this as expressing the process of evolution. He wrote, "the fundamental relation expressing the law of evolution, the historical pattern, or the system, is in this case given by the law of mass action" (Lotka 1925, p. 42), which he used in a general form as $dm/dt=F(m_1, m_2, m_3; v, T)$. This described the rate of change of mass over time as a function of the components m_1, m_2, and m_3 as well as temperature (T) and pressure (v). Lotka investigated this equation and its relevance for population growth and for cases where a predator feeds on a prey population.

Volterra, as mentioned above, had been interested in the application of mathematics to biology as early as 1900. His deeper involvement in theoretical ecology and the descriptions of oscillations started in 1925 when the marine biologist Umberto D'Ancona approached him to mathematically analyze a problem in fisheries. D'Ancona, then engaged to Volterra's daughter Louisa, had observed that the proportion of predators in the catches had increased after a pause in fisheries due to the First World War (Scudo 1971; Kingsland 1995, p. 106). Volterra published his equations in a long memoir in Italian in 1926 (translated and reprinted in Scudo and Ziegler 1978) and in a much shorter version in the same year in the journal *Nature*.

The equations

Volterra approached predator-prey dynamics by describing the encounters between predators and prey as analogous to encounters of molecules in a gas. This method of encounters used in classical statistical mechanics described the numbers of collisions of molecules as proportional to the product of their densities (Scudo 1971). Lotka came to similar conclusions based on the law of mass action.

The Lotka-Volterra equations are usually formulated:

$$dN/dt=aN-bNP$$

$$dP/dt=cNP-dP$$

where N = number of prey
t = time
a = growth rate of prey
b and c = per capita change in prey and predator population due to interaction
d = death rate of predator

These equations were based on the assumption that the prey population would grow exponentially in absence of the predator (signified in the first equation by the term aN), that predators would starve in the absence of prey, and that its rate of extinction without prey would be proportional to the number of predators (signified in the second equation by -dP).

Furthermore, the equations described oscillations of both species around a mean value that was dependent on the growth and death rates of predator and prey and their initial numbers. The oscillations were coupled and periodic as predators increased when there was a large amount of prey, and they decreased when the prey diminished. The period of the oscillations depended on the growth rate and the death rate of prey and predator as well as on the initial numbers of the organisms. Volterra called this the first law that was derived from his equations. The second was that the average numbers of the species tended to constant values as long as the growth and death rates (a and d above) as well as the interaction parameters (b and c above) stayed constant (Volterra 1926). The third law provided Volterra with evidence that his calculation had empirical proof. He interpreted the fishing activities as a decrease in the growth rate of the prey (a) and an increase in the death rate of the predator (d becomes more negative).Volterra concluded that, as long as (a) stayed positive, the prey population would increase while the predator population would decrease. In short, "the larger the mortality of the predator, the larger is the population of the prey" (Hutchinson 1978, p. 221). A halt in fisheries would produce the opposite, an increase of the predator and a decrease of the prey which was what had been observed by D'Ancona.

Lotka arrived at virtually the same equations as Volterra by using the law of mass action as a starting point. He then solved these equations with a Taylor expansion and drew the integral curves as closed ellipses in the same way as Volterra. When Volterra published his results in 1926 Lotka protested that his own contribution to the subject was not mentioned. Volterra had been unaware of Lotka's work but then acknowledged Lotka's priority concerning some aspects of the description of the predator-prey dynamics. Although using similar approaches Lotka's and Volterra's fields of research and interests were different so that no collaboration resulted. Perhaps this was also the reason the priority dispute soon lost its heat. Lotka had become more interested in the analysis of growth of human populations by then and Volterra continued with a refinement of his differential equations (a more detailed analysis of the priority dispute is given by Israel 1993).

The Lotka-Volterra equations enabled ecologists to calculate stability conditions for the predator prey relationship and sparked further research. These calculations helped to clarify whether the stability of the interactions contributed to the stability of communities, or if instability could disrupt them (Rosenzweig and MacArthur 1963). The conditions for stability were determined mathematically by setting the rate of increase for predator and prey as zero. This stationary state was the equilibrium point. Then the equations were solved, and how slight disturbances from the equilibrium state would influence the interaction was investigated. If these slight disturbances led the populations to move away from the equilibrium point the equilibrium was considered unstable. The stability of equilibrium in the equations depended on the value of the roots of the solutions, which was investigated in detail by Lotka (1925, p. 148 ff.).

Graphic representation

Calculating the stability conditions of the equilibria was a complex mathematical operation. However, one of the most striking features of Lotka's and Volterra's work was how they presented the graphical solutions to their equations making it possible for ecologists to understand the conditions for stability developed in the equations. An example is the coordinate system used to illustrate the oscillations of predator and prey populations (Figures 6 and 7). Every point in the coordinate system represents a community composition, meaning a certain number of predators and prey. It was possible to calculate at which points the predator and the prey populations maintained themselves. These points were connected to form the zero-growth isoclines. Where the two zero-growth isoclines meet is the point of equilibrium for a two-species community. The figure also shows how the two-species community behaves. The predator-prey trajectory has the form of ellipses circling around the equilibrium value in periodic oscillations. Three different oscillations are shown for three different sets of values of the parameters b and c.

The underlying model of Figure 6 was not realistic because in the equations the behavior of the prey and predator populations were immediately dependent on each other, causing the coupled oscillations. This could only happen in an undisturbed environment.

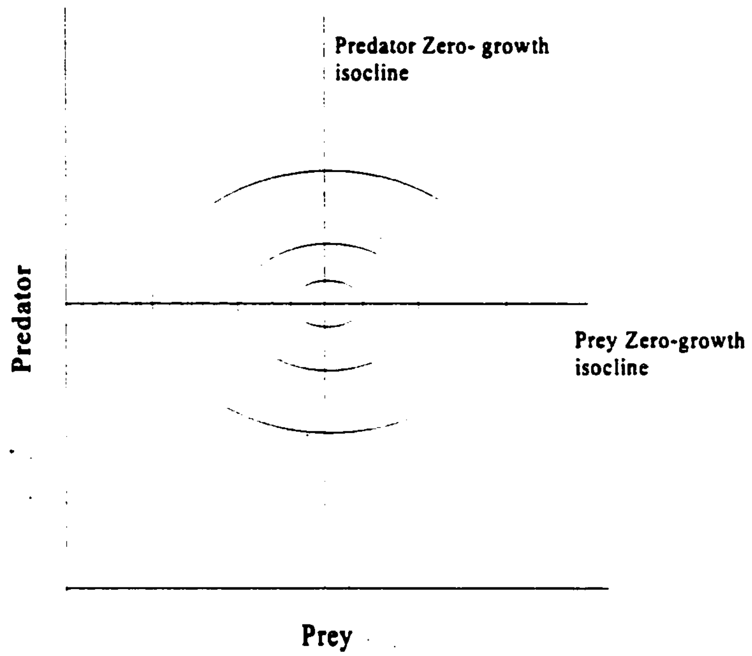


Figure 6: Predator-Prey oscillations as predicted by the Lotka and Volterra equations

Every disruption, every change in birth rate or death rate as well as a change in the rate of encounters of predator and prey, would have caused erratic oscillations. The assumption that predator and prey were limited only by each other was illustrated by the horizontal and vertical isoclines. This meant that the concept of density-dependence that was at the center of Nicholson's models was not part of the initial Lotka-Volterra equations. The addition of density-dependence, at least of the prey population, would have created a stable equilibrium, as is shown in Figure 7 where the predator isocline is still vertical but the prey isocline is slanted. This meant that the prey population was limited by its own density. The graphical representations of the underlying dynamics of predator-prey oscillations are still debated and different versions of the zero-growth isoclines are discussed. Besides density-dependence of the prey population several forms of hunting behavior by predators can be included in the graph (see Berryman 1992).

The discussion of the stability of predator-prey models had a strong impact on community ecology and the equations of Lotka and Volterra were important for the

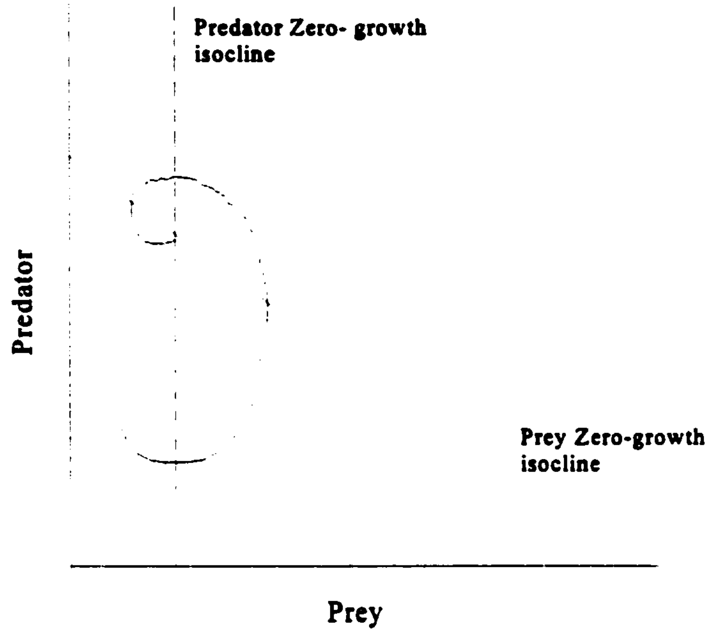


Figure 7: Predator-Prey oscillations as predicted by the Lotka and Volterra equations with density dependend growth of the prey population

justification of equilibrium in animal communities. The equilibrium solutions of the equations for predator-prey dynamics provided evidence about the rebounding behavior of the system. Assuming slight displacement from the equilibrium state, Lotka determined whether the system returned to equilibrium or departed from it. This notion of equilibrium, as an epistemic value for rebounding behavior was intensely debated by community ecologists and I will not describe this discussion here. However, the calculation of the stability conditions for equilibrium states and their graphical representations are still relevant today and formed a link between population ecology and community ecology because they enabled ecologists to understand oscillations in nature based on the interaction between predator and prey.

It is curious to see how Lotka and Volterra acknowledged the idea of density-dependent growth of populations. In his original treatment Volterra ignored it; the existence of damped oscillations as shown in Figure 7 would have violated his first law, which predicted periodic oscillations. Later Volterra included density-dependent growth in his modeling, perhaps because he became aware of other work in the field. However, it seems that his method of encounters initially did not lead him to the concept of density-dependence.

Lotka included density-dependence in his treatment of predator prey oscillations but only in mathematical form. He wrote that damped oscillations would result by including terms of second degree (N^2 or P^2) in the equations. When added to the equations above this would result in closed curves when the integral was plotted. The ecological significance of N^2 or P^2 was that they represented interactions between individuals of a population. Lotka only mentioned the second degree terms and their inclusion but he briefly referred to the work by Poincaré for the mathematical solution; he did not seem to see the ecological relevance of the higher terms.

A reason for this immediate oversight by Lotka and Volterra could have been that their analogies came from physics and mathematics. Volterra especially was not familiar initially with work in population biology by biologists, and his method of encounters did not include density-dependent growth. Lotka's case is different because he had known of the self-limitation of populations through his collaborations with Pearl. He had acknowledged density-dependent population growth by 1923 (Kingsland 1995, p. 83) and earlier he had described damped oscillations in chemical reactions in 1920. He did not include the assumption in his predator-prey models but only in his models for single population growth and particularly later in his work on the dynamics of human populations. This seems to bear out for Israel's (1993) claim that Lotka did not completely trust the analogy between chemical oscillations and those of populations. Not being an ecologist, and being more focused on the general significance of energetic exchanges in the growth processes, he might initially have missed the relevance of density-dependent population growth in the predator-prey dynamics.

Adding a quadratic term to the predator-prey equations could have been a method to represent density-dependent growth. The integral of the quadratic equation plotted against time would have resulted in a sigmoid growth curve, the logistic curve, which became a model for population growth that was at the center of a debate about density-dependence in the 1920s onward. Here equilibrium was discussed in terms of the regulation of populations by their density.

The logistic curve

The logistic curve had been developed in the discipline of demography, which investigates the growth of human populations using vital statistics. It can be traced back to the 17th century when John Graunt, in 1662, first constructed tables of birth and death rates to estimate the growth of the population for the city of London (United Nations 1973; Hutchinson 1978, p.5). The discipline of demography, especially in the 18th century, was connected to political or economical analysis (Hutchinson 1978, p.11). Knowledge about death rates and birth rates was important to make claims about the structure of a population and assess its productivity. Views on population played an important role in economic theories of the 17th century, for example mercantilistic economic theories. According to the mercantilists, a large population meant higher revenues because the work force was larger and wages could be lowered (United Nations 1973, p. 35). Michel Foucault wrote about the development of demography in the 18th century: "the biological traits of a population become relevant factors for economic management, and it becomes necessary to organize around them an apparatus which will ensure not only their subjection but the constant increase of their utility" (Foucault 1976). Foucault saw demography as part of the increasing medicalization of society which was part of general economic changes in the 18th century.

The most popular work that used the analysis of population growth as basis for economical and social principles was Thomas Robert Malthus' essay on principles of population growth, first published in 1798. The essay promoted the thesis that a state welfare system would be doomed to fail because it could never change the fact that population size increased, when unchecked, geometrically, whereas resources only increased arithmetically (Malthus 1960).

The geometrical rate of increase of a population with no boundaries was questioned by Pierre Verhulst, a Belgian mathematician. In his studies on population dynamics Verhulst was influenced by Adolphe Quetelet who had published a paper in 1835 describing the resistance to population growth as proportional to the speed with which the population tended to increase. Verhulst developed the logistic curve by constructing a simple mathematical model that described a continuously growing population with an upper limit (Hutchinson 1978, p. 20), publishing it in a memoir in 1845.

T. Brailsford Robertson, a physiologist, introduced the logistic growth curve into biology in 1908 using it initially as a model for the growth of individual organisms (Kingsland 1995, p. 66). Robertson investigated growth phenomena by looking at their underlying chemistry. He found that the growth of organisms mostly started slowly, increased in speed and finally approached a limit asymptotically. He found this to be analogous to chemical reactions whose "progress of change" (Robertson 1923, p.5) was catalyzed by their own products. For this reason he called the logistic curve 'self accelerating' or 'autocatalytic'. In 1923 Robertson applied the same logistic curve that he had applied to individuals to the growth of bacteria populations (Kingsland 1995, p. 66). The growth process described by the logistic meant that there was a limit to the growth of the population which was determined by the density of the population. The population approached an equilibrium size from both sides; a population below it increased and one larger than it decreased.

The logistic curve was much debated when it was used to describe the growth of non-human populations. One of the curve's main supporters was Raymond Pearl (1879-1940), who had discovered Lotka and had tried to bring him to Johns Hopkins University. Unlike Nicholson, Pearl did not give priority to the assumption of a balance of nature but saw the logistic curve as a good example of the connection between mathematics and biology. Through him the logistic curve took center stage for the justification of equilibrium from the 1920s onward.

Pearl and mathematical biology

Pearl's interest in this topic had been sparked during his stay in London in 1905/1906, where he was working with Karl Pearson (Kingsland 1995, p. 58). Pearson was committed to a strictly empirical approach to science as described in his major work *The Grammar of Science* published in 1892. After the publication of his book he became increasingly interested in the study of evolution. Inspired by Francis Galton, Pearson began to develop statistical methods to study variations (Provine 1971, p. 32). He became one of the founders of biometry and the first editor of the scientific journal *Biometrika*, first published in October 1901 (Provine 1971, p. 62). It should be mentioned that although Pearson was inspired by Galton, the two disagreed on the nature of evolution. They were on different sides in the debate between Mendelians and biometricians which started soon after 1900 (Provine 1971, p. 25). (This discussion included a debate about another form of equilibrium, the Hardy-Weinberg equilibrium. I do not consider here.)

The collaboration with Pearson resulted in Pearl's initial interest in eugenics and in mathematical method in biology. Later in his career Pearl criticized the eugenics movement, more for its methods than for its aims as it became increasingly propagandistic in the 1920s, which, according to Pearl, was not justified by genetic data (Allen 1991). Pearl's interests turned to the problem of rapidly increasing human population growth, and he wondered how it could be limited (Allen 1991). For this it was necessary to know how populations grew and a mathematical description of growth processes was needed.

Because of his acquaintance with Pearson, Pearl believed in the fruitful connection between mathematics and biology. As Kingsland (1995, p.59) wrote, "he saw himself not merely as a disciple of Pearson, but as a modern descendant of the mathematical tradition in evolutionary biology extending through Pearson back to Francis Galton". The mathematical illustration of logistic population growth was an important part of this tradition, although Pearl was not convinced of it at first. He initially rejected Robertson's growth curve, claiming that it did not reflect empirical findings correctly and did not really describe underlying properties of growth. Both arguments will reappear later, ironically stated against Pearl himself who, in the 1920s, became a firm believer in the logistic curve (Kingsland 1995, p. 67). It is difficult to say exactly what changed Pearl's mind, but by the 1920s he believed that the logistic curve was a law of population growth.

The logistic curve and equilibrium

Pearl and the mathematician Lowell Reed assumed that population growth followed a sigmoid path and described it in mathematical terms (Kingsland 1995, p. 68). They compared their model with data from human population growth and found that it fit well enough to announce the law-like character of the logistic curve in an article in 1920. The discipline of demography thus delivered the material for the establishment of a biological model. The introduction of the logistic curve was at the center of a debate in population biology about the control of population growth and about mathematics in biology.

The equation that describes the logistic growth of populations is:

$$dN/dt = rN(1-N/K)$$

N=number of individuals in a population
t=time
r=instantaneous rate of increase
K=carrying capacity

This translates into the graph in Figure 8, which shows that the curve approaches K, the carrying capacity, asymptotically. K in the logistic is a stable equilibrium point because, once replaced from it, the population returns to K, shown in Figure 8 by the upper curve.

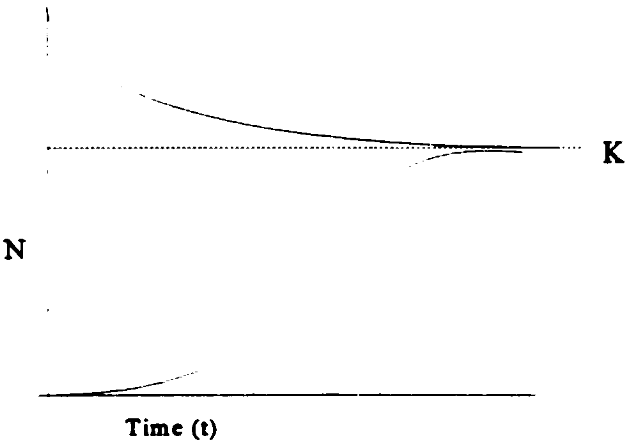


Figure 8: The logistic growth curve K= carrying capacity, N= population size

The logistic suggests a certain relationship between the rate of increase of a population and its size which leads to an equilibrium value. At the heart of the debate about the assumptions underlying the logistic curve was the variable r and its "interpretation" by the logistic model. This led to a discussion about growth rates in populations which had important consequences for the present justification of the equilibrium concept. The variable r can be interpreted in several contexts.

r as difference between birth rate and death rate and its theoretical nature

The simplest definition of r is the difference between birth rate and death rate in a population. To calculate it and make predictions about population growth, demographers tried to obtain data on birth rates and death rates in life tables, as was done in the beginning of demography, for example by John Graunt in the 17th century. This provided an estimate of the growth rate of the population.

The value of r can be calculated by subtracting the population's death rate from its birth rate. This, however, can only give an estimate of the "true" growth rate. To understand this it is useful to investigate the other definition of r which is instantaneous growth rate or per capita rate of increase.

Finite rate and instantaneous rate of increase

Malthus' hypothesis was that unchecked population growth is exponential or geometric. This was based on the assumption that every organism left more than one successor. Assuming that the size of a population at time 1 is λ times bigger than the population at time 0 we arrive at the equation:

$$N_1 = \lambda N_0$$

The same can be said for the population at time 2

$$N_2 = \lambda N_1 = \lambda^2 N_0$$

and for time 3

$$N_3 = \lambda^3 N_0$$

λ denotes the finite rate of natural increase, the ratio between the population size at one point in time to the population size at a previous time. For example, a population with $\lambda = 1.2$ will be 1.2 times larger than the population in the previous interval (Pielou 1974, p 2). If, however, we model population growth as continuous, we use differential equations.

The time steps become infinitely small, and the equation for population growth is now:

$$dN/dt = rN$$

The letter r in the continuous model takes the place of λ. It is now called the instantaneous rate of increase. The unit of r is individuals/time, and thus r measures the per capita rate of increase, the rate of individuals added to the population over time. Pielou (1974, p 2) compared the growth of a population to an amount of money earning interest, expressing the rate of interest as r. The value of λ is the ratio between the amount of money in the second year divided by the amount of money in the first year (remember here Foucault's statement cited above). The mathematical relation between λ and r is: $\lambda \approx \ln r$. This relation, however, is only approximate.

The theoretical r

Today ecologists use r and λ interchangeably but this blurs important differences between the two variables. One difference is that r can be transferred to different units, whereas λ cannot (Gotelli 1995, p. 5) An annual rate of 12% charged by a bank, which would symbolize r, can be translated into 1% a month. A number for λ for one year cannot be transferred into a monthly value. Thus r makes the comparison between populations possible.

This comparison, however, only makes sense if r is considered to be some characteristic of a population that does not change with the composition of the population but gives some estimate of the "true" ability of the population to increase. This cannot be measured in the field because this hypothetical "true" r depends on the age distribution of populations in which reproduction as well as death and birth rates are dependent on the age of the organisms. The value of λ, on the other hand, can be measured in the field by simply dividing the number of organisms in one year by the number in another year. A concrete value is gained. This, however, provides only a momentary picture of the growth rate in a population. If this finite rate is transferred into r, a misleading estimate of the "true" r is arrived at.

The problem of r in demography was illustrated in a 1925 article by Louis L. Dublin and Lotka. They claimed that the American population had a high birth rate because of high immigration rates of people who were in and about mid-life (Dublin and Lotka 1925), a factor that had to be taken into account when calculating r. The immigration rate, however, was subject to change. If it declined, then the birth rates would have been smaller as well and, r had to be recalculated. The high immigration rate thus 'inflated' the value of the 'true r' because the immigrants contributed to a relatively high proportion of the birth rate.

How then can the value of r ever be calculated? Dublin and Lotka assumed that an age distribution could eventually become stabilized:

> Certain age distributions will practically never occur, and if, by arbitrary interference, or by a catastrophe of nature, some altogether unusual form were impressed upon the age distribution of an isolated population, the irregularities would tend shortly to become smoothed over. There is, in fact a certain stable age distribution about which the actual age distribution varies, and towards which it returns if through an agency disturbed thereupon (Lotka 1925, p. 110).

The assumption of a stable age distribution presupposed assumptions about stability in the first place. Dublin and Lotka (1925, p. 311) wrote that: "it can be shown that with a fixed schedule of maternity rates for women of different ages, and a fixed age schedule of mortality, the population will gradually settle down to a fixed age distribution". This meant that the *relative* not the *absolute* numbers of individuals in each age class remained constant. Assuming this, Dublin and Lotka could calculate r for the stable population and compare the true natural rate of increase with the rate of increase of the actual population, which was distorted because of immigration and other factors.

The main characteristic of r was its theoretical nature. Its importance did not lie in its immediate measurability or observability but in its usefulness as an assumption of how a population would behave under specific conditions. These assumptions could then be compared to the actual state and conclusions could be drawn. In Dublin's and Lotka's case these conclusions were that the immigration is important to keep the growth rate of the American population high.

The debate about r

The theoretical nature of r caused some dispute. Thompson, who in the beginning of his career, was an advocate for mathematical ecology found that the abstraction in the case of r went too far. He rejected its use because it could not be observed and it thus had no ecological significance (Thompson 1931 quoted in Cole 1954). Other ecologists tried to incorporate r and its estimation from life-tables into their discipline and this created a discussion about the concept of equilibrium. To calculate r from life tables the assumption of a stable age distribution was necessary, otherwise one could never be sure how close the calculated r was to the real r. This seemingly technical issue had an important effect on the discussion of the concept of equilibrium because it was assumed that a population that had reached a stable age distribution was growing exponentially and not in a density-dependent manner. The two assumptions of a stable age distribution and exponential growth were connected. Initially density-dependence was not the focus of the life-table estimation of r. On the contrary, the logistic curve with its interpretation of r was contradictory in parts to the life table approach.

r and the logistic

The logistic equation consisted of two parts, the first of which described exponential population growth (rN), the second, the limit that is set to the population (1-N/K). The second term in the equation modeled the approach to K. This could be illustrated graphically by plotting population growth rate (dN/dt) against population size and by comparing the model for exponential growth and logistic growth (Figure 9). Comparison between Figure 9a and 9b shows the initial increase in the rate of population growth (dN/dt) and the subsequent decrease until the population reached K in the logistic curve, whereas it had no limit in exponential growth. How did the per capita growth rate depend on population size? This can be seen in Figure 10 where the difference between exponential growth and logistic growth in relation to per capita growth rate is plotted, r being expressed as (1/N) (dN/dt). Figure 10a shows that for exponential growth, r remained constant, meaning that population size had no effect on the per capita increase of the population. In a population that was

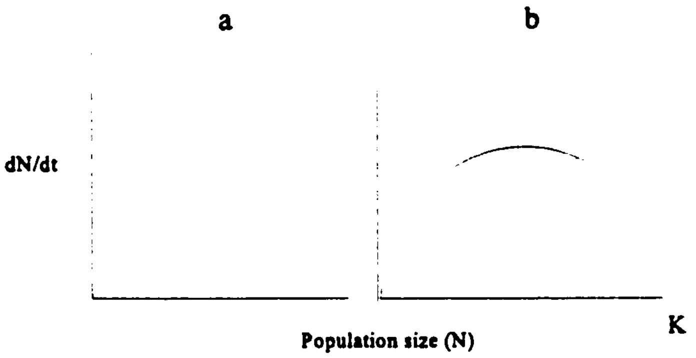


Figure 9: Growth rate (dN/dt) in relation to population size modeled as exponential growth (a) and as exponential growth (b) (from Gotelli 1995, p. 33)

growing exponentially, the difference between birth rate and death rate stayed constant, no matter how large the population was. A constant r was assumed when calculating r with the help of life-tables. Density-dependence was not part of the model. In contrast to this, Figure 10b shows that r_m declined linearly with population size in logistic growth until r reached K

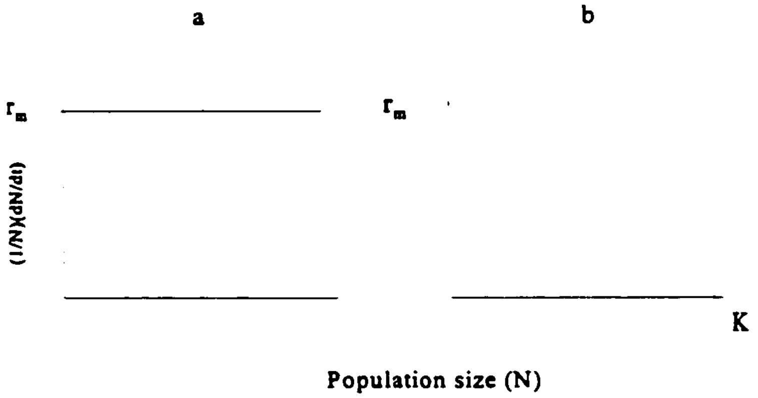


Figure 10: Per capita growth rate (1/N)(dN/dt) as a function of population size (N) for exponential growth (a) and for logistic growth (b)

and the population ceased to grow.

It seems counterintuitive that the per capita growth rate declined according to the logistic equation even if the population was still growing. However, the model assumed that the birth rate of the population declined from its initial value and the death rate increased. The relationship between the birth rates and death rates according to the logistic is given in Figure 11.

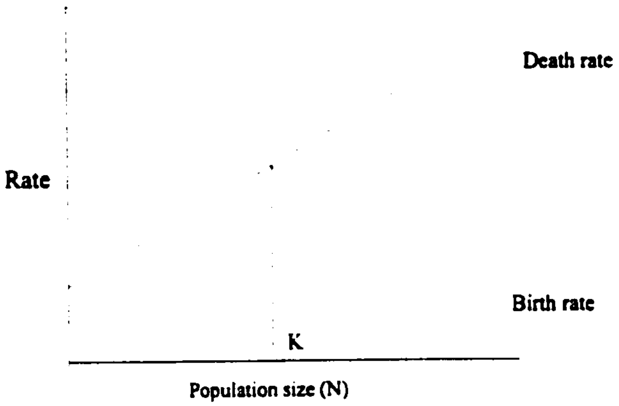


Figure 11 : Density dependent birth and death rates according to the logistic curve. K is the equilibrium point or the carrying capacity (adapted from Gotelli 1995, p. 31).

According to the logistic, the maximum value of r was only reached in the initial stages of the growth process (signified by r_m in Figure 10). The linear decline of r during population growth was interpreted as showing that density influenced the growth rate; but how would it be possible to estimate r? This could only happen in the initial phase of population growth or when the population had reached the stable age distribution and grew exponentially. For the calculation of r in this form, however, the logistic was of little help because of its emphasis on density-dependent growth.

The Australian ecologists H.G. Andrewartha and L.C. Birch used the emphasis on density-dependent growth of the logistic model in their criticism of logistic and density-dependent growth in general. They are usually described as the opponents of Nicholson's concept of density-dependence. Their arguments have to be understood, however, in the context of the limitations of the logistic curve for the calculation of r.

Andrewartha and Birch and the deconstruction of r

Andrewartha and Birch's focus was population ecology. They claimed that "the distribution and abundance of a species cannot be explained by studying only its relations with the plants and animals in its 'community'. There are certain other important components of environment which also require to be considered" (Andrewartha and Birch 1954, p. 4). According to them, questions about abundance and distribution of animals had to be treated together in investigating populations. Their argument went as follows. A species could produce the most offspring in the most favorable habitat. The numbers of individuals were the highest where an animal found the most favorable conditions and the numbers decreased where the conditions became less beneficial. The limits of this most favorable habitat were set by environmental conditions which changed constantly (Andrewartha and Birch 1954, p.8). Population biologists, according to Andrewartha and Birch, had to analyze environmental conditions of the animals and how the organisms reacted to them.

In this spirit they rejected the distinction between density-dependent and density-independent factors, arguing that there were no density-independent factors. Even climate would influence a larger population more than a smaller one (Andrewartha and Birch 1954, p. 18), which would suggest that all factors were density-dependent in one way or another. However, later in their book they rejected the influence of climate as acting in a density-dependent way (p. 592). This apparent contradiction stems from the fact that these ecologists did not argue that it was never the case that a population was likely to decrease because of its size. According to them, sometimes climate might have acted in a density-dependent way because a population had grown so large that a phase of unfavorable weather had a more severe effect than if the population had been smaller. Their main concern was controlling factors in populations and they disagreed with how Nicholson and the logistic equation related population size to the growth rate, the first describing regulation via density-dependence, the second assuming a linear decrease of r during the growth of the population.

The way Andrewartha and Birch arrived at their argument is complicated and it is based on an ambiguous understanding of r.

Before publishing his 1954 book with Andrewartha, Birch visited the Bureau of Animal Population in Oxford in 1948 and published an article in the same year in which he stated his approval of the use of r as a concept in population biology (Birch 1948). However, he also claimed that a stable age distribution could rarely be found in insect populations because of environmental changes. According to Birch, the use of r made sense only as an "intrinsic rate of increase" of a population, which described its exponential rate of increase under ideal conditions. Here Birch's argument followed Dublin's and Lotka's work in demography, in which Lotka postulated the difference between the true r and the actual r. Birch claimed that for populations in the field the rate of increase could not be determined because conditions kept varying and no stable age distribution could be achieved. Ecologists thus had to use r differently than demographers.

The two r's

Andrewartha and Birch elaborated on these thoughts. They referred to r as a *statistic*, following the definition of R.A. Fisher because its value could never be known exactly, voicing similar concerns about r as did Thompson. However, they did not reject the use of r but emphasized its abstract nature, which was nevertheless useful for ecological studies if one distinguished between the true r and the actual r as did Dublin and Lotka. Andrewartha and Birch called one r the "innate capacity for increase" as defined above in the equation for the logistic curve. This was the true r, the maximum rate of increase a population can reach without any interference from other animals or the environment. It was denoted by r_m, where m stood for maximum possible increase and it was intrinsic to a population; it was its potential for increase, but it could never be reached in nature. The statistic r_m summarized the "physiological qualities of an animal which are related to its capacity of increasing" (Andrewartha and Birch 1954, p. 43). The ecologists regarded r_m as a characteristic not only of a population but of an entire species, and it could be used to compare different species.

The letter r (without the subscript m) was used by Andrewartha and Birch to denote the actual rate of increase in a population. Andrewartha and Birch's book aimed to show how environmental factors affected the value of r, and they used results from laboratory experiments to make their point. For example, they described how temperature and moisture influenced the value of r of a population of grain beetles (Andrewartha and Birch 1954, p. 47). The fact that r changed depending on environmental factors led them to a criticism of the logistic curve, which is at first surprising because the logistic also assumed that r_m decreased. The argument has to do with the methodology that Andrewartha and Birch suggested for the estimation of r_m.

Methodology and r

Andrewartha's and Birch's approach was to estimate r_m from life-table data which assumed the stable-age distribution and exponential growth. It is confusing though, how they used the stable age distribution, writing "in nature we do not find populations with stable age distributions" (Andrewartha and Birch 1954, p. 53). However, they defined their r_m as the "rate of increase of a population with stable age distribution" (p. 43) and they claimed that r_m "may be accepted as a real and consistent attribute of a species" (p. 383). How then can r_m ever be known without assuming a stable age distribution? They conceded that r_m could never be known exactly but it could nevertheless be calculated from life tables. This provided a close enough approximation of the innate capacity of increase of a species and it could be determined in the laboratory. Andrewartha and Birch admitted that their "definition of r_m is arbitrary" (p. 53) but they saw it as the only way to use it as a meaningful theoretical statistic and as a measurable factor at the same time.

Andrewartha and Birch criticized the logistic curve by claiming that the experimental verification of logistic growth was not justified because "[t]he logistic theory requires that the uncrowded population commence its growth with an innate capacity of increase which we have called r_m. But, since the fecundity and expectation of life for the individual inevitably vary with its age, the actual rate of increase, r, will be the same as r_m only if the population has a certain age distribution known as the 'stable' age distribution" (Andrewartha and Birch 1954, p. 356). According to the authors this stable age distribution was never realized in the experiments that were supposed to verify the logistic curve because these researchers started with small populations to show the dynamics of growth (Andrewartha and Birch 1954, p. 356).

The detailed discussion of Andrewartha and Birch's concept of r_m is important because they used it to criticize the logistic curve as a model of density-dependent population growth. The logistic curve assumed that r_m was influenced by the size of the population. Andrewartha and Birch denied this and said that the experimental verification of the logistic curve was not valid. Their distinction between actual r and r_m showed that the decisive question was to explain why r_m differed from r. They answered the question by referring to a disruptive environment. A disruptive environment, however, did not require the postulation of regulating factors. With their deconstruction of r they wanted to show that the concept of a balance in nature was misleading and its associated idea of an equilibrium useless. They also suggested a different method for the study of population growth. Their emphasis was on the construction of life tables and the approximate estimation or r_m.

Other problems with the logistic curve

Two approaches emerged from the debate about the logistic curve. One was to assume density-dependence and see how populations with simple life-histories grow. The other was to assume a stable age distribution and determine the rate of increase of a population as an innate capacity of increase. The relationship between the per capita rate of increase and population size remained a mystery. Or, as McLaren (1971, p. 4) pointed out:

> The problem in population regulation then, is to understand why r should over the long term generally average close to zero, even though r_m is positive within the natural range of most species.

Although the logistic provided a model for the decrease of r with population size it did not convince ecologists in this respect either. It was questioned whether the logistic curve was useful in telling ecologists about regulation in nature. Hajnal (1957) claimed: "if population growth accelerates, it usually slows down after a while. The fact that S-shaped curves, and the logistic in particular, fit many population series means no more than this"

(Hajnal 1957). Pielou argued that "a sigmoid growth curve is what we would expect on common sense grounds without any appeal to mathematical argument" (Pielou 1974, p. 52). According to its critics, the logistic curve simply described the growth process in a way that did not shed light on its underlying features, especially when applied to populations. Even if a sigmoid growth could be observed in some cases, for example in bacteria populations, mathematically minded ecologists claimed that arguing from an observed sigmoid growth curve back to a mathematical equation that described growth was impossible:

> Consequently, since one sigmoid curve is very like another, it is rarely, if ever, possible to argue back from a growth curve to a model. An empirical growth curve usually resembles, more or less, several possible theoretical growth curves and without additional observations on different kinds of data it is impossible to choose among them. Guesses as to the model underlying a particular observed growth curve are no more reliable than guesses as to the contents of an unopened parcel. (Pielou 1974, p. 52).

Thus, population biologists could use the logistic to show that equilibrium was achieved but it did not help to explain in detail how density-dependence would affect a growing population.

The logistic today

The logistic, although not convincing in all its aspects, is still used to describe the growth of populations of organisms with simple life histories. It has also served as an important stimulus to the ways ecologists discussed how density-dependence affected population size. Begon et al., for example, questioned the linear density-dependence assumed by the logistic equation. They understood density-dependence such that as the population was growing the death rate started to increase at a certain threshold and eventually exceeded the birth rate (Figure 12). The point where death rate and birth rate met was the equilibrium point, or the carrying capacity. Below this point the population increased and above this point the population decreased. Equilibrium, however, was not a single point as shown in Figure 12a (Begon, Harper et al. 1990, p.204). Figure 12b shows a more realistic version, according

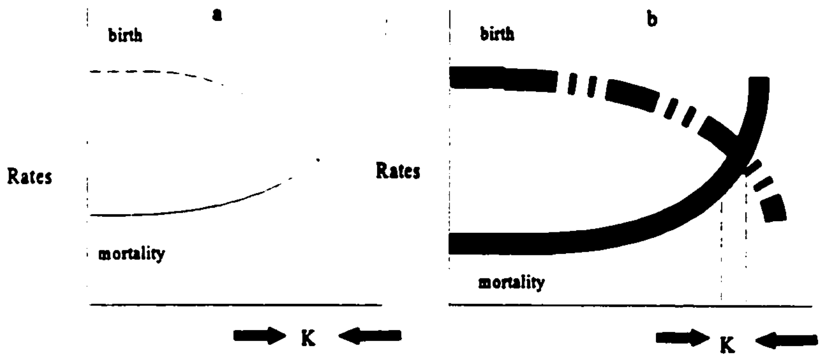


Figure 12: Graphical representation of density dependence. Figure 12a shows an exact illustration where K.which describes the carrying capacity or the equiibrium point is a closely defined area. Figure 12b is a broader interpretation where K stretches over a larger range (adapted from Begon, Harper et al. 1990, p. 204)

to Begon et al., in which the equilibrium point is not as clearly defined. Another effort to describe density-dependence, which took uncertainties into account, was made by D.R. Strong (1986) who argued for "density vagueness". Vague density-dependence emphasized the variance "around any line of central tendency in density function" (Strong 1986). Figure 13, shows the variances of the population densities with time.

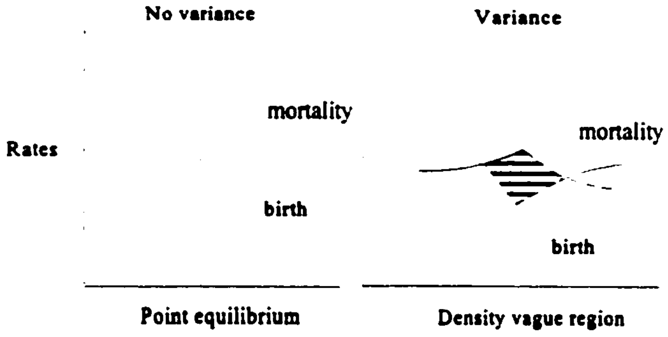


Figure 13: Vague density dependence, according to Strong (1986) showing the difference between point equilibrium and the density vague region (shaded). In the figure on the right only the birth and death rates are shown.

The logistic curve is also still relevant today through the concept of maximum sustainable yield in fisheries management. According to the logistic model, a population's maximum growth occurred if the population size was held at half of its carrying capacity

(Gotelli 1995 p.48). Following this, the carrying capacity of a fish population was predicted, and the maximum sustainable yield was calculated. It was expected that a population could be reduced to half of its carrying capacity and would then rebound to its original size. As this method of resource management failed, scientists today have modified or abandoned the calculation of sustainable yield.

Discussion and summary

In this chapter the mathematical justification of the concept of equilibrium was discussed. The concept was relevant in different contexts, one being its use for the mathematical description of predator-prey oscillations. Here the work of Lotka and Volterra inspired biologists because it provided opportunity to calculate the nature of equilibria in a community. The mechanism that was attached to the concept of equilibrium at this stage in community ecology was rebounding behavior. The epistemic value was stability and the concept of equilibrium provided a way to explain the stability of predator-prey interactions.

Regarding equilibrium in populations, the epistemic value was control of population size (N), which meant that N limited the growth rate (r). The logistic curve provided a mathematical justification for this through its modeling of the relationship between r and N. Assumptions that were inherent in the logistic curve were discussed among population ecologists, especially concerning the role of the variable r. Andrewartha and Birch, for example, emphasized the importance of discriminating between an innate r and an actual r. They rejected the epistemic value of control and thus rejected the concept of equilibrium as well. According to their metaphysical framework, the environment determined population size, which was reflected by their methodology of life-table analysis. This assumed exponential growth of populations with a stable age distribution, density-dependence not being the primary concern. Both elements made them reject the logistic curve with its simplistic assumption of linear density-dependence. A certain ambiguity can be found in their work because they claimed on one hand that a stable age distribution could rarely be found in nature. On the other hand they used it as a theoretical assumption to be able to compare different populations based on their intrinsic r.

Despite Andrewartha and Birch's critique, the concept of density-dependent regulation leading to an equilibrium state is still in use. Because the logistic provided a simple model for population control it became very influential and served as an inspiration to ecological research. Ecologists, however, have modified assumptions made in the logistic curve.

The logistic and the predator-prey equations were discussed in this chapter as a form of mathematical justification of the equilibrium concept. The equilibrium state, defined as setting the growth rate to zero and subsequently solving the equations, provided important insight into the dynamics of predator and prey. These relations could also be described in graphical form, which was done by ecologists to summarize the behavior of the two populations.

Regarding population growth, the logistic curve was influential in illustrating a certain growth pattern of populations and then providing the mathematical description of it. Both elements were important for the justification of the concept of equilibrium. Even if it was later discovered that the logistic was not clear on the exact form of density-dependence, the mathematical justification of equilibrium concept was successful.

However, this justification did not follow established rules. Volterra's laws, for example, were not laws for population dynamics but rather descriptions of what would happen if the laws were correct, although he himself initially was not aware of this. Other biologists, however, were less trusting of his predictions because some of the assumptions involved did not seem to be realistic (Israel 1993). Mathematical justification took many forms and was much debated. Thus, it is not useful to refer to a certain context of discovery which can be separated from a context of justification because there is no evidence for any a priori rules for justifications of the concept of equilibrium.

Volterra's and Lotka's approach to mathematical justification used deterministic methods. This caused criticism by Andrewartha and Birch, and 'equilibrium' was increasingly discussed in probabilistic terms following the 1950s when it was suggested that statistical thinking be incorporated into ecology. This also influenced the debate about the equilibrium concept as will be discussed in the next chapter.

Chapter 5: Density-dependence, equilibrium, and regulation in today's population biology

In the last chapters I showed how equilibrium in nature was discussed by early population biologists. According to Nicholson and Lotka, it was the result of regulation processes and was expressed in the sigmoid growth curve (the logistic) and in the competition curve of Nicholson. The logistic curve assumed a linear decline of the per capita growth rate while the population was growing, and it offered a simple mathematical and graphical representation of density-dependence. It did not make clear, however, how density-dependence worked. Andrewartha and Birch argued that a heterogeneous environment made it impossible to determine the nature of density-dependence. Their criticism centered on the justification of the variable r and the assumptions made in the logistic equation. Other ecologists saw the logistic curve as too simplistic regarding its assumptions about density-dependence.

The controversy

Although a variety of studies showed that populations were kept in bounds, evidence for regulation was difficult to find experimentally and because regulation was disputed so was the assumption of equilibrium. Experiments were conducted to prove the existence of the balance of nature, for example by Nicholson (1950) who tested his concept of self regulation with populations of the fly *Lucilia cuprina* in the laboratory. He concluded on the basis of these experiments that "...there is a single dominant controlling mechanism, namely density-dependent reaction". Field experiments, so called convergence experiments, were conducted by Eisenberg (1966) who fenced in different densities of snails and observed that the differences were maintained at first but disappeared after the snails reproduced once. This led Eisenberg to the conclusion that the populations adjusted themselves. However, the question was whether the factors that were limiting the densities in the laboratory or in the confinements were indeed present in nature (a criticism made by Den Boer and Reddingius 1996, p. 66).

Other methods to detect density-dependence included sampling data from populations in the field and applying simple tests to see if the data set provided evidence for regulation These tests, however, were not successful (Murdoch and Walde 1989). The relative stability of populations was all the evidence there was and the question remained how stability was accounted for and if the density-dependence concept provided a good explanatory framework for the persistence of populations. Opponents of the concept argued that stability could be achieved by mechanisms that did not require reference to the equilibrium concept.

Arguments for equilibrium

To discuss the justification of the equilibrium concept it is necessary to investigate different understandings of density-dependent regulation and proposed mechanisms leading to it. Murray (1994) claimed that ecologists did not clearly define 'density-dependence'. He asked whether birth rates or death rates or both were regulated by the density of the population. The difficulty was that density-dependence functioned differently in different populations, and it was the ecologist's task to find out how it worked. Should regulation be seen as the "the actions of repressive environmental factors, collectively or singly, which intensify as the population's density increases and relax as this density falls" as Huffaker and Messenger claimed (quoted in Pollard, Lakhani et al. 1987)? Or should it be seen as a mechanism implying "there is some dependence of per capita growth rate on present and/or past population densities"(Murdoch and Walde 1989, p. 114)?

The definition by Huffaker and Messenger (1964) assumed the existence of environmental factors which acted more severely on a large population than on a smaller one. Murdoch and Walde (1989) seemed to have a more immediate density-dependence in mind. They claimed the size of a population directly acted upon the population itself. They wrote, however, about "*some* (my italics) dependence of growth rate on population densities"(Murdoch and Walde 1989, p. 114). Sinclair and Pech (1996, p. 165) used Murdoch's and Walde's definition more rigorously, claiming that "density-dependence occurs when the per capita growth rate of a population depends on its own density". This would be closer to the idea of "self regulation" assumed by Nicholson. The difference in wording between these authors indicates an uncertainty about what exactly density-dependence mechanisms are and how they can be detected.

Feedback in ecology

A suggestion about how to relate equilibrium and density-dependent mechanisms was made by Murdoch (1994), who postulated the existence of feedback mechanisms between succeeding population densities. He wrote, "the feedback mechanism creates an equilibrium" (Murdoch 1994, p. 273), which seemed comparable to the equilibrium concept of Nicholson-Bailey. Murdoch, however, pointed out that the equilibrium he referred to was not necessarily stable. A population might undergo extreme fluctuations and perhaps even collapse, but, according to Murdoch, this did not imply that the population followed non-equilibrium dynamics. He claimed that his view was supported by the fact that populations in general persisted over a long time period. Although a crash of a population could occur on a local scale, invading sub-populations of the same species could replace their unfortunate cousins. Thus, the population as a whole could persist and be regulated by feedback mechanisms, equilibrium being a necessary consequence. However, these regulatory mechanisms need not necessarily affect the local population.

According to Murdoch, whether or not we could detect regulation depended on the scale of the investigation. The larger the scale the more likely that regulation would be detected: "The theory ... suggests persistent species must consist of regulated single populations or regulated collections of sub-populations. Regulation should therefore be ubiquitous in natural populations, provided we look for it at the appropriate spatial scale" (Murdoch 1994, p. 275). The idea that local sub-populations could be replaced by other sub-populations of the same species is the concept of *metapopulation*, which was introduced into ecology in the 1970s by Richard Levins (Hanski and Gilpin 1991). According to his mathematical model for 'populations of populations' (Hanski and Gilpin 1991, p.1) the area inhabited by a population was subdivided into patches, and the effect of extinctions in these patches was calculated.

Murdoch claimed that the only alternative to the feedback relation was a chance relation, random walk dynamics, between subsequent population sizes. Random walk assumed that no dependence between the size of a population and its growth rate existed; a population would grow or shrink governed by chance only. This meant that population size rarely returned to its original value, a situation also called a drunkard's walk (Royama 1992, p.10) because the drunkard only remembers the last position in his/her walk. Random walk models describe populations whose fluctuations are unbounded and without equilibrium.

Murdoch's distinction between random walk and feedback adds a new dimension to the mathematical justification of equilibrium, according to which populations can follow equilibrium dynamics even if they do not persist. Murdoch (1994) and Murdoch and Walde (1989) wrote, "field ecologists tend to use 'density-dependent' and 'stable' as synonyms, whereas the rigorous mathematical definition of density-dependence implies only the existence of an equilibrium, which need not be stable or regulated" (Murdoch and Walde 1989).

The mathematical definition of density-dependence

To understand the relevance of the mathematical definition consider the simplest equation describing density-dependence, given by May (1976):

$$X_{t+1}=F(X_t)$$

The size of population X at time t+1 was a function of the size of the population at time t (the definition of density-dependence given by Murdoch and Walde (1989)), the feedback Murdoch referred to expressed by $F(X_t)$. This sort of feedback is described for other disciplines as well, for example economics, in which the equation is the basis for models of commodity and price, or genetics, in which the function describes the change in gene frequency in time (May 1976). In these fields, as in ecology, equilibrium assumptions play an important role.

The significance of the mathematical definition was that it could be used to calculate the stability conditions of equilibrium. This was done algebraically by setting $X_{t+1}= X_t$ which was the "ideal nirvana of non population growth"(May 1976). Graphical (May 1976) or algebraic (Lotka 1925) methods could be used to determine whether the equilibrium point was stable (May's mathematical definition of equilibrium is very close to Lotka's, described in the last chapter, who derived the equation from his law of mass action and regarded it as an underlying fundamental law of the redistribution of matter using differential equations).

The alternative to equilibrium, random walk dynamics, was expressed by Murdoch (1994) as:

$$\ln X_{t+1} = \ln X_t + r_t$$

where $\ln X_{t+1}$ stands for the natural logarithm (used to make the variance constant) of the size of the population at time t+1, and r_t denotes the per capita rate of change, which varies at random and is unrelated to current or past densities. This does not mean that a population performing random walks perishes. However, the return time to the original value (equilibrium value) of a random walk "increases with time unboundedly" (Royama 1992, p. 10), which means that the population is not in equilibrium.

Regulation: weak and strong definition of equilibrium

Thus far Murdoch's definition of density-dependence is seemingly nothing more than a relation between reproductive rates and population size. Murdoch (1994) used the notion of feedback to illustrate the relationship between past and present population densities, and contrary to earlier definitions, density-dependence did not imply regulation. It was a necessary but not sufficient condition for regulation (Murdoch and Walde 1989, Murdoch 1994). I will call the mathematical definition of equilibrium a *weak definition* because it does not imply regulation or negative feedback. The function F(X) could predict that a local population will not persist for very long. This, as has already been shown, was the case for the original Nicholson-Bailey models and also for the Lotka-Volterra equations. They predicted that a prey population that was completely destroyed by its predator would crash as would the predator population shortly thereafter. However, stabilizing mechanisms were postulated and incorporated into the basic predator-prey models (Murdoch and Oaten 1975). A stabilizing factor, for example, was a refuge for prey organisms. When a certain number of prey organisms escaped the predators, the prey population could sustain itself. Another stabilizing factor was migration. As mentioned above, in the context of metapopulation dynamics, a local population that had crashed could be replaced by invaders from a different sub-population. Migration served as a stabilizing factor and was density-dependent in that more migration presumably occurred when the population was smaller. The stabilizing factors could be described as 'negative feedback' mechanisms because they regulated the size of a population. Assuming negative feedback is what I will call the *strong definition*. It claims that density dependence leads to regulation and that equilibrium is the outcome of such regulation processes. For regulation to occur there has to be a negative feedback in such a way that "the sum of the negative feedbacks between components be stronger than the sum of the positive feedbacks" (Berryman 1991, p. 141). Negative feedback mechanisms are stabilizing and have a control function, for example, in predator-prey systems. As proposed by Nicholson, these mechanisms are density-dependent.

It seems difficult to reject Murdoch's weak definition. Some relation between subsequent populations must exist because we would, for example, presume that individuals are adapted to certain risks of extinction and we would refer to those adaptations to explain why populations have persisted. Random walk cannot account for the persistence of populations that can be observed regularly.

The mathematical definition offers an account of feedback that is not to be equated with regulation or stability. It is merely claiming that there is some relationship between population sizes which is a weak definition of density dependence. Arguments against equilibrium, however, are often made against a stronger claim defining equilibrium as the outcome of regulatory mechanisms in nature. This was often equated with a deterministic approach to nature, exemplified by Lotka's and Volterra's equations, which was regarded as inadequate.

Arguments against density-dependence

Stochasticity in ecology and the spreading of risk

Arguments by Andrewartha and Birch introduced previously, that notions like 'density-dependence' were not necessary to describe population dynamics, seemed to reject even the weak definition of density-dependence. According to them, the size of a population does not depend on the size of the population previously but on environmental factors, and the abundance of animals has to be seen in connection with their distribution. Andrewartha and Birch's reasoning was further elaborated by the Dutch population biologists J. Reddingius and P.J. den Boer in the late 1960s and early 1970s. Reddingius and den Boer, however, did not argue against the weak definition of equilibrium but focused on the introduction of 'stochasticity' into the modeling of equilibrium.

The term 'stochastic' describes a process in which random variations play an important role (Kendall and Buckland 1971, p.146) (see 'stochasticity' in the Appendix to Chapter 5). The use of deterministic models like Nicholson-Bailey's and the logistic curve had already been questioned by the 1950s, and arguments for the inclusion of chance were made for example by Andrewartha (1957), and Skellam (1951), who discussed random dispersal in populations in 1951. Although Leslie (1958) used stochastic models for the analysis of life-tables, stochasticity did not play a major role as part of ecological models until the late 1960s, when the importance of stochastic processes was increasingly emphasized and electronic data processing became accessible.

Den Boer saw stochasticity as an alternative to density-dependent mechanisms because the latter, according to him, ignored the heterogeneity of nature. Den Boer did not claim that the persistence of populations could not be explained at all because nature was too unpredictable; instead he offered alternative explanations to the stability of populations by postulating that the heterogeneity of nature allows populations to persist. Because nature is not uniform local populations can be eliminated, but others find refuge and the populations as a whole survives. Den Boer called this "spreading of risk" in space (Den Boer 1969). Heterogeneity in the organisms spread the risk in time through the development of several life stages. Phenotypic variation also helped to spread the risk because the population could face a multitude of environmental variations, and the chance that some organisms might be able to cope with them were higher than in a homogeneous environment. The spreading of risk leads to the balance of nature, but it is a different balance than Nicholson's. Den Boer (1969, p. 174) wrote that "this important feature of the so-called 'balance of nature' of which every biologist and layman has some vague notion, is therefore the result of a complex and highly intricate 'system' of spreading the risk within populations and between populations of the same and especially of different species. Hence, the balance of nature is not a balance but rather a relatively high degree of stability".

Den Boer did not completely deny the existence of density-dependent mechanisms; he claimed, however, that increasing heterogeneity in nature reduces the efficacy of density-dependence. In homogeneous habitats density-dependent mechanisms would have been more important. This was the reason for den Boer's claim that ecologists should not investigate how density is limited, but how density fluctuations are restricted. Although den Boer based his work on the notion of stability he rejected the concept of regulation. Discussing regulation, according to den Boer, is only justified if negative feedback processes like density-dependence are observable, which rarely is the case. Den Boer agreed with Murdoch that the persistence of populations required explanations but den Boer rejected the notion of feedback as a mechanism. "Spreading the risk" accounts for stability of populations. According to den Boer the organisms "out chance" the environment.

Gambling for existence

In a similar approach J. Reddingius (1971) described this "out chancing" of the environment by the organisms as 'gambling for existence'. He claimed that deterministic population biology is not realistic because of variations arising from demographics and the environment (described above as demographic and environmental stochasticity) and wrote: "[i]f population ecology is to have anything to do with living nature outside laboratories, it has to become a statistical science" (Reddingius 1971, p.9). He clarified the notion of statistics by saying:

> mathematical statistics is an application of mathematical probability theory to certain decision problems that in themselves can be formulated in purely mathematical language....probability theory and statistics as such are purely formal disciplines in which no statements about the real world are made...A 'collection of chance events' mathematically is a collection of undefined entities called 'events' that has certain set-theoretic properties and on which a set function called a probability measure is defined that also is required to

have certain properties (Reddingius 1971, p.39).

Reddingius rejected the deterministic approach to nature and replaced it with a statistical one according to which nature was not uniform but should be described by a Markovian chain. This assumption seems to be close to the weak definition of equilibrium by Murdoch in that the size of a population at time t_{+1} was not independent of the size at t_0 (see "Markovian chain" in Appendix to chapter 5). Where Reddingius uses 'Markovian chain', Murdoch talks about 'feedback' to describe equilibrium.

The modern debate

The modern debate about equilibrium is about mechanisms leading to the stability of populations. Murdoch suggested feedback which can but must not have a regulative function. Only negative feedback acts in a density-dependent way. Reddingius and den Boer rejected the notion of density-dependence claiming that the heterogeneity of nature enables populations to persist. According to Murdoch, the use of the equilibrium concept was justified but, according to Reddingius or den Boer, it was not.

Ecologists on both sides discuss the issue by referring to metaphysical and epistemological issues which both play an important part in the justification of the concept of equilibrium. Murdoch's and Walde's (1989) definition of density dependence does not clarify what mechanism leads to equilibrium. They describe how we can know about such a mechanism, that there is some dependence of per capita growth rate on present or past densities of a populations. This is an epistemological argument. Murdoch's postulation of feedback processes is metaphysical because it describes how nature works, how it is structured. Reddingius also uses epistemological arguments in referring to statistics as telling us how nature works. His metaphysics is that the heterogeneity of nature leads to stability in populations.

It is not surprising that metaphysical and epistemological issues play a role in the justification of equilibrium. I have pointed out in earlier chapters that they are connected. However, it is helpful to see how scientists view this connection and how they discuss justification. Reddingius, for example, said equilibrium approaches, using deterministic equations, were not realistic, and he found that equilibrium is not useful as a theoretical concept. However, in the quotation above he stated that mathematical statistics makes no statements about the real world. If the lack of realism in mathematical statistics is no obstacle why not use equilibrium a theory as well in which no statements about the real world were made? Reddingius endorsed the statistical approach because it reflects the probabilistic structure of nature but he also claimed that the theory makes no statements about the real world. Reddingius is not clear on the issue of justification.

When the participants in the debate about equilibrium refer to justification it is often simplified, for example, when it is claimed that the equilibrium proponents rely primarily on logical reasoning, whereas the other side allegedly leans toward empiricism. Supposedly empirically minded critics of the equilibrium concept are Andrewartha and Birch, and C.J.Krebs.

Andrewartha and Birch stated that generalizations about density-dependent factors "were not a general theory because they [did not] describe empirical facts"(Andrewartha and Birch 1954, p. 649), claiming that they were dogmatic and not testable. According to them, the defenders of the concept of density-dependence merely described what would happen if the dogma were true but did not demonstrate its truth (Andrewartha and Birch 1954, p. 19). The authors claimed further that the density-dependent theory did not explain the observed facts, which was the aim of a sound theory.

Another criticism of the equilibrium assumption as a useful theory was Krebs's (1991) rejection of the density-dependent paradigm because it was "descriptive and a posteriori". He claimed that the "density-dependence paradigm is bankrupt" and argued for an approach to ecology based on field experiments. Krebs approached scientific activity supposedly more empirically. According to him, the underlying mechanisms of nature could only be uncovered by field experiments which had to be designed properly and by the collection of data in an unbiased manner (Krebs 1991).

Krebs argument that the concept of equilibrium was questionable because it was a posteriori refers to the way knowledge is justified; a posteriori knowledge through experience, a priori knowledge, on the contrary, being possible without the involvement of experience. Discussion about the possibility of a priori knowledge is ongoing, but Krebs seemed to confuse the terms: how can the testing of theories lead to knowledge which is not a posteriori? Gaining knowledge through experience is the main motivator to perform experiments. Collecting data in an unbiased manner, as Krebs demanded, is also questionable. Scientists should eliminate sampling errors and try to obtain representative data; however, it seems that Krebs has a way of sampling in mind that is devoid of theory. How can experiments be performed without any theory in mind? Krebs followed the assumption that data alone can speak for themselves, which is questionable because background assumptions are part of scientific theories and cannot be detached from the hypotheses to be tested. The experimental approach to nature that Krebs is suggesting is certainly not free from theory: the statistical nature of theory testing in ecology and the increasing use of electronic data processing add theory to the observation of data.

On the other side, ecologists in favor of equilibrium sometimes emphasize the logical connection between data and hypothesis, as, for example, does Berryman (1991). He, by quoting Royama (1977), argued that the existence of density-dependence was "derived through logical deduction from one major premise, the persistence of populations in the wide sense". Berryman concluded that it "thus seems pointless to test for density-dependence as it is to test the hypotheses that organisms eat each other" (Berryman 1991, p.142).

Andrewartha agreed with Berryman's claim but regarded the logical connection between equilibrium and evidence as a reason to reject equilibrium. His criticism of the idea of density-dependence rested partly on the argument that density-dependence was a logical deduction. As he said, "my chief criticism of the 'theory' of density-dependent factors is that it is unscientific because its authors have depended too much on insight and deduction and not enough on experiment and observation" (Andrewartha 1961, p.178).

That density-dependence is a logical deduction from an established premise seemed to imply for Berryman that density-dependence is true. A valid deductive argument shows that if the premises are true the conclusion cannot be false. However, the premise for density-dependence is not merely that populations persist as Berryman suggests. Many additional premises have to be true to decide on the truth of the equilibrium concept. These, however, are disputed.

The authors cited simplify the problem of the justification of theories. Andrewartha's and Krebs's emphasis on observation is misleading because observation cannot lead to the establishment of theories (Carnap 1966, p. 230). One can observe regularities in nature and describe empirical generalities but this does not result in theoretical advancement because theories are supposed to describe underlying unobservable features that lead to the regularities. Recent views in the philosophy of science have questioned the explanatory ability of theories but as far as their generation goes even philosophers of science who are empiricists, for example Carl Hempel, conceded that, scientific theories "are not derived from observed facts but invented in order to account for them"(Hempel 1966, p.15). Berryman's justification of equilibrium as being deductive is also questionable because theories are not developed deductively but inductively. The inductive establishment of theories is problematic and has been discussed by philosophers and scientists for a long time because induction does not have the same logical necessity as deduction. Numerous efforts have been made to face the challenge of justifying inductive knowledge on solid grounds. The positivists addressed the problem of justification by separating the discovery from the justification of theories, a strategy that I have rejected for the analysis of equilibrium earlier.

Characterizing the debate about equilibrium as one between empiricists and rationalists would not do justice to the issue. Elton, in a review of Andrewartha's and Birch's book, pointed out that "the notion of innate capacity for increase, with its stable age distribution, is really quite as theoretical and abstract... as the equations for the logistic curve or Volterra's predator-prey theories" (Elton 1955, p. 419). I agree with Elton in that Andrewartha and Birch were not more empirical than Lotka and Volterra or Nicholson. Both sides presented different theories that either justified or failed to justify the equilibrium assumption, and both sides implicitly had a certain understanding of how theories should relate to the evidence. In general, some misunderstanding regarding justification can be observed in the debate about the equilibrium concept. Both sides in the dispute expressed erroneous views of the power of deduction (Berryman) and misrepresented the problem of observational evidence (Krebs) (I do not mean that ecologists do not understand the status of empiricism. The exchange mentioned here so far merely suggests that terms like observation and deduction are used in a rhetorical sense). For this reason I argue that the debate about the justification of the equilibrium concept cannot be analyzed by saying that one camp is empirically minded, while the other prefers rationalism. The debate cuts across this boundary and has to include an analysis of how theory is justified, which is part of a critical appraisal of empiricism.

The justification of theory

The nature of empiricism cannot be discussed here in detail, but since it is a theory about justification elements of it play a role in the debate about the concept of equilibrium. The reason for Berryman's referring to the deductive nature of equilibrium and Andrewartha's rejection of it have the same root: the ambiguous status of the justification of theories, and scientists' uneasiness about extra-observational elements in theories. This can already be observed in early ecological works, for example by Elton in 1927:

> One of the recent trends of biology has been a series of revolts against the practice of theorizing without sufficient facts, and such revolts undoubtedly result in a very beneficent feeling of exhilaration derived from the direct contact with raw facts, unhampered by the weight of dogmatic theories. This is certainly the case with animal ecology (Elton 1927, p. 10).

More recently, the marine biologist Paul Dayton voiced a strong dissatisfaction with the amount of theorizing in ecology: "Ecology has become an extremely narrow and elitist discipline and rigid Popperian religion. In addition, religious statistical zealots have trivialized my field to the point that I often think about retiring and escaping into the natural history that I love" (Dayton 1997 pers. comm.). And Den Boer and Reddingius (1996) promoted what they called a "natural history paradigm"as an alternative to the equilibrium approach to provide a better way of understanding the stabilization of populations.

I argue that because of this uneasiness towards theory, ecologists like Berryman (1991) either propose a logical necessity of a theory or, like Andrewartha (1961) they claim to rely on the observational evidence and reject theoretical constructs such as equilibrium as "metaphysical" because they are not based on observation. To clarify this point another reference to the positivists' philosophy of science is useful. Although they were divided on the issue of the status of theoretical terms, the instrumentalists among them claimed that theoretical terms can only have "cognitive value" if they are translatable into observational terms. If a statement cannot be defined in terms of its observational consequence then it is metaphysical and unscientific.

Two aspects of this view are problematic. At first the positivist's notion of metaphysics is itself metaphysical because it is based on the metaphysical position of nominalism. Besides that, the positivists thought that any reference to objects transcending immediate experience had to be avoided, aiming at constructing a scientific language based on verifiable sense experience alone. This, however, as critics of the positivists showed (one example of many is Putnam 1962), proved to be impossible. The remedies that the positivists suggested to save their account of observational language were mostly too complicated to lead to a clear definition of observational terms, and the distinction between theoretical and observational language was abandoned. Leading positivists later questioned the foundational structure of observations in science in general (Hempel 1993).

I have shown so far that a definition of equilibrium in ecology is difficult to establish in purely observational terms. In addition, even if this could be done it would not reflect the use of the concept. One of the benefits of the concept is that it is a speculative entity that is used to account for mechanisms such as the regulation of populations. Equilibrium is then translated into notions such as feedback that are not observable either. I introduced the notion of epistemic value earlier to describe the characteristic of equilibrium to be more than just a translation of observations.

The discussion has revealed that the debate about the justification of equilibrium concerns the relationship between theory and evidence. It is not that one group proposes a rationalistic justification whereas the other group suggests empiricism. Both groups present different theories about the persistence of populations. The equilibrium concept is an example of theory being underdetermined by the data (see Duhem-Quine thesis in

Appendix). What underdetermination exactly amounts to has been debated (see for example Laudan 1990), but the discussion so far has shown that the equilibrium concept should not be criticized because it is not based entirely on observations or because it contains background assumptions or values. These are all part of scientific theories. The question is whether the underdetermination of theories leads to scepticism about any scientific knowledge or if we can justify the equilibrium concept through scientific testing.

Testing for density-dependence

Difficulties

A general problem in testing density-dependence arose from the fact that density-dependent mechanisms could be manifold, for example intraspecific or interspecific competition, or predation (Sinclair and Pech 1996). The forest biologist R.F. Morris, who worked for the Forest Entomology and Pathology Laboratory in Fredericton, New Brunswick, tried to find a way out of this dilemma by distinguishing between two kinds of factors controlling a population. One kind caused a relatively constant mortality of the population over the years, the other kind, more variable, caused less mortality but contributed more to the observable changes in population density (Morris 1959). The latter factor was, according to Morris, a key factor because it could be used to predict population change. As he said, "changes in population density from generation to generation are closely related to the degree of mortality caused by this factor" (Morris 1959).

Morris' argument is reminiscent of Nicholson's distinction between density-legislating and density-governing factors (Nicholson 1954 b), the latter being density-dependent because they react to changes in population size. Density-legislating factors could have a more severe influence on the level of density but they had no regulative effect. It seemed that Morris' key factor could be, in Nicholson's terms, a density legislating factor, for example, a climatic factor. However, by investigating the dynamics of defoliating insects like the black-headed budworm (*Acleris variana* (Fern.)) Morris found that the key factor in this case was predation by parasitic insects, suggesting that even a density legislating factor could act in a density-dependent manner. This point might not be crucial for an assessment of density-dependence but it hinted at a shift in the justification of the equilibrium concept brought about by testing for density-dependence.

The test by Morris

Morris' method was based on the Malthusian assumption that unlimited growth is exponential so that one could illustrate exponential population growth graphically as a straight line by using the logarithms of the population sizes. Using logarithms also stabilizes the variance of the population sizes, which is lower regarding the number of individuals in a sample with few individuals than in a sample containing more individuals. The use of logarithms avoided this statistical nuisance, and the equation for exponential population growth became:

$$\log N_{t+1} = \log \lambda + \log N_t$$

(equation 1)

where N_{t+1} = the size of the population at time t+1, λ= finite rate of increase, and N_t= size of the population at time t.

Because Morris worked with insect populations which reproduced in discrete intervals he used difference equations to model their population growth, plotting log N_{t+1} versus log N_t and performing a regression analysis investigating the functional relationship between the subsequent population sizes. He chose N_{t+1} as the dependent variable, N_t being the independent variable. The equation of the linear regression which expressed the relation between the two variables was:

$$\log N_{t+1} = \log \lambda + b \log N_t$$

(equation 2)

This is the same equation as equation 1, except for the inclusion of b which describes the slope of the regression line. Normally the slope of a regression line is used to investigate if the independent variable determined the dependent variable. Morris performed a linear regression analysis, reasoning that a slope of $b=1$ would mean that no density-dependence occurred because it would suggest exponential population growth. A slope of $b<1$ would suggest some form of regulation. Figure 14 shows a plot of an exponentially growing population with a finite growth rate of 1.2. The slope of the regression line is close to 1.

Referring to the equations above can make Morris's argument more obvious. If b=1 equation 1 becomes

$$N_{t+1}/N_t = \lambda$$

This is the equation for exponential population growth. If b<1 the equation for population growth translates into:

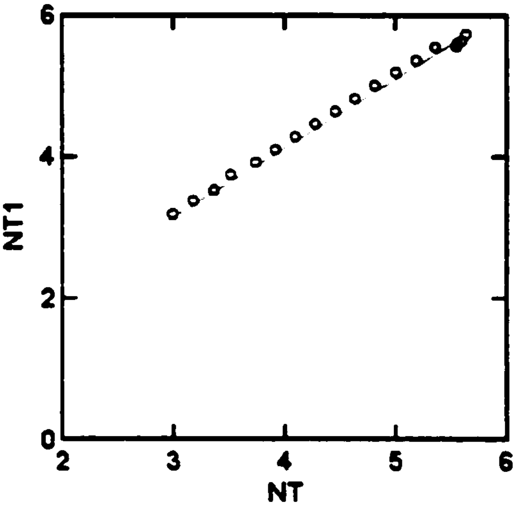


Figure 14: The logarithms of subsequent population sizes of an exponentially growing population. NT1=logarithm of population at time t+1, NT=logarithm of population size at time t. The slope of the fitted regression line is close to one.

$$N_{t+1}/N_t = \lambda\, N_t^{b-1}$$

This means that the ratio N_{t+1}/N_t is not independent of population size but that the ratio between N_{t+1} and N_t gets smaller as population size increases (Pielou 1974, p.55).

Morris (1959; 1963 a) used this method to detect factors that had regulatory functions (key factors) by starting with the logarithmic population equation, including b, and then step by step incorporating different mortality factors. For example, he added the proportion of larvae killed by parasites (Morris 1963 a). If this addition brought the slope of the regression line significantly closer to one, then parasitism was a key factor. Morris also developed methods to incorporate weather as a possible key-factor (Morris 1963 a). He wrote that this key-factor analysis made "no commitment as to the precise mode of operation of the factor" (Morris 1963 b) that limited populations. Despite Morris's claim that he was primarily interested in the prediction of population change his test served as a starting point in the statistical testing of density-dependence. More tests arose out of the criticism of Morris's approach.

Criticisms of Morris' test

Criticism of Morris's method voiced in 1970 by Maelzer and St. Amant focused on its characteristic as a test for density-dependence. Maelzer (1970) simulated density independent populations with the help of a computer that produced random growth rates and found that the regression analysis of the data resulted in a value of $b<1$. The statement that was tested was whether the growth rates and the population sizes were connected. Random growth rates should not have "passed" the test designed by Morris. Whether population models could be applied legitimately to simulated populations could be questioned. Maelzer anticipated this critique and further investigated data from natural populations. He found evidence that not only density-dependent processes, but also sample size influences the value of b. St. Amant also voiced this criticism (1970), claiming that short data sets were more likely to show regulation than longer data sets when tested with Morris's method.

Pielou (1974) showed that not only the size of the data set, but also its quality mattered. She criticized Morris's method by showing that the slope b of the regression line was influenced by the degree of scatter of the data points. Pielou modeled two density independent populations and found that the one that had more scattered data points resulted in a slope of less than 1. The regression line through the less scattered plot had a slope of closer to 1. Morris's test predicted that one population was regulated by density-dependent factors, whereas the other one was not; however, both were not regulated at all (Pielou 1974, p.57).

The arguments against Morris's test were based on simulations of populations which were not regulated in a density-dependent way although the test judged them to be so. The test could be fooled if, as St. Amant (1970) said, the "variation in numbers of animals is large compared to the total population change over the period measured". A scattered data set could also cause a higher variation in numbers in relation to total population change and thus also indicate density-dependence. Pielou dismissed the regression technique entirely because she thought stochastic variation in nature caused data sets to be "fuzzy" and would always fool the test.

Another challenge to the test came from St. Amant who argued that it was difficult to find a null hypothesis against which the hypothesis of density-dependence could be tested. The null hypothesis, the hypothesis under test, said that the population was not regulated. This however, was difficult to distinguish from regulation via density-dependence. As St. Amant pointed out,

> 'An unusually high population density is more likely to be followed by a decrease than an increase [in density].' This is not true of a regulated population but of almost any more or less irregular series of numbers. The very fact that a census value is followed by a decrease makes that value more likely to be unusually high, compared to all the other census values (St. Amant 1970, p. 826).

By saying it is difficult to find a null hypothesis St. Amant pointed to a problem in the testing for density dependence in that the tests could not distinguish between an irregular set of numbers and a regulated population. It was difficult to tell why a population was kept in bounds. Remember, the critics of the density-dependence approach did not deny that populations were kept in bounds; instead they questioned the existence of density-dependence. Whenever a population was not increasing indefinitely or went extinct the values fluctuated somehow and a test could not tell why. Thus, the test could not tell whether density-dependent mechanisms were present in nature. Tests after Morris's were designed to overcome this problem, which seemed to be of statistical nature. However, as the discussion of further tests will show, density-dependence was transformed into a statistical concept.

Bulmer's test

M.G. Bulmer developed an improved test for density-dependence in 1975 (Bulmer

1975). He rejected the approach of measuring the slope b the way Morris did, but suggested determining the correlation between subsequent population sizes. He assumed that the alternative to the equilibrium approach was that populations perform a random walk, meaning they did not return to an equilibrium value. For such a population the growth rate would be negatively correlated with population size. This idea led to the construction of two models:

$$x_{t+1} = x_t + z_t$$

where x is the population size and z describes independent random variables with zero mean and variance σ^2. This model describes an unregulated population. The model for density-dependent growth is

$$(x_{t+1} - x_t) = -\alpha\, (x_t - \mu) + z_t$$

where μ= equilibrium value and $-\alpha$= the growth rate which, in this model, is negatively correlated with population size, expressed by the term $(x_t - \mu)$or

$$(x_{t+1} - \mu) = \beta(x_t - \mu) + z_t$$

where $\beta = 1 - \alpha$

Which model is correct? In every statistical test the predictions that are made have to be tested by comparing them to a theoretical probability distribution providing evidence about the null hypothesis, which describes a frequency distribution distinguished by a rejection and an acceptance region. Usually the boundaries are set at 95%, or $p = 0.05$, which means that the probability of rejecting a correct null hypothesis is 5% (meaning the determined data are lying in the area of the frequency distribution where only 5% of the expected values will be found). If we make the mistake of rejecting a true null hypotheses we have committed a Type I error. However, if we set our standards to reject a true null hypothesis too high we might commit a Type II error, accepting a false null hypothesis.

Bulmer solved the problem regarding the null hypothesis by calculating its probability distribution according to a test statistic he called R, which described the expected values of the population size, given assumptions of the model (Bulmer 1975). To calculate R Bulmer used the assumptions of the random walk model, determining the shape of the probability distribution R and the significance values by computer simulations of R with different population sizes. Thus, he provided a probability distribution for the null hypothesis which said that no density-dependence existed based on his own models. The test statistic was, according to Bulmer, almost equivalent to the first serial correlation coefficient r and was an important step in the testing of density-dependence.

Significance of Bulmer's approach

There were two important changes in Bulmer's modeling strategy compared with Morris's. First, Bulmer did not use a regression analysis but analyzed the correlation between two values, an approach apparently more suitable for the analysis of population sizes because it did not assume that N_{t+1} depended on N_t but that both variables covaried. (This meant that the variance of N_{t+1} changed in the same way as the variance of N_t. The variance of N_{t+1} was "explained" by the variance of N_t only in the sense that both variables covary. One did not depend on the other as in the case of regression. Correlation went both ways. A third factor, besides N_t and N_{t+1}, for example, could have caused the variance in both variables.)

A second important aspect of Bulmer's test in which he differed from Morris was his use of the serial correlation coefficient through his test statistic R. This measured the correlation between members of a time series. This analysis formed a significant part of the justification of the equilibrium concept.

Time series analysis and autocorrelation

Time series analysis is often used for data that occur in a time sequence. This poses statistical difficulties for the experimenter because statistical procedures normally are based on the requirement of random sampling, assuring the independence of the sample events from each other. If this requirement cannot be fulfilled, it is the task of experimental design to randomize data. However, if the data have to be collected in a certain order, no randomization can take place. For successively collected data the independence assumption is violated: it has to be assumed that the census data are statistically connected (Pankratz 1983, p.8). In the case of density-dependence tests, a randomization of data would destroy exactly the dependence between subsequent data we want to investigate. Randomization, possible in other kinds of experiments, seems to be impossible here (although I will describe later how the idea of randomization can also be used in time series).

A benefit of time series analysis is that periodicity in the data can be detected. To investigate periodicity an autocorrelation analysis is used that measures the strength of the correlation between serial observations. However, it is important to understand that an autocorrelation analysis can only be performed if the data set fulfills certain criteria, for example the time series has to be stationary and possess a constant variance (for examples, see Time series analysis in the Appendix to Chapter 5).

Criticisms of Bulmer's test

Bulmer designed his test with the assumption that a test should reject the hypothesis of density-dependence if a trend was present (Figure 16 a and b show a time series which follows a trend). This was criticized by other ecologists who claimed that density-dependence could still be present even if a population was growing or declining for a while (Pollard, Lakhani et al. 1987). Pollard et al. argued that Bulmer's test would be fooled by the trend, and the null hypothesis which says that density-dependence is absent would be accepted, meaning a type II error would have been made too easily. This debate was not only about statistics; it was also about how the characteristics of the data set should be translated into ecological properties of a population and how a null hypothesis was formulated.

The test by Pollard et al.

Pollard et al. tested the correlation between the change of density of a population (d_i) and the size of the population (x_i), calling the correlation coefficient $r_{(dx)}$. If density-dependence occurred, the correlation should have been negative, i.e. an increasing density should have resulted in a decreasing change in density. The test defined density-dependence as "the actions of repressive environmental factors, collectively or singly, which intensify as the population density increases and relax as the density falls"(Huffaker and Messenger 1964 ; quoted by Pollard, Lakhani et al. 1987). To construct a probability distribution for the null hypothesis Pollard et al. used a randomization test which "reshuffled" the data set (Potvin and Roff 1993)0. I said above that it is not possible to randomize time series data because they are collected in chronological order; however, Pollard et al. (1987) used a randomized data set to create the null hypothesis. The randomization was based on the idea that "the observed set of x_i [population size] values should be judged as a significantly extreme arrangement when compared with all possible arrangements of x_i values"(Pollard, Lakhani et al. 1987). If we randomly listed values for different population sizes, they should have differed significantly from a time series that was statistically connected. The random data set was obtained by reshuffling the observed values for population density. Because the possible combinations of population size data was immense, a sample of the permutations was sufficient.

After the reshuffling procedure two data sets existed, one of observed data and one of created data. The value of $r_{(dx)}$ was determined for both data sets, and Pollard et al. suggested that if less than 5% of the values for $r_{(dx)}$ from the simulated data were smaller than $r_{(dx)}$ from the observed data the null hypothesis of density independence should be rejected. Thus the value of $r_{(dx)}$ for data from a population that was regulated through density-dependence was expected to be below 0. Pollard et al. wanted to detect negative density correlation between population change and population size. They justified their approach by showing that the test statistic $r_{(dx)}$ was equivalent to a test statistic used in a maximum likelihood approach. Maximum likelihood tests were used to measure the agreement between expected and observed results. Expected results were calculated for each model and test statistics had to be constructed in order to determine the null hypothesis. The expected results were then compared with the observed results and it was decided which model represented the data better. Although Pollard et al. only used the likelihood ratio test to justify the use of their test statistic $r_{(dx)}$, the likelihood tests played an important role in a third test to be discussed, and the strategy of likelihood testing was different from the testing strategy discussed so far.

Likelihood ratio tests

The hypothesis testing that has been described so far was based on methods of regression and correlation. The method determining the goodness of fit between data and model was the "sum of squares". Further it assumed a certain probability of the occurrence of our data which depended on the probability distribution of the expected data. A probability distribution was chosen to be the null hypothesis, the hypothesis under test. The test asked: given a certain expected probability distribution, what is the probability of occurrence of my data? Hilborn and Mangel (1997) used the following notation for this kind of testing:

$$Pr(Y_i /p)$$

which translated into the statement: given a particular parameter p which was determined by the underlying expected probability distribution, what was the probability of observing value Y_i ? (Hilborn and Mangel 1997, p.132)

As Hilborn and Mangel pointed out, the subscript i signified that various Y's but only one parameter value 'p' was possible. The likelihood approach constructed a different hypothesis. According to Hilborn and Mangel, the likelihood testing asked: "given these data sets, how likely are the possible hypotheses" (Hilborn and Mangel 1997, p. 132). The likelihood equation was:

$$L(\text{data/ hypothesis}) \text{ or, as } L(Y/ p_m)$$

where L stood for Likelihood (Hilborn and Mangel 1997, p. 132).

The difference between the two approaches lay in the subscript m of the parameter p. It indicated the possibility of various hypotheses (i.e. models) given one set of data. The authors claimed: "the key to the distinction between likelihood and probability is that with probability the hypothesis is known and the data unknown, whereas with likelihood the data are known and the hypothesis unknown"(Hilborn and Mangel 1997, p. 133).

The question regarding density-dependence tests was: "given the set of data for population sizes, which model fits best?" For their maximum likelihood approach Pollard et al. (1987) chose three different models. One (model 1) described purely random walk dynamics; another described random walk dynamics with a drift, which accounted for cases where a trend in the population dynamics exists (model 2). The third described density-dependent growth.

We already have encountered the random walk model (model 1) in describing

Bulmer's test. The equation for the random walk model with drift (model 2) was:

$$x_{i+1} = r + x_i + e_i$$

where x_i stood for the natural logarithm of the population size at time i and r was the drift parameter (the growth rate) and e was a random variable with normal distribution. Model 3, which described density-dependent population growth, was:

$$x_{i+1} = r + \beta x_i + e_i$$

where β was the factor that described density-dependence when $\beta \neq 1$. The β used in model 3 was not the same as the b in the regression test by Morris, although it was in the same place in the equation as in Morris's model and it also described the slope of the regression line. Morris used b in the regression as an estimate of β, which led to the flaws in his test. In Pollard et. al's case β was a model parameter, and its magnitude was not estimated by regression. The letters b and β meant the same, but their context and their estimation was different.

To decide which model fit the data better a likelihood ratio test was conducted in which model 1 was tested against model 2, and model 2 was tested against model 3. Pollard et al. found that mathematically the test statistic for testing their model 2 against their model 3 was equivalent to the correlation coefficient $r_{(dx)}$ in their randomization test.

Criticism of Pollard et al.'s test

Murdoch and Walde (1989) compared Bulmer's and Pollard et al.'s test by analyzing data from Gaston and Lawton (1987), who had analyzed 11 studies of insect populations in which the authors had claimed to have found density-dependence. However, only five of these passed Bulmer's test and three of them Pollard et al.'s test. The two tests contradicted each other in several cases, for example Bulmer's test sometimes detected density-dependence in cases where Pollard et al's test did not detect any and vice versa. Dennis and Taper (Dennis and Taper 1994) objected that the test by Pollard et al. did not have enough power, i.e., that the possibility of a Type II error was too high. They suggested a third test which again used a different testing methodology and made different assumptions about population growth.

Dennis's and Taper's test and bootstrap

The test by Dennis and Taper (1994) was different from Pollard et al.'s test in several aspects. One aspect is the use of the likelihood ratio test by Dennis and Taper. Pollard et al. used the likelihood ratio test only to derive their test statistic d_{rx} from it (Pollard, Lakhani et al. 1987), whereas in Dennis's and Taper's test the likelihood ratio was more important. Besides the likelihood ratio test, Dennis and Taper also used a different equation than Pollard et al. (1987) to model density-dependence. Translated into the notation I used for the density-dependent model by Pollard et al., Dennis and Taper used the following equation for density-dependent population growth:

$$x_{i+1} = x_i + r + \beta e^{xi} + z_i$$

where x_i stood for the natural logarithm of the population size at time i, r was the drift parameter (the growth rate) and z was a random variable with normal distribution. The factor β described density-dependence when $\beta \neq 1$ (equation 3).

The difference from Pollard et al.'s model of population growth was that in Dennis and Taper's approach the factor that expressed density-dependence influenced x_i directly and not the logarithm of x_i. (see Pollard et al's equation for Model 3). Dennis and Taper claimed that this allowed for stronger density-dependence. They suggested three models to choose from for a data set. The basis of the models was equation 3 above. Model 0, describing random walk, was realized if parameter $r=0$ and parameter $\beta=0$. Model 1, describing random walk with a drift; for example a constantly growing population, was realized if $r \neq 0$ and $\beta=0$. Finally the third model describing density-dependent growth contained the parameter values of $r \neq 0$ and $\beta \neq 0$.

The test by Dennis and Taper consisted of two steps. In the first step maximum likelihood estimates for the parameters in each model, for example r or β, were constructed. This step was necessary to determine which values of the parameters could be reasonably expected, given the models they were part of. For example, in the case of model 0 Dennis and Taper assumed that the population counts were distributed randomly when the logarithms of the numbers were used. With this assumption the maximum likelihood of the variance of model 0 was the variance calculated for a normal distribution. The variance was the squared sum of all observed population changes, divided by the number of observations. The maximum likelihood estimate for the variance in model 0 thus was

$$\sigma^2=1/N \sum d^2$$

where σ^2= variance and d= changes in density of the population.

The likelihood estimates for the variance in model 1 and model 2 were different because the models made different assumptions. In specifying the maximum likelihood estimates Dennis and Taper were able to define the confidence limits of the parameters. For models 0 and 1 the confidence limits could be deduced from a known distribution because Dennis and Taper assumed that in a randomly growing population the values of the population sizes over time were independent of each other. However, as discussed in detail previously, this was not the case for model 2 because of the assumption that the data were autocorrelated. How could the confidence intervals be found for the parameters in model 2? Dennis and Taper used a technique called 'bootstrapping' which was similar in spirit to the resampling method used by Pollard et al. (1987) allowing them to multiply their data set and make estimates of the data that could be expected, and constructing the confidence limits for model 2. At the end of this first step the models were complete. The confidence intervals of the parameters were determined, and the models had complete likelihood estimates or likelihood functions used in the likelihood ratio test, which formed the second step.

The likelihood ratio test helped to decide which model fit the data best. The ratio of the likelihood functions decided which model was better. For example, the likelihood function of model 1 was divided by the likelihood function of model 2. Dennis and Taper used the following notation:

$$\Lambda=\text{likelihood function model 1/ likelihood function model 2}$$

The decision was made in favor of model 1 if $\Lambda > c$. The parameter c represented a cutoff point "chosen by the investigator"(Dennis and Taper 1994, p. 211) (The probability distribution of c had also to be determined, but basically it could be said that the higher Λ, the more likely was model 1 because the likelihood ratio Λ decreased with increasing likelihood of model 2.)

The test by Dennis and Taper consisted of two steps. The first step determined the maximum likelihood of data given the three models. The acceptance and rejection values for the likelihoods were gained by bootstrapping, which was a resampling of the data in a different order. After the likelihood functions of the models were determined they were compared with the data in the second step and the model which best conformed to the data was chosen. Because of the two steps involved, the test by Dennis and Taper was called a parametric bootstrap likelihood ratio test (PBLR test).

Differences in the three tests

The tests for density-dependence show an increasing sophistication of statistical analysis. It is disputable however, which one provides the best justification of the equilibrium concept. Turchin (1995) claimed that "conceptually the differences between the two most recent tests (Dennis and Taper's and Pollard et al's.) appear to be minor". Dennis and Taper, however, found that their test was superior to that of Pollard's et al. because of its higher power, which meant that it could detect density-dependence more efficiently than other tests. Fox and Ridsdill-Smith (1995), on the other hand, preferred the test by Bulmer. They compared the performance of Bulmer's test with other available tests and came to the conclusion that it performed better in certain situations than the tests by Pollard et al. (1987) and Brian and Taper (1994). They argued that it was possible to ignore the first few data points when applying Bulmer's test and thus reduce "start-up effects": in case the population is just returning to its equilibrium value, ignoring the first few data points would let the test detect the equilibrium value. Fox and Ridsdill-Smith (1995) saw advantages in Bulmer's test and claimed that it was not surprising that the test did not perform well if its assumptions (no trend in the data) were violated. According to them, it was often the case that statistical tests had strict assumptions; for example, many tests were based on the assumption that the data were normally distributed requiring remedial actions to be taken to make the test useful. This could also be done with Bulmer's test. An advantage to Bulmer's test was that it was computable with the help of a calculator, whereas the tests by Pollard et al. and Dennis et al. required intensive computer power because of the resampling procedure (Pollard et al.) and the bootstrapping (Dennis and Taper).

Differences in the tests can be attributed to differences in methodology and in assumptions about density-dependence. For example, Bulmer's test regarded a population with a trend as not being in equilibrium. Pollard et al. allowed a trend in the data which they included in their second model, meaning a population could grow or decline and would still have been considered regulated. Dennis and Taper offered a slightly different model than Pollard et al. for a population that is regulated by density-dependent mechanisms. The background assumptions of the tests differ but as I have discussed, according to philosophers of science, these are part of scientific testing. The main question for this analysis is whether the tests for density dependence justify the assumption of equilibrium.

The tests for density-dependence and the justification of equilibrium

To assess the status of the tests for density-dependence in the justification of equilibrium, the tests should be judged against norms of scientific testing described by scientists or philosophers. The notion of testing is important for the justification of theories. The philosopher of science, Ronald Giere, wrote that "a good test is a test that provides the basis for a JUSTIFICATION either of the hypothesis or its negation"(Giere 1984, p. 101). There is no doubt that scientists also regard the testing of hypotheses as an important part of justification. Good testing is the focus of many textbooks and graduate courses in ecology.

The testing of theories does not deny the thesis of the underdetermination of theories. Testing does not mean that observations are completely independent from theories or that background assumptions are not part of theories. However, to create a good test of a scientific theory rules have to be followed. These were described by Giere (1984) in the second edition of his *Understanding scientific reasoning* (the third edition does not spell out the conditions for a good test as clearly).

1. The hypothesis has to generate a prediction and this prediction has to be logically deducible from the hypothesis together with the initial conditions. This condition is fulfilled but does not amount to much in the case at hand because the prediction from the models is

that a time series has a certain pattern. The pattern, however, is not created by deduction. The time series merely describes it.

2. Relative to everything else *known at the time* (excluding the hypothesis being tested), it has to be improbable that the prediction turns out to be true. This condition has two purposes. At first the test should provide an independent justification of the hypothesis. That is why what is known should not include the hypothesis being tested. What counted as known at the time was knowledge that had been previously justified (Giere 1984, p. 104). The improbability of the hypothesis added to its justification. (Giere 1984, p. 113).

Another interpretation of the 2nd condition is that it ruled out false positives (Campbell 1994). If the prediction gained through the hypothesis was improbable and it was correct the probability that another hypotheses made the same predictions was small. Giere used Halley's Comet as an example. The British astronomer Edmund Halley predicted in 1705 that a specific comet would reappear in 1758. This was a bold prediction based on Newtonian mechanics and only Newtonian mechanics could make such a precise prediction. The less bold the hypothesis the more likely would be the false positive. If Halley had predicted that, based on Newton's laws sometime in the next 30 years a comet would appear, everybody would have said that this was likely to happen based on other theories as well. Thus, Giere wanted to exclude with the second condition the possibility that the evidence, the outcome of the experiment, fit another hypothesis equally well (in the 3rd edition of his book this is step six on page 39).

The second condition, avoid false positives, is often mentioned in the discussion about equilibrium tests and its importance and relevance cannot be denied. It underlies the main criticism against the tests by Morris and Bulmer. Critics of the equilibrium approach also base their arguments on the false positives apparently produced by the later tests. As Wolda and Dennis (1993, p. 590) said, "we have given ample evidence that, for data where density-dependent regulation clearly is not the appropriate explanation, the density-dependent model often provided the best description of the fluctuation pattern". According to Wolda and Dennis, Giere's second condition of a good scientific test is not fulfilled.

3. The outcome of the experiment has to be verifiable independently of the hypothesis

itself. This condition does not assume that the evidence has to be observable independently of any theory but only of the theory in question. Giere admitted that confirming observations could not always be made as easily as in the case of Halley's comet: "in modern science, the predictions that justify current hypotheses are often quite complex and require millions of dollars worth of equipment to verify. That doesn't matter. All that matters is that it can be done"(Giere 1984, p. 104).

Giere's third condition is fulfilled, especially in the more recent tests, because a verification of the test prediction is possible. This is expressed in the likelihood of a model fitting the data. The fit of the data can be verified by looking at the result of the likelihood-ratio test which tells how well the model predicts the data.

In particular, Giere's second condition for a good test played an important part in the justification of the equilibrium concept. One motivation for developing better tests for density-dependence was to eliminate false positives, as seen in the criticism made against the early tests by Morris and Bulmer. The second condition still underlies most criticisms of the equilibrium approach, which claim that because even the most recent tests produce false positives, the equilibrium concept is not justified.

One could argue that the tests for density-dependence have to improve to justify the assumption of equilibrium. Instead of regarding the tests as moving towards answering whether the equilibrium assumption is justified I interpret them as part of a change in the justification of equilibrium. I claim that the tests play an important role in justification but their importance is not captured by the conditions for a good test.

The problems with tests for density dependence in general was to formulate a null hypothesis, as pointed out by St. Amant (1970). Although it seems obvious that the null-hypothesis was that no density dependence existed it was not an easy task to translate this into statistical terms. I claim that the development of tests resulted in a definition of density-dependence in terms of the tests which is a change in reference of 'density-dependence'. This points towards a change in justification of the equilibrium concept which means that ecologists today use the concept for different reasons than did Nicholson. The change of reference becomes obvious when it is understood what the tests for density-dependence attempt to detect.

What is detected in tests for density-dependence ?

Figure 15 summarizes the characteristics of the time series that the tests detect. Model

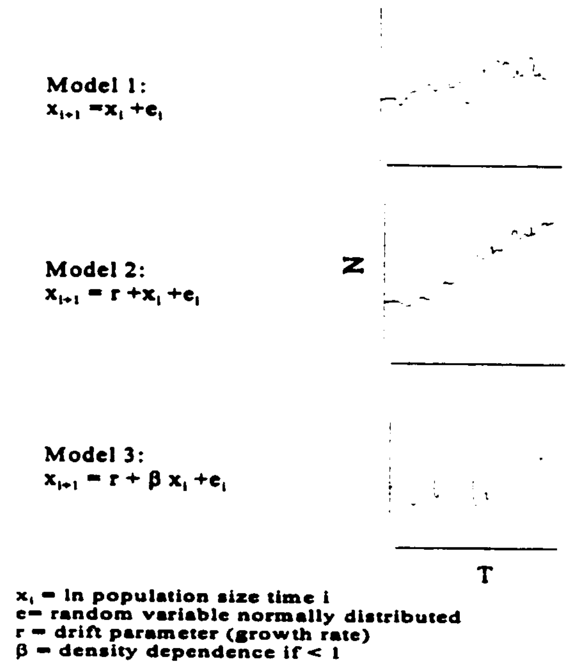


Figure 15: Sketch of population dynamics described by the different models used for tests for density dependence by Pollard et al. (1987)

1 describes a population that follows a random walk. The data points are scattered and do not show any consistent trend or return function. Model 2 describes a random walk with drift. The data points still follow a random-like walk but one can detect an upward trend in the data. Model 3 shows a regulated dynamic which oscillates around a mean value. Figure 15 shows that in model 3 the parameter β has to be smaller than 1 to produce the kind of graph that is drawn beside the equation. The tests reveal whether "the added parameter in model [3] produces noticeably improved description of the data" (Dennis and Taper 1994, p. 208).

Change of reference

Dennis and Taper's statement model 3 produces a better description of the data suggests that the tests do not detect equilibrium in Nicholson's sense but a new equilibrium, which describes the characteristic of a time series. I call this a 'change of reference' of the term equilibrium. The new definition of equilibrium is that "a population is in equilibrium if its dynamics follow a time series model, described by the equation: $x_{i+1} = r + \beta x_i + e_i$ in which $\beta < 1$". I interpret this new definition as a change in reference because scientists now refer to a characteristic in a data set rather than to a the result of a mechanism in nature. The change of reference is the result of statistical testing and the fitting of models has contributed to it.

The problem with Giere's conditions for a good test becomes obvious now. According to Giere's conditions the equilibrium assumption is not justified because the tests for it produce false positives. However, although Giere's conditions are helpful in analyzing the dispute, they miss important aspects of justification. To understand this we have to further investigate the change in the concept , and this points to a change in justification. Proponents of the equilibrium concept use it now with a different motivation than Nicholson and this is criticized by their opponents. Thus, to understand the debate we have to ask 'why' (or 'why not') in a historical or ultimate sense the models fit. Giere only asks 'why' in a proximate sense.

The disagreement about equilibrium indicates that a process that I call 'negotiation' is taking place. This involves interpreting the relation of the evidence (data set) to the theory (equilibrium) in a certain way. The testing is a historical process which has partly led to a new reference of the term equilibrium. I will show in the next chapter why the notion of negotiation is appropriate and why this does not mean that scientists are 'bending the truth'.

Summary

This chapter describes the arguments about the assumption of equilibrium in the present. I claim that the arguments are about the relation between evidence and theory, although these issues are hidden behind the arguments. Terms like 'a priori' and 'empiricism' are used more as rhetorical devices than as a means of giving insight into the issue at hand, which is the problem of induction. Although the problem cannot be solved it is often assumed that scientific observation can provide us with a foundation on which knowledge can rest. This foundational view has been criticized and this criticism reopened the debate about the justification of theories. With this background I investigated if norms of scientific testing can justify the equilibrium assumption. This I claim is not the case, although the norms of testing play a role in the development of the tests. However, the testing process itself led to a change in justification of the concept detectable by a change in reference of the term, a subject analyzed in more detail in the next chapter.

Appendix to Chapter 5

Stochasticity

In the 16th century 'stochastic' referred to a person who could forecast the future. It was revived with a new meaning in the 20th century and still plays an important role in ecological modeling. Pielou (1974, p.7), for example, pointed out that birth and death events in populations are stochastic events because their occurrences are not precisely predictable. She concluded that the calculation of population dynamics becomes increasingly inaccurate if deterministic models are used. Besides demographic stochasticity, described by Pielou, ecologists also incorporated environmental stochasticity (May 1974, p.34). Lande (1993) defined demographic stochasticity as "caused by chance realizations of individual probabilities of death or reproduction, whereas environmental stochasticity is described as perturbations in the environment".

Markovian chain

Kendall and Buckland define a Markov process as: "A stochastic process such that the conditional probability distribution for the state at any future instant, given the present state, is unaffected by any additional knowledge of the past history of the system" (Kendall and Buckland 1971). This definition claimed that it was necessary to know only the present state of the system in order to make claims about its future state; thus, the size of population at time t_{+1} was not independent of the size at t_0 although it was not necessary to know previous population sizes before t_0. The additional assumption that the Markovian process was stationary meant that "it is completely unaffected by a shift in the time origin. In particular, a stationary series varies about some fixed mean μ. It exhibits no change in its mean and no drift" (Box and Jenkins 1969, p. 93).

Duhem-Quine thesis

The underdetermination of theory by the evidence was emphasized by the historian of science and physicist Pierre Duhem in his book *The Aim and Structure of Physical Theory*, originally published in 1906 (I will refer here to the English translation of 1954). According to Duhem, when a physicist conducts an experiment he or she uses certain instruments and abstract notions to describe what is happening during the experiment. In some cases the outcome of the experiment, for example, smoke coming out of a container, could be verified by an observer who does not know the hypothesis under test. However, the verification merely concerned the smoke and the container. What that meant in terms of the abstract notions of the theory was not accessible to the lay-spectator. According to Duhem, every experiment in physics already presupposes the truth or adequacy of other theories it is based upon. These theoretical assumptions were 'background assumptions' made by the physicists. Duhem claimed that physics was like a whole organism of connected theories in which one theory could not work without its connection to another (Duhem 1954, p. 187).

Furthermore he claimed that if a theory was tested and verified the scientist did not know whether this system of theories was correct or if perhaps a different system would also predict the outcome of the theory (Duhem 1954, p. 190). If a theory was falsified it was not knowable whether the theory itself or one of the background assumptions was wrong. It was impossible to test all the background assumptions which themselves had other background assumptions.

Duhem concluded that one experiment by itself could not decide a debate about which theory was to be rejected and which was to be accepted. There was no crucial experiment that made us choose between one system of theories or another. The thesis that whole theories could not be refuted by crucial experiments and that the theories had to be seen as systems being composed of several theories was called the 'Duhem- Quine thesis' because the philosopher Willard van Orman Quine came to a similar conclusion as Duhem's.

The Duhem-Quine thesis had a strong effect on justification and it has to be discussed to understand how ecologists could decide on which system of theories to chose. Quine's approach to the relation between theory and evidence was more radical than Duhem's. Duhem cautioned physicists against accepting theories as true too quickly. Quine, however wrote that "[a]ny statement can be held true come what may, if we make drastic enough adjustments elsewhere in the system"(Quine 1953). As Harding (1976, p. xii) pointed out, Quine's thesis was stronger than Duhem's because Quine seemed to say that a "saving hypothesis always exists" which is a further statement that one cannot expect a decisive experiment that can solve the debate about equilibrium. The thesis that evidence alone cannot determine which theory is true is often called the 'underdetermination thesis'.

Time series analysis

According to Box, Jenkins et al. (1994) and Weigend (1994) the method of time series analysis goes back to an article by G. Udny Yule published in 1927. He investigated sunspot activity assuming that activity at a certain stage was influenced by sunspot activity at an earlier stage. Another influence was random disturbance. The important change in data analysis that Yule introduced was the estimation of noise in the data and how the noise affected periodic behavior. If underlying periodicity in data could be detected, forecasting was much easier. The "...ability to model dependence can lead to the solution of problems in forecasting, feedback control, and intervention analysis "(Box, Hunter et al. 1978, p. 584). Those problems existed, for example, in engineering, as Box et. al (1994, p. 3) pointed out because an engineer could estimate the random error that caused variations in the output of a technical process.

Autocorrelation analysis is frequently used in population ecology because it offers a method to investigate patterns in data which are not perfectly cyclic but where some regularities are assumed. The way in which the data are correlated is described by the shape of the autocorrelation function which provides evidence of the form of periodicity that the population displays (Turchin and Taylor 1992). Nisbet and Gurney (1982, p.252), for example, described how a perfectly cyclic population dynamic results in a perfectly cyclic autocorrelation. Non-cyclic behavior results in an autocorrelation function that decreases to zero for long time lags. Population ecologists are interested in the cases between these two extremes. Like the diagrams of Lotka and Volterra predator-prey interaction, the graphic representation provides fast access to the results of the analysis.

Figure 16 shows the result of an autocorrelation analysis of the numbers of passenger using an airline (I have taken the example from a statistical software program called "Systat for Windows®", Volume 7.0. I refer to the example on pages 673-681.) Autocorrelations are measured for subsequent observations, for example, the correlation between population size at t and t+1 or between population size at t and t+2. If the autocorrelation is plotted against the time lag we obtain an autocorrelation function of the time series. The autocorrelation analysis in Figure 16 shows that the values 12 months apart are highly correlated. This indicates that the time series has seasonal regularities.

Autocorrelation analysis thus offers an important tool to investigate patterns in data sets that display patterns. However, to perform an autocorrelation analysis the data set has to have certain characteristics which are important for an understanding of the change in the equilibrium concept. The analysis requires a stationary time series which has a constant mean and a constant variance (W. Blanchard, pers. com.). Taking the example of the raw data for passengers using in airline we can see in Figure 17 a that the variance of the data is not constant and that the data set displays a trend. One can eliminate both attributes by using the logarithms of the data, which stabilizes the variance. To remove the trend in the data one

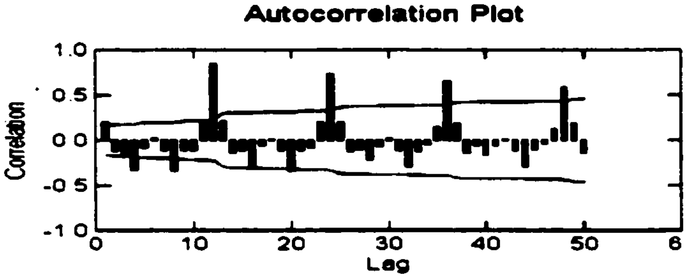
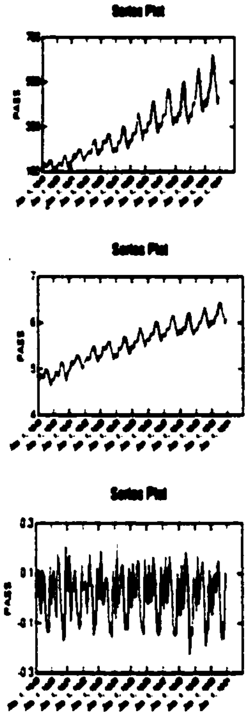


Figure 16: Autocorrelation function of numbers of passengers using an airline . The autocorrelation function is plotted against the time lag. The horizontal lines mark the significance level of the correlations

determines the differences between "each value and its previous value" (Systat manual p.

679). The different steps in the treatment of the data set are summarized in Figure 17, c of which shows a stationary data set on which the autocorrelation analysis, shown in Figure 16, is performed.



a: Raw data of a time series. Numbers of passengers using an airline

b: Logarithms of raw data. The x-axis now shows the logarithms of the numbers of passengers

c: Differences in subsequent values of Figure b.

Figure 17: Treatment of raw data for autocorrelation analysis

Chapter 6: The scientific negotiation of equilibrium

In the last chapter I described the testing of the equilibrium concept and claimed that the testing led to a change in reference of the term. This was not accepted by all ecologists and I describe the ensuing discussion about the change as 'negotiation'. Scientists and some philosophers often disagree with an analysis of science as a negotiation process, believing it implies that data are used inappropriately or that the outcome of negotiation processes cannot be truthful. The use of the term 'negotiation' is often understood to mean that scientific knowledge is underestimated. I do not think that scientific data, once agreed upon, are manipulated but their relation to theories is. The negotiation of equilibrium is not a negative aspect of science but rather an essential part of it. In this chapter I investigate the change of reference and the negotiation process further.

Turchin's translations

My investigation into the negotiation of equilibrium is based on an article by Peter Turchin, "Population Regulation: Old Arguments and a new Synthesis", published in 1995. Turchin's synoptic paper summarized the recent debate about density-dependence, illustrating how the reference of key terms in the debate about equilibrium has changed. The article also provided insight into the process of negotiation and its effect on the phenomena investigated and offered a translation from the old definitions to the new ones. On the surface, Turchin made claims similar to Nicholson's about the regulation of populations. A closer look, however, revealed that his definition of key terms ('regulation' and 'density-dependence') led to an interpretation of population processes that differed significantly from Nicholson's.

Regulation and density-dependence

According to Turchin, a population is regulated if its population dynamics fit a stationary probability distribution, of which the equilibrium state is the mean. A regulated population is in equilibrium, so that: "... being regulated and having equilibrium is one and the same thing" (Turchin 1995, p.26). The criterion of having a stationary probability distribution is important to distinguish a data set with equilibrium from a data set that performs a random walk (Figure 15 (Chapter 5) shows curves that describe a random walk and a curve with a stationary dynamic).

The other key term besides 'regulation' is 'density-dependence' which Turchin defined as return function in the data set. He wrote: "...return tendency is a generalized notion of direct density-dependence" (Turchin 1995, p. 27). Thus, if a data set has a strong return function, we can say that density-dependent mechanisms act upon the population. Equilibrium is present.

I believe that Nicholson would have agreed with Turchin that populations return to their equilibrium value and that this can be connected to density-dependence. It is, however, interesting how Turchin described the equilibrium state: "[e]ven if the endogenous structure of the model with which we represent population fluctuation is characterized by a stable equilibrium, this point has no special status, and will be visited by the population trajectory as frequently... as other points nearby" (Turchin 1995, p. 25). This statement is in opposition to Nicholson's belief that the equilibrium state indeed has a special status.

Turchin's claim about equilibrium not having a special status is puzzling; it has to do with his concept of stationarity in a data set, meaning the data set has to have a return function. It follows that density-dependence is a necessary condition for equilibrium and here Turchin agreed with Nicholson. Turchin, however, said that the presence of density-dependence is necessary but not sufficient for regulation. This claim is a divergence from Nicholson, who thought that density-dependence is necessary and sufficient for equilibrium. Despite an acknowledgment of other factors determining the size of a population, later in his career Nicholson believed that density dependence can occur only if density-dependent mechanisms, sufficient for equilibrium, are present (Nicholson 1954 b). He did not loosen his ontological commitment to equilibrium via density-dependence.

The shift in reference

I argue that the change in definitions is significant because it indicates a shift in reference of the term 'equilibrium' from equilibrium in nature to equilibrium in the data. This point has to be discussed further. To understand the difference in Turchin's reference for 'equilibrium' from Nicholson's, it is necessary to distinguish exactly when Turchin was talking about equilibrium in the real world and when he referred to equilibrium in the data. His use of the word 'regulation' is confusing, for example when he wrote that "regulation is not equivalent to return tendency" (Turchin 1995). How can return function in the data set (density-dependence according to Turchin) not be sufficient for stationarity (regulation according to Turchin) in the data set? What else is a stationary data set than a data set with return function?

In a discussion of this issue, Hanski et al. (1993) said that a population can show a return tendency while possessing a declining trend. This means there can be return function but no stationarity. Wolda et al. (1994, p.230) pointed out, however, that "if there is a declining trend, then there is no return tendency".The density-dependence tests would indicate that a population with a declining trend is not density dependently regulated because the dynamic is not stationary.

Turchin claims that density-dependence is return function. How then can density-dependence not be sufficient for regulation? What kind of regulation had Turchin in mind? The solution to this confusion is that Turchin implicitly used two notions of 'regulation', one notion was statistical and one was ecological.

Statistical and ecological regulation

The difference between the ecological and the statistical notion of 'density dependence' is that a regulated time series in statistical terms is not necessarily regulated in ecological terms. In this sense statistical regulation is a necessary but not sufficient condition of ecological density-dependence. Statistical regulation is a property of a data set, ecological regulation is a property of a real population. Turchin sometimes blurred the distinction between data set and nature. He said that statistical regulation means that the data comes from a bounded distribution, meaning there are upper and lower limits in the data set. In this sense we can say that statistical regulation implies boundedness of a real population. The validity of this claim will be discussed later. But the distinction between ecological and statistical regulation needs amplification. It has also been the concern of earlier discussions about tests for density-dependence (for example St. Amant 1970).

The concept of autocorrelation is helpful to understand the difference between statistical and ecological regulation. Autocorrelation denotes the correlation between subsequent data in a time series. A set of random data does not show autocorrelation but, and this is the important point, can be stationary. Imagine the throwing of two (or more) dice. After each throw the numbers of the individual dice are added up. Then a frequency diagram is constructed with the value of the throws on the abscissa and their frequencies on the ordinate. After a long series of throws the bar diagram shows a normal distribution. The value seven will appear much more often than the value two for example. Treating the values of the dice as a time series would thus result in a stationary probability distribution. However, the data are not correlated with each other.

Could autocorrelation of the data be used as a definition of ecological regulation? This is doubtful because, as Williams and Liebhold (1995) pointed out, it is difficult to distinguish between autocorrelation in exogenous factors such as weather patterns and autocorrelation in the population. If we find autocorrelation we might not have ecological regulation.

So far the statistical notion merely offers a description of density-dependent regulation. The question which remains unanswered is why the data are stationary. We want to know why, how, or if the data set gives evidence for mechanisms in the real world. However, Turchin had not made any statements about the real world simply by using the data set. If equilibrium does not have special status according to Turchin, why use the term equilibrium at all? He equated return function in the data with equilibrium in the data. This does not mean that the return function, a property of the data set, is an explanation for equilibrium, supposedly a property of the real world population under investigation. Turchin's notion of statistical regulation may seem to be a description of a data set that would perhaps indicate ecological regulation or give evidence for regulation in the real world but, again, it does not add any new information that would indicate that the data is regulated.

I conclude that Turchin is only superficially in agreement with Nicholson.

Resistance to Turchin's translations

The statistical notion of 'regulation' and Turchin's interpretation of 'equilibrium' was criticized by Wolda and Dennis (1993), who were critical of the equilibrium approach in general. They wrote that a stationary probability distribution can originate from a sample of a normal distribution, or a log-normal distribution. Statistical density-dependence is of little help if we want to find out if a population is regulated in the Nicholsonian sense. The test for density-dependence, they argued, would tell us that the throws of the dice in the example given above are regulated by density dependent mechanisms. But the values are merely a set of random numbers; they have no connection to each other. Thus, the statistical definition of regulation, according to the critics, does not make sense ecologically. All that is tested is statistical density-dependence. Did Turchin misinterpret the limited utility of the tests for density-dependence? No, he knew that statistical density-dependence can not be equated with ecological density dependence. The motivation for Turchin's definition of density-dependence in statistical terms becomes more obvious if it is shown how the same data were interpreted differently by him and by Wolda and Dennis.

Disagreement in the interpretation of data - Rainfall in Panama

An example of diverging interpretations of test results is rainfall data for an island in Panama. This example was used by Wolda and Dennis (1993, p. 589) to discredit the tests for density-dependence or, at least, to caution the users of the tests. Turchin, however, interpreted the tests differently.

The density-dependence test by Dennis and Taper, applied to rainfall data from an island in Panama, detect density-dependence (there might have been a motive for the choice of the data set: I suspect the rain fall data promised that the test by Dennis and Taper would diagnose density-dependence). This test result does not make sense because, as Wolda and Dennis argued, it is odd to assume that there is some mechanism that controls the amount of rainfall in the same sense that a population is controlled. Dennis and Taper argued that caution has to be used in applying density-dependence tests because the findings might even be absurd.

Turchin, on the other hand, used the rainfall data as a good example of density-dependence. He claimed that it makes sense that the tests picked out the data as density-dependent because rainfall is regulated in the sense that "the earth's climate (of which rainfall is a manifestation) is a well-regulated system" (Turchin 1995). Turchin's definition of regulation here was that the amount of rainfall is not limitless; it has an upper and a lower limit and this property is detected by the tests.

It is unclear which kind of regulation Turchin referred to in this case. The rainfall data shows statistical density-dependence. Both parties agree on this, Wolda and Dennis cautioning against equating rainfall data with population data because the latter could be statistically regulated but not ecologically regulated. Turchin claimed that the regulation detected by the test for density-dependence can tell us something about the real world which is that the rainfall is bounded.

One could say that the tests detect density-dependence in rainfall data because the data set also displays autocorrelation. Although autocorrelation is a questionable indicator for ecological regulation, one clarification is necessary: Williams and Liebhold (1995) found, based on simulations, that weather data are indeed autocorrelated on a limited time scale. The autocorrelation, however, disappears the longer the time series lasts. It seems that both camps have a point in referring to weather data as support for their arguments. For my purpose it is sufficient to see that the nature of rainfall is interpreted differently by both sides and the different interpretations have to be seen in the context of the differing motivations about what the weather data is supposed tell us.

What were Turchin's motivations? He admitted that statistical equilibrium is necessary, not sufficient for ecological equilibrium. Even the weaker claim that the tests show that the data comes from a bounded time series is disputed: Wolda et al. (1994) claimed that the tests will detect density-dependence even from a set of unbounded numbers. I claim that Turchin was aware of the limitations of the tests and that he offered a different justification of the equilibrium concept than Nicholson. The process through which he introduced a different justification was the negotiation of the evidence regarding the theory. That the tests for density-dependence play a role in the justification becomes obvious if Turchin's approach to the modeling of population dynamics is analyzed

Turchin's modeling approach

Turchin agreed with the critics of the equilibrium assumption that the density-dependence tests only detect statistical density-dependence. This is not immediately obvious in the article discussed because he did not clearly distinguish between ecological and statistical regulation. For him the main point in testing for density-dependence is not to immediately detect density-dependence in the population, but only to take the first step in a row of investigations of the time series. The distinction between evidence for and evidence against the presence of equilibrium is a distinction that serves to create an initial classification of data sets but is not an answer to the question whether or not there are indeed density-dependent mechanisms that regulate a population. Turchin described the procedure as follows:

> Depending on the test outcome, we know that we need to model fluctuations of the population as either a stationary or non-stationary dynamical process. If it is non-stationary, then we need to make another decision: Should we model this population as a density independent stochastic growth/decline process, or as a density dependent process in which some parameter is following a temporal trend? (Turchin 1995, p. 31).

Further tests for the structure of density-dependence are not possible without initial density-dependence tests. As an example of these further tests, Turchin (1990) suggested the use of autocorrelation functions to detect direct density-dependence and also delayed density-dependence (but, again, it is debated whether an autocorrelation analysis can decide whether a population is regulated in Nicholson's sense). These tests, however, can only be used if we know whether or not the population is stationary. According to Turchin's definition mentioned above, stationarity and being regulated is synonymous to 'equilibrium'. Thus, by definition, the tests for density-dependence pick out statistical equilibrium which is a property of the time series. Although Turchin claimed that tests for density-dependence pick out a property of the population, I interpret his strategy as shifting the reference of 'equilibrium' from a result of a mechanism in nature to a property in the data. Turchin did not ignore that the tests for density-dependence pick out statistical equilibrium rather than ecological one. The detection of statistical equilibrium is part of his research strategy.

Interpretation of Turchin's research strategy

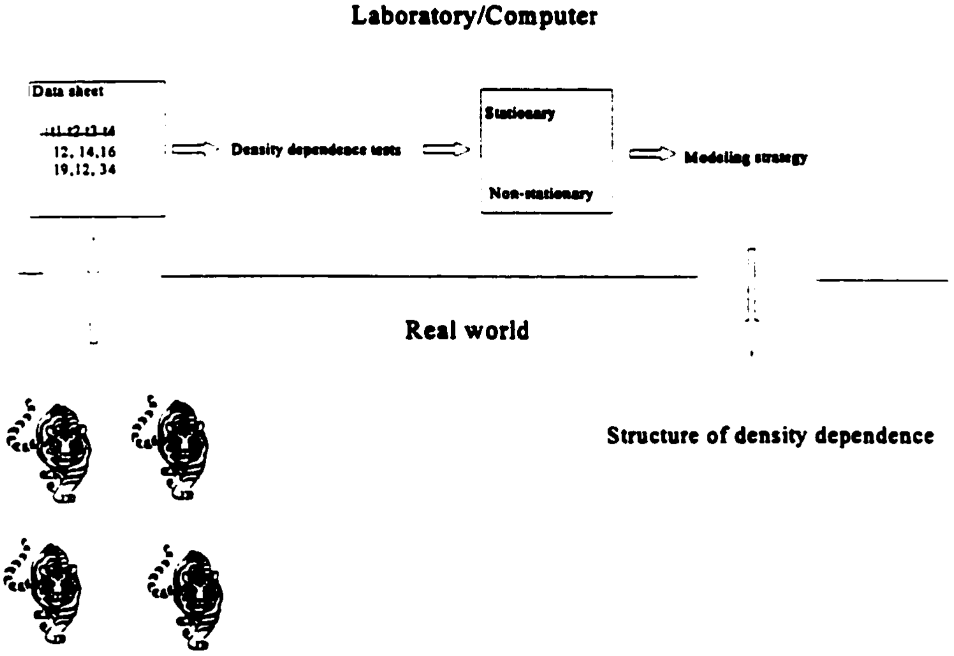


Figure 18: The analysis of density dependence according to Turchin (my interpretation)

The critics of the equilibrium approach cautioned against the tests of density-dependence which detect statistical equilibrium. However, Turchin saw the difference between statistical equilibrium and its counterpart in nature. My interpretation of Turchin's argument is summarized in Figure 18, showing how equilibrium in the data relates to equilibrium in nature. The lower part of the figure illustrates the content of the real world according to Turchin and the upper part describes the steps of data analysis in the computer or the laboratory. The four tigers symbolize an animal population in the real world whose abundances are recorded on a data sheet. Density-dependence tests in the laboratory or a computer allow scientists to make decisions about the modeling strategy they want to pursue. Knowledge about autocorrelation in the data can indicate patterns in the time series (see Figure 16 in Appendix to Chapter 5).

The investigation enters the real world again when the modeling strategy supposedly leads to insight into the type of density-dependence. Deeper insight, according to Turchin, might come from field experiments that are designed based on the statistical analysis of the data. Turchin's discussion and definition of 'equilibrium', however, was centered on data analysis and the attribution of equilibrium was justified because it made the classification of data sets possible. I conclude that the change in reference of the term 'equilibrium' is from the mechanism in nature to the characteristic of the data set. This is a significant change because Turchin now justifies the equilibrium concept differently than Nicholson did. Figure 18 illustrates the negotiation process that is part of this change in justification.

Arguments against negotiation

My description of the change in justification is based on an analysis of the debate between proponents and opponents of the equilibrium assumption. However, one could interpret the debate differently: critics of the equilibrium view, such as Wolda and Dennis or Den Boer and Reddingius, thought that Turchin's modeling was not sufficient to justify equilibrium, and they rejected his approach to detecting ecological equilibrium. One could claim that the debate is simply semantical in that different scientists interpret words like 'equilibrium' and 'density-dependence' in different ways, which is unfortunate but can be remedied by agreeing on a certain usage. Clarification can be achieved if it is made clear that ecologists have to distinguish between statistical equilibrium and ecological equilibrium.

Indeed, evidence can be found in the ecological literature that some scientists might question my claim that the change of reference of 'equilibrium' is to be interpreted as part of a negotiation process. For example, my illustration of Turchin's argument unintentionally bears a strong resemblance to a figure in a book on ecological modeling by Hall and Day (1977, p. 16) who did not interpret the split between data and nature in the same way I did.

They wrote that the distinction between data and the world is merely an abstraction, a model, of the world whereas I claimed that this constitutes a change in reference of 'equilibrium' implying, as could be argued, that scientists use theoretical terms like 'equilibrium' to describe nature directly.

One could claim that I take the definition of the theoretical term 'equilibrium' too seriously, which points to an important argument against my view concerning change of reference as an indicator of change in justification of the equilibrium concept. This claim, made by the positivists, that theoretical terms are connected to the world via meaning relations to observable data is, however, not defensible. One could treat the equilibrium concept as not having any meaning relationship to nature but as an abstract model. Ambiguity about models, however, exists among ecologists as revealed in the statement by Zeng et al. (1998, p. 2194) who wrote that the tests for density-dependence may be "far too simple and removed from biological reality to cover the various complex population dynamics encountered in the field". How does the idea of equilibrium as a model bear on justification?

Models in ecology

Levins, Maynard Smith, and Hilborn and Mangel

A description of how ecologists see models as some kind of idealization of nature was given in an influential article by Richard Levins in 1966 (Levins 1966), in which he described different modeling strategies. He claimed that models can not be simultaneously precise, realistic, and general. Instead, the modeler has to make choices. Levins claimed that a simulation that incorporates many parameters to give as precise a prediction as possible is following a "naive, brute force approach" (Levins 1966, p. 421). Those models sacrifice generality for realism and precision. A second type of model sacrifices realism for generality and precision, examples being predator-prey models like those of Volterra or Lotka. Levins suggested using a third group of models, preferably sacrificing precision for realism and generality. These are mostly graphical and flexible, in that, instead of exactly specifying their mathematical form, they describe phenomena as functions that are decreasing or increasing convex or concave.

Levins admitted that models always simplify representations of nature. To preserve realism, he claimed that it is possible to test several models with different simplifications, if they all have in common a certain outcome which was considered a "robust theorem", such as that a species will evolve broad niches and tend toward polymorphism in an uncertain environment. The term 'theorem' suggested that Levins had something like a logical deduction from axiomatic models in mind, but he did not expand on this.

More important in this context is the point that a mathematical model, according to Levins, is neither a hypothesis nor a theory because it is not verifiable directly. A model, he said, is neither true nor false. All it has to do is generate testable hypotheses. Thus, the conflict between different modeling strategies "is about method, not nature, for the individual models while they are essential for understanding reality should not be confused with reality itself"(Levins 1966, p. 431). In this way Levins avoided the discussion about theories and their status, and to obtain testable hypotheses used abstract models which are realistic but not to be confused with reality.

John Maynard Smith (1974) also distinguished between practical and theoretical use of mathematics in ecology. According to him, practical use consisted of simulating population dynamics, for example, determining how many fur seals could be culled. These simulations are good for special cases but for deeper questions we need "different kinds of mathematical descriptions, which may be called models."(Maynard Smith 1974, p. 1). Like Levins, Maynard Smith thought that models serve to discover more general ideas, in that they provide an abstract picture of underlying features in nature that can be tested.

Although Maynard Smith's arguments were somewhat similar to Levins', he was not concerned with Levins' distinctions between generality, realism, and precision of models. This can be seen in Maynard Smith's arguments regarding the differences between stochastic and deterministic predator prey models. Although he admitted that using deterministic models is only justified by "mathematical convenience" he was not too worried about the simplification. Maynard Smith described his general attitude as being to "assume that if the deterministic models shows a stable equilibrium, the corresponding stochastic model would predict long-term survival, whereas if the deterministic model shows no equilibrium or an unstable one, the stochastic model would predict extinction with high probability" (Maynard Smith 1974, p. 13). This displays a certain pragmatism toward the idea of stochasticity and its incorporation into models, using as an example Volterra's predator-prey equations and their graphical representation as a phase plane (discussed in Chapter 4, Figures 6 and 7).

More recently, Caswell (1988) argued that models might not tell us a lot about the world but they tell us "something very important indeed about the possible relations between stability and complexity". As an example he cited work by Robert May (1974) which mathematically investigated the connection between the stability and complexity of ecosystems, arguing for the legitimacy of theoretical studies in ecology because, even if they do not make quantitative prediction possible, they help to generate new, interesting hypotheses that were worth testing.

Levins, Maynard Smith, and Caswell had varying approaches to modeling but shared a common view that models are not describing exactly what is happening in nature, but are idealizations. According to these authors, models serve as hypothesis-generating devices but do not make any direct statements about the world. Because the biologists mentioned did not talk about theories at all, it is difficult to understand how they viewed the way that models, theories and the real world are connected.

Hilborn and Mangel (1997) discussed this problem in more detail, defining theories, quoting Webster's dictionary, as "considerable evidence in support of a general principle". But they did not further discuss the idea of theory, turning instead to the definition of model as "a stylized representation or a generalized description used in analyzing or explaining something" which serves as a tool for the evaluation of hypotheses. A hypothesis, which can be represented by several models, is less stringent than a theory and more tentative (Hilborn and Mangel 1997, p. 25). For example, the hypothesis "birds forage more efficiently in flocks than individually" can be described by different mathematical models, consumption being proportional to flock size, or being saturated as flock size increases, or other possible scenarios. Each can be represented mathematically by a model. In their discussion of different sorts of models, Hilborn and Mangel differed from Levins and Maynard Smith in that, although they also distinguished between stochastic and deterministic and between quantitative and qualitative models, they did not separate the use of the models as decisively. Hilborn and Mangel recognized that some models are used for prediction and some for understanding, but their discussion did not attach any priorities to one rather than the other. (It could be that the development of computers made it possible to use quantitative models as easily as qualitative ones. Data processing is so fast that it does not matter how many more parameters are included in the analysis. This was not the case when Levins and Maynard Smith published their work).

So far I have described how the biologists regarded models as idealizations and as different from hypotheses in that they provide a representation of a hypothesis. Thus, the claim that the equilibrium models are "removed from biological reality" (Zeng, Nowierski et al. 1998) is beside the point. Still,the models, however abstract, have to be tested against data collected from the real world.

How models meet data

Hilborn and Mangel suggested first determining which probability distribution can be used to describe the probability of the observed events. For this the data are plotted. Socalled Monte Carlo methods can be used to create a data set of which the scientist know its origins (described in Chapter 5). How is it determined which model fits best? Hilborn and Mangel claimed that the maximum likelihood approach is more suitable for modern model testing than the methods of sum of squares. Usually the method of sum of squares is used to distinguish between two hypotheses but, as I have described, density-dependence tests often employ several models and the maximum likelihood approach assesses which model has the most likelihood to fit the collected data. As Hilborn and Mangel pointed out, likelihood analysis turns the methodology of testing around. They described the procedure of normal probability testing as first deciding on a hypothesis, then gathering data, and finally accepting or rejecting a hypothesis based on the probability that a Type I or Type II error is avoided. In likelihood testing, however, the procedure, according to Hilborn and Mangel, is to present the data with a variety of models. As quoted earlier, they claimed that in the old probabilistic approach the hypothesis was decided on and then confronted with the data; in the likelihood approach the data are gathered first and then a model is chosen (Hilborn and Mangel 1997, p. 133). The scientist decides which model to fit. A variety of models can be fitted to a certain data set and the likelihood of which model fits best determined, rather than one hypothesis being tested against another. Wolda and Dennis (1993) remarked with respect to this procedure that ecologists not only have to be concerned about Type I and Type II errors but also about Type III errors, as Wolda and Dennis called them, i.e. the error that is committed when the wrong model is fitted to the data. This could be a model, for example, that describes density-dependence in a wrong way. In addition to likelihood ratio tests, Hilborn and Mangel proposed to use Bayesian analysis if prior information about the likelihood of one of the models is available. The goodness of fit then depends partly on the prior information the scientist has (Hilborn and Mangel 1997, p. 203).

The account by Hilborn and Mangel suggests that it is the role of the scientists to match the models with the data. Abstract models, require scientists to use them. The representation of equilibrium is not automatically justified but dependes on the activity of the scientist who uses a certain model to fit it to population data. I argue that the choice of models and what they are supposed to represent is part of the negotiation. To understand the negotiation process a closer look at the concept of a model from the perspective of the philosophy of science is helpful.

. Equilibrium according to the semantic view

A recent view of the structure of scientific theories is called the semantic view. The name is used to distinguish it from the syntactic view, which regards a theory as consisting of an axiomatic system in which non-logical terms, for example equilibrium, are defined via socalled correspondence rules. The axiomatic system provides the rules of how the terms of the theory relate to each other, but it does not prescribe any meaning to the terms. Correspondence rules specify how the theories relate to the world. According to the semantic view, theories relate to the world through models. As Thompson (1989, p. 71) puts it, the semantics of the syntactic view were provided by the correspondence rules and the semantics of the semantic view were provided by models.

Theories as set-theoretic entities

Inspired by the work of Patrick Suppes and Everet Beth, some philosophers of science classified scientific theories as set theoretical entities (Suppe 1989, p. 3; Thompson 1989, p. 69), sets being "collections of entities of any sort" (Suppes 1957, p. 177). The motivation to classify scientific theories in this way was to express the idea that scientists compare sets of theoretical entities with sets of phenomena rather than applying scientific laws to the world. Suppes (1967, p. 59) illustrated this in reference to quantification in science, saying "we cannot literally take a number in our hands and apply it to a physical object. What we can do is show that the structure of a set of phenomena under certain empirical operations is the same as the structure of some set of numbers under arithmetical operations". The task of scientists is to determine the degree of fit between theoretical sets and sets of phenomena.

Equilibrium as idealization

The relation between the sets forms the most important feature of the semantic view. It describes how theories relate to the world and it can best be explained by contrasting it with the syntactic view. According to the latter, theories are seen as linguistic entities such as the equation F=ma meaning that "force equals mass times acceleration".

The linguistic formulation caused problems because, for example, no strict distinction exists between theoretical and observational terms. Furthermore, Thomas Kuhn (1970) pointed out that changes in the meaning of terms like 'mass' in subsequent theories would mean that the theories that share the term describe different things in the world. Thus, the theories would be incommensurable and one cannot say that a later theory got it more right than its predecessor.

Incommensurability was often interpreted as implying irrationality in science, and partly for this reason Suppes and others argued that theories are not linguistic structures. According to Thompson (1989, p. 71) 'models' in formal semantics "are entities that satisfy an axiomatic structure and by doing so provide an interpretation for that structure. A model satisfies an axiomatic structure if it renders the theorems of the structure true". Models of formal structures are always true in terms of the formal system they interpret (Thompson 1989, p. 29).

An example from geometry is given by Thompson. Since the mid-nineteenth century two different forms of geometry besides traditional Euclidean geometry have existed. These are abstract and difficult to visualize or formalize linguistically in the way Euclidean geometry can be. They can be treated as models that share the same formal structure, itself an abstract mathematical entity, and they apply to different situations (for the visualizations of the different geometries see Salmon 1975).

This concept is applicable to scientific theories, in that theories are merely sets of equations or non-mathematical structures that are without any meaning in themselves, being neither true nor false. Theories are "formulae with holes in them, bearing no relation to reality" (Cartwright 1983, p. 159). Thompson claimed that theories can have meaning, but some might have no empirical application. Despite the differences on this point, Thompson's claim points to an important feature of the semantic view, that it separates a theory from its application. This is supported by Beatty's claim that "the empirical claims of science are not considered to be components of theories" (Beatty 1980). Theories do not tell the scientists what the world is like. Scientists themselves have to fill in the models with empirical claims.

With the semantic view in mind, the argument about the change in the equilibrium concept can now be that different models are chosen from an idealized mathematical structure. I claim that this structure was described by May (1976) and Lotka (1925), as introduced in Chapter 5. It consisted of the equation: $X_{t+1}=F(X_t)$,. This structure does not have any meaning in itself but, it can be interpreted to mean that the size of population X at time t+1 is a function of the size of the population at time t. Once interpreted, several models can be derived from it, for example, those used by Pollard et al. (1987). Thus, one could say that the semantic view offers an account of theories that is consistent with ecologists negotiating a choice of models. One could claim that 'change of reference' amounts to saying that the form of representation of equilibrium in the models has changed. According to the semantic view and the way ecologists use models, change is no surprise because a multitude of models are possible. However, to demonstrate the significance of the change in justification, I still have to show what the change of reference, negotiated by Turchin, entails. An investigation of the relationship between theories, models and data according to the semantic view is necessary to show why the change of reference is part of a change in justification of the concept of equilibrium.

Relationship between theories and models

First a comment on what the relationship between models and theories is not. Although I have described the semantic view so far using examples of axiomatic systems, for example the different models of geometry, models are not necessarily interpretations of axiomatic systems. The models of density dependence chosen in the tests described are not deduced from the theory. In this regard, Giere explicitly denied that links between models and between models and theory are logical relationships, claiming that there are no clear rules that determined which "models or hypotheses were part of the theory" (Giere 1984, p. 86). He defined theories exclusively in terms of models, claiming that they are a population of models plus a hypothesis that links the model to the world (Giere 1988, p. 85). Although Giere seemed to combine theories with their application, his conception of model was also one of an extralinguistic structure, and he did not think that statements about models are part of the models.

Theories define models; Van Frassen and Suppe

The question remains, how do we get from theory to the model? Different approaches to this can be found in the literature. One way was described by Suppes as defining models with set-theoretic predicates (Thompson 1989, p. 74). Another approach was given by Stegmüller but I will concentrate here on the approach by Van Fraassen (1980) and, in more detail, on Suppe (1989).

According to Van Fraassen's approach theories define a state space which is determined by the parameters of the theory and describes the dynamics of the system. The state space system is the model, an example being the predator-prey equations of Lotka and Volterra. Referring to Figures 6 and 7 in Chapter 4 one can see how the theory defines a coordinate system which consists of the densities of predator and prey populations. I have discussed how the different assumptions of predator and prey behavior could be included in the models (Figure 7 included density dependent growth of the prey population) showing how changes in the theory can easily be incorporated in the state space (model).

For the understanding of equilibrium it is helpful to use the approach by Suppe (1989), which is similar to Van Fraassen's in claiming that theories specified systems. For Suppe the way from theory to model is less direct, although also based on the idea of abstraction. According to Suppe, a theory, or science in general (Suppe 1989, p. 65), is concerned with what he called a "physical system", which is an abstract construction based on a few parameters. It never describes what is happening in detail; it does not deal with all the complexities in nature.

Suppe suggested that with the help of theories physical systems are described by scientists, choosing idealized parameters from the phenomena to be investigated. The physical system is confronted with hard data, the collection of which includes correction procedures such as the log transformation in the case of population data. Suppe did not claim that models directly translate into state spaces but that models are replicas of the theory (Thompson 1989, p. 71). This would mean that equilibrium models come from an idealized system as described above ($X_{t+1}=F(X_t)$). The parameters chosen are the subsequent sizes of the population and the physical systems in more detail are the models of density-dependence.

Relations between theories and models: examples used in biology

Philosophers of biology have embraced the semantic view because it describes important aspects of theorizing in the discipline and how evidence is related to theory. This not only applies to equilibrium but also to so called 'laws' in biology. An example is the Hardy-Weinberg law in genetics, which, although called a law, is a model of how genotype frequencies would behave under certain conditions named by the law itself, namely random mating, and independence of each allele (Lloyd 1984). These conditions are not met in nature yet the Hardy-Weinberg law is still used as an idealization.

Mendel's laws, according to Lewontin (1991), are also to be understood as models and not as universal laws. They are, according to Lewontin, "contingent on the particularities of cellular mechanics" which are not always met (Lewontin 1991), so that in many cases Mendel's laws are wrong. Used as idealizations, however, Mendel's laws can be seen as calculation devices in which the parameters presented by the model enable predictions and the confirming or disproving of theories.

Not only should biological laws be interpreted as models, but the semantic view applies also to physics, as pointed out by Cartwright, who used as an example Newton's law: F=ma. Following a different version of the semantic view, which was less strict than Suppe's or Van Fraassen's, she believed that models indeed describe what actually happens in nature. Theories, however are idealizations that are never true because they are abstractions, connected to the world through models. For example, in Newton's law, Cartwright (1994, p.358) wrote, "force is connected with real systems only via a set of models that assign force functions to specific kinds of situations". To make sense of Newton's laws we have to create models that are based on them, for example, systems that describe simple harmonic or damped harmonic motion.

Equilibrium as a law

Following the discussion about Mendel's and Newton's laws we could interpret the concept of density-dependence as having a law-like status as well. But what does that mean? Density- dependence is part of a model that is neither true nor false but could be compared to the dynamic of real populations. However, the models never fit completely; they still are idealizations, describing how the "phenomena *would have been* had the abstracted parameters been the only parameters influencing them" (Suppe 1989, p. 83). Conditionals like this are called counterfactual because they describe events of which I know the premise will be false; for example, if I jumped off the Empire State Building I would be dead. The activity of comparing models to the world is not unlike arguing from a premise that is regarded as false because the models are not exactly as the world is. However, falseness provides scientists with important insight. The equilibrium concept has to be interpreted this way. The population models fit but what represents the equilibrium assumption in the models is an abstraction. It is important to notice that laws, according to the semantic view, are regarded as internal to the abstract system rather than as governing nature as a whole.

Mapping

Although I agree that equilibrium has to be interpreted as an abstraction, the relevance of negotiation for a shift in reference becomes obvious if it is investigated how models are supposed to relate to the world. The relationship between model and nature is called a 'mapping relationship', another important component of the semantic view. Suppes (1957) uses the analogy of mathematical functions, which can serve as maps describing how a dependent variable varies when the independent variable is changed. The same relation, according to the semantic view, exists between a theory and the world. The mapping is done by using models, which, however, have no influence on how the mapping is done; "the laws of the theory do not specify the mapping relation" (Suppe 1989, p. 4). This again shows that the theory is independent of its application.

Different views about the character of the mapping relationship exist in the literature. Van Fraassen required the abstract system to be isomorphic to the real word. The requirement of isomorphism is strong. According to Van Fraassen it means that between a model and the world exists a "total identity of structure"(Van Fraassen 1980, p. 43). This means, for example, that the predator-prey equations by Volterra, which can be plotted in a coordinate system, has to be in total identity with actual predator-prey populations. This was hardly the case. Ecologists used the equations merely as starting points in their analysis of population dynamics.

Van Fraassen claimed that for a theory to be true there has to be an "exact correspondence between reality and one of its models" (Van Fraassen 1980, p. 197). On page 68 in the same book he said that to have a true theory is "to have a model which is a faithful replica, in all detail, of our world". The conditions for the truth of a theory seem to be very stringent in this account. (Perhaps this is the reason for Van Fraassen's anti-realism.)

According to him, for scientists to accept theories they do not have to be true, merely empirically adequate in that they describe correctly what is observable. For example, if we arrive at correct predictions from predator-prey models we deem the equations empirically adequate, although they might not have been true if we had interpreted them literally. This, according to Van Fraassen, does not have to bother scientists.

Suppe claimed that even Van Fraassen's conditions for empirical adequacy cannot be met because theories are abstractions (Suppe 1989, p. 102). He asked how abstractions could be faithful replicas of the world if they never really covered all the complexities of nature. Suppe's conditions for empirical truth of a theory require that the intended scope of a theory has to be phenomena which form natural kinds, a natural grouping in nature (Suppe 1989, p. 98), which does not necessarily follow from Suppe's version of the semantic view. It illustrates Suppe's commitment to science finding out about the true divisions of nature. On the other hand, Suppe admitted that he did not think that theories have to be interpreted literally. (Suppe called his position quasi-realism because he thought it is realistic in spirit. However, it contains the anti-realistic element of theories as not being literally construed (Suppe 1989, p. 101).)

A different version of the mapping relationship was given by Giere (1984) who agreed with Suppe that theories are not to be interpreted literally. Giere also rejected the notion that models has to be isomorphic to the real world because of the abstractions involved in theory construction. Giere suggested that the relation between theories and the world is one of similarity (Giere 1984, p. 81). (He dubbed his version of the semantic view 'constructive realism': constructive, because the models, as Giere claimed, were social constructions; realism because he believed that models are representations of a reality independent from our representations of it).

So far the discussion of the semantic view allows us to interpret the debate about equilibrium as a question about which models fit nature. This is consistent with what scientists say. Wolda and Dennis (1993, p. 589) wrote that to test for equilibrium is to make a "data-based choice between two models". This is an important step in the analysis of equilibrium. But, as the discussion about mapping shows, it leaves several questions unanswered. Here, I do not mean questions regarding realism: it is doubtful that those can ever be solved. Instead, I mean questions about the justification of the equilibrium concept.

Justification, negotiation, and the semantic view

The semantic view gives an accurate description of equilibrium as an abstraction, but there are ambiguities in how the abstraction relates to the world according to the interpretations of the semantic view by Van Fraassen, Suppe, and Giere. Three different accounts of 'equilibrium' are possible according to these interpretations. Following Van Fraassen we should interpret 'equilibrium' literally, saying that $\beta<1$ in the model by Pollard et al. constitutes equilibrium but if the model fits what is observed, this does not mean that density-dependence really occurs in nature, only that the equilibrium model best describes the phenomena. According to Suppe's interpretation, the models are idealizations which somehow fit, but that we do not have to interpret $\beta<1$ literally as constituting an equilibrium. Thus, we should not talk about density-dependence. Giere would say that the models with density-dependence exhibit the causal structure of the phenomena. What exactly in the model corresponds to the causal structure? Does $\beta<1$ correspond to the causal structure, and if so, does it justify our density-dependence assumption? However, we know that this interpretation is not tantamount to saying that populations are regulated in Nicholson's sense by density-dependent mechanisms.

I agree with Churchland's claim that, seen in isolation, the semantic view "takes theories even farther into Plato's heaven, and away from the buzzing brains that use them" (Churchland 1990). Churchland, like Giere, interprets theories as representations and connects the investigation of representation with a study of the human brain. Thus, his remark about buzzing brains is meant literally.

I follow a different strategy, connecting the semantic view with a historical account of the justification of equilibrium. What is lacking in the interpretations of the semantic view just discussed is the context in which the models were developed. The modeling of equilibrium is part of a larger research strategy. Density-dependence tests are not testing equilibrium right away but are one step in the modeling of population dynamics.

The semantic view provides part of an account of justification and it indeed suggests the inclusion of several elements of justification. Because it implies a separation of theories from their applications, it underlines the importance of understanding how scientists apply them. For this reason an analysis of the negotiations of theories is necessary. The semantic view, more than the positivistic view, encourages an analysis of what scientists want to use theories for. Suppe, Van Fraassen, Giere, and Cartwright all acknowledge the importance of scientific practice in justifying scientific theories; Cartwright (1983, p. 13) claimed that fundamental theories have to be corrected all the time by "the applied physicist or the research engineer". This correction has to be part of an account of justification.

I call the exchange of arguments between Turchin and the critics of the equilibrium approach *negotiation* because it concerns the relationship between evidence and claims about equilibrium. I focused on arguments by Turchin because I believe his approach is typical of modern scientific data analysis. Turchin suggested a new way of thinking about equilibrium, new because the statistical equilibrium is not necessarily Nicholsonian and because the relation between theory and the data is discussed and interpreted in a different way than before. Furthermore, the negotiation is about the justification of claims about equilibrium. It provides reasons to hold on to the equilibrium framework: to model population dynamics. Equilibrium in its new form has important diagnostic value. Understanding the new modeling is possible only if seen in its historical context. Otherwise the change in reference is undetected. How important the change in justification is can be seen by looking at how it affects which phenomena are investigated by ecologists.

The effects of the new reference

To understand the importance of the change in justification, I will focus on the new reference of equilibrium chosen by Turchin. I interpret his modeling approach in a larger context of his research strategy. Why is it important to use density-dependence tests that tell us whether $\beta<1$, as in the models by Pollard et al. (Pollard, Lakhani et al. 1987)? Modeling of density-dependence has to be understood by describing the effects of time-series modeling on the grouping of the phenomena to be investigated.

Time series modeling creates new groupings

The time-series approach made the comparison of very disparate phenomena possible. Weigend (1994) described how data from different origins could be treated with the same analysis. In the "Santa Fe Time Series and Prediction and Analysis Competition", data from physics labs, physiological data from patients with sleep apnea, high-frequency currency exchange rate data, and J.S. Bach's final (unfinished) fugue from *The Art of the Fugue* were grouped for the same analysis (Weigend 1994). With the aim of analyzing the data in the best possible way, different models were tested and it was determined which one made the best predictions about a data set. This was similar to a test of density-dependence, just that the data came from very heterogeneous sources.

The effect of the new grouping of time series phenomena is that equilibrium is not discussed in terms of populations alone. The boundaries between phenomena are drawn in a different fashion, as data from physics or medicine can be analyzed collectively. It is also the case that phenomena from the same origin might be seen as very different. For example, the similarity between two data sets from two populations might be smaller than the similarity between two data sets from a population and a medical chart. Another example is the data set of a regulated population which is more similar to rainfall data from Barro Colorado Island in Panama than to a non-regulated population. This is a novel grouping of phenomena that presumably never would have occurred to Nicholson.

What does the new grouping tell us?

Turchin compared the rainfall data from Barro Colorado Island to the fluctuations of the Dow Jones Industrial Average between March 1993 and September 1994. The rainfall data was regulated, whereas the Dow Jones Industrial average was not. Turchin concluded that the stock exchange is a "non regulated system" and the earth climate a "regulated system".

This seems misleading to me. Perhaps during another time period or over a longer time span the Dow Jones would fluctuate around a mean value or the rainfall data for another location in a certain period would perform a random walk. Would we then conclude that the first system is bounded and the latter is unbounded? Is it permissible to make inferences from the time series about the behavior of a whole system, of which the time series forms a part? Can one system not incorporate regulated and non regulated dynamics at once? A case in point is the data illustrated in Figure 19, a race chart of the American baseball league (east). The figure shows the development of competing baseball teams throughout the months from April until August 1998. The value of 500 on the ordinate means that the team has the same number of wins and losses. The plus or minus values indicate either more wins than losses or more losses than wins. I chose the example because, according to Turchin's definition of regulation, the figure shows two systems of regulated dynamics and three of non-regulated dynamics. The teams of Baltimore and Toronto are regulated, whereas New York, Boston and Tampa Bay are not regulated since their dynamics are not stationary.

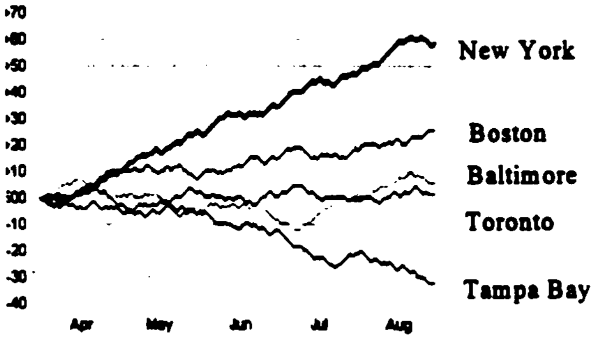


Figure 19: Race chart of the American league east from August 1998, taken from (http://espn.sportszone.com/mlb/standings /index.html).

We could ask further whether the successive values of each team are correlated. Does the performance of a team in August allow any predictions regarding the performance in September or October? Are there any periodic dynamics? The actual analysis should be left to the domain of sports analysts and I do not doubt that interesting patterns could be observed. My point, however, is that the system "Baseball league" can exhibit regulated or non-regulated dynamics. Thus regulation is not a characteristic of a certain system but is a characteristic of a certain set of numbers, which either returns to a mean or does not. Unless we do not know already if the whole system is regulated, it seems impossible to judge from the time series data whether they are part of a regulated system or not. Statistical regulation in Turchin's sense is a statistical property of time series. Making inferences from a times series to the system that it contains overstates the possibilities of the time series diagnostic.

Admittedly the notion of 'system' is vague. We could, of course, describe a time series as a system and then make assumptions about a system, given the time series data. For example, we could say that the time series of Toronto in the above example forms a system, but then what if Toronto suddenly started continuously losing? The time series would no longer be regulated. In his claim about the regulation of rainfall Turchin seems to have a more encompassing definition of system in mind. He does not seem to pay tribute to the new boundaries that are erected by the time series methodology, which do not allow statements about larger systems but describe patterns in time series data. Turchin's claim that a short time series of fluctuations of the Dow Jones index allows inferences concerning the system stock exchange seem to be overly ambitious. Time series methodology allows for a different way of individuating phenomena. On the other hand, time series analysis also prohibits certain forms of individuation, ways or guidelines by which phenomena are singled out. If we find a stationary probability distribution of a population, certain statements can be made and further tests are necessary. But it cannot be said that a population is in ecological equilibrium, and it cannot be said that the system of which the population is a part is regulated.

Data mining

Turchin's analysis gives important insight into the task of the modern ecologist. A recent article in the *American Scientist* begins: "[o]ne of the most important parts of a scientist's work is the discovery of patterns in data. Yet the databases of modern science are frequently so immense that they preclude direct human analysis. Inevitably, as their methods for gathering data have become automated, scientists have begun to search for ways to automate the analysis as well"(Brodley, Lane et al. 1999, p. 54). The process Brodley et al. are referring to is data mining, the strategy many scientists, and not exclusively ecologists, are using to describe nature. The new definition of 'density-dependence' and 'equilibrium' is part of the approach to data mining and is framed in those terms.

Conclusion

The new equilibrium concept makes sense only if it is understood in the context of the general research strategy of data mining. This development has led to the point that equilibrium is defined as a model of the form $x_{i+1} = r + \beta x_i + e_i$ in which $\beta<1$ fits the data. Have we lost equilibrium while searching for it? I claim that the testing of equilibrium indeed has led to its redefinition and to a deconstruction of the old equilibrium concept, and that this can be seen in the new reference of 'equilibrium'.

Detecting the change in reference is important because it leads to a new justification of equilibrium, resulting in a shift in what phenomena are investigated by ecologists. This process, however, is negotiated. Thus, ecologists like Wolda and Dennis argue against the new definition of equilibrium and oppose the new grouping of phenomena. The discussion among scientists, moreover, is rarely in those terms. The complexities of research strategies, interests, relation of theory to data are usually ignored although often the disagreements about equilibrium are rooted in those complexities. An account of equilibrium in terms of its justification helps to focus on the issues at hand and describes scientific activity as a social negotiation process allowing the existence of hard data that are not the fabrication of scientists but are not simply observed either.

Chapter 7: Conclusion; the status of equilibrium

In this thesis I claim that the justification of equilibrium has changed over time and that this change is relevant for an understanding of the concept. This concluding chapter will focus on justification as a historical and philosophical concept and what it can contribute to the debate about the equilibrium concept in population ecology.

The assumption of a balance in nature was imported from physics and chemistry where several definitions of equilibrium exist. I described the definitions and claimed that the concept of equilibrium in physics and chemistry plays a role in explaining mechanisms associated with it. For example, in statics and dynamics the equilibrium assumption explains rebounding behavior, in thermodynamics it explains the directedness of energy exchange processes. This power to explain gives the concept theoretical importance which I labeled as 'epistemic value'. The concept helps us to know why certain processes take place.

I investigated the relevance of equilibrium in ecology by discussing different approaches to the concept by two influential ecologists, Elton and Nicholson. Elton regarded the balance of nature as fictitious, whereas Nicholson saw it as a fundamental aspect of nature. The latter saw the equilibrium notion as important to explain regulation in nature. Elton believed in regulatory mechanisms as well; their description was one of his major contributions to ecology, but he made no use of the equilibrium concept to understand regulation. These differences in attitudes towards equilibrium, however, were not only epistemological but ontological as well. Elton regarded nature as too disruptive for the regulatory factors to lead to a balanced state, while Nicholson saw equilibrium as the outcome of density-dependence through intraspecific competition. To accommodate the ontological and the epistemological aspects of equilibrium I used the term 'justification' which describes the reasons ecologists use the equilibrium concept.

One major aspect of Nicholson's approach was his mathematical justification of the balance of nature. He used equations to describe oscillations in nature, an approach not uncommon in biology in the early 20th century. For example, mathematics played an important role in the investigation of balance between predator and prey populations which was important in community ecology. Regarding mathematical justification of equilibrium in populations, I focused on the debate about the logistic curve. It was a controversial description of the growth of organisms and it was later used for populations as well. At the core of the logistic was an interpretation of the factor r, which stood for the growth rate of the population. In the logistic, r was interpreted as declining linearly, which was a simplified description of density-dependence. This provided a starting point for further investigations of the relationship between growth rate and size of a population. Critics argued that the logistic curve was not useful because its experimental validation violated its own assumptions. I showed that an important issue in this debate was the interpretation of r based on different methodologies for estimating population growth. Criticisms of equilibrium, especially Andrewartha's and Birch's, have to be understood in this context.

I included a discussion about mathematical description of growth processes in my investigation of justification. This could be criticized, claiming that the justification of the equilibrium concept using mathematics is a different kind of justification from that described in the chapter on Nicholson and Elton (Chapter 3). Positivistic philosophy of science, for example, which is still influential among scientists, would claim that the justification described in the section on Nicholson belonged to the context of discovery, whereas testing via mathematical models would belong to the context of justification. This view has consequences for a historical view of justification because only the context of discovery would be interesting for a historical analysis, whereas the context of justification has to be judged by the rules of logic. This view seems to be at the core of Sharon Kingsland's statement:

> The history of population ecology is one of a continuing dialectic between mathematician and biologist. The mathematician, trained in the physical sciences, sees equilibrium and uniformity, often at the cost of ignoring individual differences. The biologist, on the other hand, may see individuality; heterogeneity; constant, unpredictable change. The crucial difference between these two points of view is that the first is ahistorical, the second historical (Kingsland 1995, p.207).

The analysis of the mathematical justification of equilibrium, however, shows that mathematics is not ahistorical but subject to discussion and interpretation. Although perhaps the rules of arithmetic will not change over the course of history this does not mean that population biology has any ahistorical aspects. Mathematics had to be used by ecologists and its use defended. This happened with the logistic equation and is still the case with equilibrium, as can be seen in recent discussions about the concept of density-dependence. Creating two contexts is not helpful in analyzing the concept of equilibrium. Justification includes the context of discovery; it is not separable from it.

With the rejection of the division of contexts I also reject the possibility of a priori justification of the equilibrium concept, choosing instead a naturalistic approach. I look at what scientists consider to be a justification rather than at a priori connections between evidence and theory. Discussion about the a priori is ongoing amongst epistemologists and I grant that part of the justification of equilibrium could be construed as resting on a priori grounds, for example concerning some definitions about the models used. However, as the discussion showed, a priori grounds have to be understood in their historical context, which makes the notion of 'a priori' of limited use.

The rejection of the a priori is often brought forward by empiricists. Some ecologists, skeptical about the use of theory in the empirical sciences, argue for strictly empirical justification of the equilibrium concept. However, I have pointed out some inconsistencies in the ecologists' plea for empirical method by describing their confusion about the problem of induction and underdetermination.

Despite the underdetermination of theories, empirical testing of theories should be possible and a good scientific test should determine whether the assumption of equilibrium is justified. I described Giere's norms for scientific testing and applied them to the testing of density-dependence. Although his conditions for a good scientific test are relevant for the justification of equilibrium one has to carefully look at what exactly is tested. The role of the tests in the justification of equilibrium is not as indicated by Giere because a change of reference of the term 'equilibrium' is ignored by Giere. Contrary to earlier usage, testing for density-dependence is now a choice of a model which describes the data set the best.

Equilibrium is represented by a parameter in the model which has a certain value and the model either fits or it does not. The ontological commitment of scientists has switched from density-dependence to stationary probability distribution in the data. I claim that this change indicates a change in justification over time.

My claim about a change in justification is open for criticism based on recent philosophy of science. If I mean by 'change of reference in theories' that subsequent theories each talk about different things, as was emphasized by Kuhn, I presuppose a positivistic philosophy of science in that theories are connected to the world via meaning relations. However, according to a more recent view in the philosophy of science, the semantic view, theories are non linguistic abstract constructs and as such have no meaning at all. They are related to the world through models. According to this view, what I call a 'change in reference' would merely involve choosing a different model to represent equilibrium. This would invalidate my claim that the change in reference implies a change in the justification of equilibrium.

The semantic view indeed describes how ecologists regard the nature of theories, namely relating to the world like a map to a landscape. Abstract models are used in genetics and evolutionary studies, as well as in ecology, and the equilibrium concept has to be regarded as such a model. However, I found that most interpretations of the semantic view describe only a part of the justification of equilibrium because they ignore the historical context in which models are developed. The claim that models are merely abstractions does not prohibit analyzing the change in reference as a part of a change in justification. The change in justification, however, cannot be detected if one merely inquires whether models fit the data.

The historical aspect of justification of the equilibrium concept becomes obvious if one investigates how scientists negotiate the relevance of the models. I examined the case of Turchin whose approach to the equilibrium concept I took as an example of negotiation. He primarily focused on the classification of data sets in the modeling of population dynamics, a process used in other sciences under the name of data mining. It is important to understand this step because classification generates new groupings of phenomena, expressed as time series. Different time series from various origins can be compared and they are separated by their characteristics (such as stationarity) rather than by their origin. Such a shift in research topic and emphasis cannot be understood if it is not seen that a change of reference has occurred, one that has to be investigated as indicating a change in justification.

With 'justification' I describe the reasons scientists give to use the equilibrium concept. These reasons cannot be determined by pointing to the evidence alone (the persistence of populations), or by relying on rules of scientific inference. Both are important but have to be treated together with what I called 'negotiations' as aspects of justification. I focus on how scientists use the evidence and what kind of scientific inference they suggest.

This form of analysis lends itself to a naturalistic approach which was suggested by Quine. His naturalism is criticized by Alcoff and Potter (1993, p. 10) as being individualistic, in that it treats individual brains as scientific agents. This might not do Quine justice, because it could be argued that the evolutionary study of brains need not necessarily be individualistic. Perhaps evolutionary psychology or neuropsychology will discover that our brains are connected and form a large network. Although this is not how neurophysiology is currently done, it does not undermine Quine's argument. However, I agree with Alcoff and Potter that the Quinean approach to naturalization "puts the epistemological cart before the horse" (Alcoff and Potter 1993, p. 10). Quine's understanding of scientific activity is ahistorical, and a consequence of his sometimes realist standpoint. He underestimates the importance of convincing colleagues and the negotiations that scientists have to enter into before they can arrive at a justification.

Not only Quine underestimates the significance of negotiations. Scientists themselves would argue that the change in justification is not as I have described. For example, it could be argued that Turchin's modeling approach merely emphasizes prediction of data sets but does not provide a causal explanation of the data. One could say further that the prediction is one step in a better understanding of density-dependence as it was envisioned by Nicholson. According to this view the change in justification is explained by increased computer power, as for example in a statement by Levin et al. (1997, pp. 334) who wrote: "mathematical and computational approaches to biological questions, marginal a short time ago, are now recognized as providing some of the most powerful tools in learning about nature". In the case of equilibrium, the computational approach refers to computer-aided modeling and to the recent tests for density-dependence which require a high degree of computer power to perform the randomization and bootstrapping procedures. The view by Levin et al. has to be taken seriously because it seems to reflect what Turchin had in mind with his interpretation of the equilibrium concept. He admits that statistical equilibrium is not ecological equilibrium and that he is interested in ecological equilibrium, claiming that the analysis of data sets will eventually lead to a causal explanation of density-dependence. For many ecologists (for example, Levin et al.) the increasing use of statistics is a simple matter of improved methodology. What do we then make of the change in justification?

To answer this I will explore the claims that Turchin merely predicts or describes equilibrium rather than explains it and that the statistical tests are tools in the detection of equilibrium in nature. Although I agree that Turchin does not tell why populations are in equilibrium, the terms causality and explanation are highly debated in the philosophy of science. One could argue that the new use of equilibrium is explanatory in that it unifies by applying to more phenomena than before, and not only to the dynamics of populations, unification being one characteristic of scientific explanations. About causality, one could claim that theories do not causally explain anyway, as van Fraassen (1980) pointed out, but are appropriate descriptions in the right context. One could also say that the fitting of models is explanatory. The data fitting the density-dependence model behave in a way expressed by the equation (Chapter 5, model 3) in which $\beta < 1$. The models then describe possible state transitions which show how a system could behave in a certain state at a certain time. According to Suppe (1989), in showing how a system would behave we have given an explanation. Suppe does not aspire to give a philosophical account of explanation, and his view sounds, indeed, as if a description of a system could serve as an explanation.

It is imaginable that scientists would answer the question: "why is this population in equilibrium?" by pointing to a stationary probability distribution even though this equilibrium is a statistical one. Chaos theory uses patterns in the data as explanatory and it does not explain any underlying features of the dynamics. Rather, it provides a graphical description of the dynamics, trying to find order in seemingly chaotic data sets (Pickering cites Kellert on this issue 1995, p. 24). My point is that Turchin's predictive strategy does not imply that an explanation remains to be found: scientists could settle for a prediction which could then take the place of an explanation.

This perspective also questions the claim that tests for density-dependence are just tools in the investigation of equilibrium. The tool-metaphor suggests instrumentalism regarding the statistical tests for density-dependence. However, the tests are more than mere instruments to get closer to the original question. Tools, one would think, do a job and then can be put back into the toolbox. The statistical tests for density-dependence, however, have modified the question they were developed to answer. The importance of such instruments in the justification of scientific statements has been emphasized by sociologists of science such as Pickering, who emphasize the performative aspect of scientific activity (Pickering 1995, p. 21). This means that computers, models, and statistical tests are chosen for a reason. Scientists could use other approaches to equilibrium but they think that statistical tests are helpful. Using these instruments, they keep having to adjust them as I have shown by discussing the statistical tests. This fine tuning of the tests develops its own dynamics and eventually leads to the observed change in ontological commitment. The scientific tests and electronic data processing are not merely tools but formative elements in the justification of the equilibrium concept.

The testing, however, is only one of several aspects in the dynamics of justification. Other factors worth investigating are, for example, funding politics or institutional frameworks. The social relevance of increasing emphasis on the prediction of population dynamics rather than their causal investigation is also an important aspect. This suggests that my inquiry into justification is pluralistic since it avoids determinism in explaining the choice of scientific concepts, which makes it difficult to state necessary or sufficient conditions for being justified as it is attempted by epistemologists.

Philosophers and sociologists of science have aimed at explanation, and focusing on the kind of justification I am suggesting might not lead to considerable progress in this regard. Explanation as a questionable goal for the analysis of science was mentioned by

Bruno Latour (1988), and although I will not follow his account of explanation, I think that an investigation into the justification of the equilibrium concept provides important insight if it is regarded as a route to understanding rather than a route to explanation.

I refer to 'understanding' rather than 'explanation' because the former comes from within whereas a causal explanation suggests to me that I can transcend the field of science and look at it from a privileged vantage point. I do not think this is possible. I do not claim to be able to explain all of a scientist's motives or his or her intellectual development. Rather I have tried to see things from the scientists' angle and then perform an analysis (one not usually done by scientists themselves) to attempt to understand why they used the equilibrium concept, and why they developed it in the early days of ecology. These efforts to understand equilibrium then included an analysis of why the justification of equilibrium has changed.

To clarify my use of 'understanding', I consider my study as a psychoanalysis of equilibrium imagining equilibrium as a patient with an identity crisis. The psychoanalyst tries to understand the patient in that he or she takes the patient seriously. This involves an analysis of justification, in which the patient is asked why he /she feels the way he /she does. If the patient thinks he/she is Napoleon then the analyst has to understand what the justification of this assumption is. The analyst does not really believe that the patient is Napoleon but has to take seriously the justification that the patient offers .

Justification and history

The psychoanalysis of equilibrium includes an investigation into its history and the arguments scientists use to justify it. Thus, my approach depends on a connection between history and philosophy of science and I argue that history matters. First, I claim that a change in reference in the concept of equilibrium has occurred. My second claim is that this change is important because it points to a change in justification of the concept, which is not noticeable if one only focuses on the present. Justification combines several elements and its analysis helps to understand what scientists focus on in the world and how they judge the available evidence.

The historical nature of justification deserves emphasis because it has been debated in science studies for a long time: how can scientific knowledge can be granted a historical context without undermining the possibility of knowledge in general (as pointed out by the sociologist of science Karl Mannheim in the 1930s)? To resolve this, philosophers and historians of science have taken refuge in dichotomies to either allow history a role in science or to disregard it. I have mentioned the division between a priori and a posterior in Kingsland's view of the history of population ecology and I have argued that the use of mathematical reasoning does not make the justification of the equilibrium concept a priori. The positivists' (and some present epistemologists') version of justification reduced history of science to the context of discovery which was marginal for the development of scientific concepts. Another strategy to create a history/science dichotomy is to postulate some form of essentialism; equilibrium in nature has to be distinguished from its mere appearance, the stationary probability distribution being the appearance of equilibrium. This view is not helpful in the case at hand because the change in reference constitutes a change of research object, with equilibrium in nature possibly disappearing from the agenda.

Kuhn (1970) uses a historical dichotomy between normal and revolutionary science, the latter introducing a paradigm shift. He emphasizes a change in meaning, but I question his positivistic assumption that theories are connected to the world via meaning relations. My account uses the semantic view of theories to describe the relation between theories and the world. Although I describe the change in reference of the models as important, I only regard this as an indication of a change in justification.

Additionally, I cannot detect a revolution in the development described for the equilibrium concept. The change in justification of equilibrium is the result of historical processes which are gradual changes. This image of history is expressed by the poet Anne Michaels in her book *Fugitive Pieces*: "Nothing is sudden. Not an explosion - planned, timed, wired carefully - not the burst door. Just as the earth invisibly prepares its cataclysms, so history is the gradual instant" (p. 77). The idea of scientific revolutions mythologizes the dynamics of science rather than leading to understanding.

The gradual historical aspect of science needs emphasis but I think its advancement is not only the task of historians of science. During the last decades the horizon of justification has opened up and many approaches to the sciences have been developed, so much so that the interdisciplinary project of science studies has developed its own disciplines with the academically necessary creation of boundaries. However, some philosophers have attempted to include a historical approach in their philosophy of science (especially Cartwright 1983; Hacking 1983). In focusing on justification I have tried to approach the concept of equilibrium from an angle that borrows from many disciplines in an attempt to further the understanding of equilibrium as a concept and its relevance for the dynamics of science in general.

Bibliography:

Alcoff, L. and E. Potter (1993). Introduction: When feminisims intersect epistemology. In: *Feminist epistemologies.* L. Alcoff and E. Potter, (eds.) New York, Routledge: 1-14.

Allen, G. E. (1991). Old wine in new bottles: From eugenics to population control in the work of Raymond Pearl. In: *The expansion of American biology.* K. R. Benson, J. Maienschein and R. Rainger, (eds.) New Brunswick, Rutgers University Press: 231-261.

Andrewartha, H. G. (1957). The use of conceptual models in population ecology. *Population studies: animal ecology and demography*, Cold Spring Harbor, Long Island Biological Association: 219-231

Andrewartha, H. G. (1961). *Introduction to the study of animal populations.* Chicago, University of Chicago Press.

Andrewartha, H. G. and L. C. Birch (1954). *The distribution and abundance of animals.* Chicago, University of Chicago Press.

Beatty, J. (1980). Optimal-Design models and the strategy of model building in evolutionary biology. Philosophy of science **47** : 532-561.

Begon, M., J. L. Harper, et al. (1990). *Ecology.* Boston, Blackwell Scientific Publications.

Bensaude-Vincent, B. and I. Stengers (1996). *A history of chemistry.* Cambridge, Harvard University Press.

Berryman, A. A. (1991). Stabilization or regulation: what it all means! Oecologia **86** : 140- 143.

Berryman, A. A. (1992). The origins and evolution of predator-prey theory. Ecology 73 (5): 1530 -1535.

Birch, L. C. (1948). The intrinsic rate of natural increase of an insect population. Journal of animal ecology **17** : 15-26.

Borsellino, A. (1979). Vito Volterra and contemporary mathematical biology. *Vico Volterra Symposium on mathematical models in biology*, Rome, Springer Verlag: 410-417

Box, G. E. P., W. G. Hunter, et al. (1978). *Statistics for experimenters.* New York, John Wiley & Sons.

Box, G. E. P. and G. M. Jenkins (1969). Some recent advances in forecasting and control. Part 1. Applied statistics **17** : 91-109.

Box, G. E. P., G. M. Jenkins, et al. (1994). *Time series analysis.* Englewood Cliffs, N.J., Prentice Hall.

Brodley, C. E., T. Lane, et al. (1999). Knowledge discovery and data mining. American Scientist **87** (January-February): 54-61.

Brown, T. L. and J. R. H. E. LeMay (1981). *Chemistry.* Englewood Cliffs, Prentice-Hall Inc.

Bulmer, M. G. (1975). The statistical analysis of density dependence. Biometrics **31** : 901- 911.

Campbell, R. (1994). The virtues of feminist empiricism. Hypatia **9** (1): 90-115.

Carnap, R. (1966). *Philosophical foundations of physics.* New York, Basic Books Inc.

Cartwright, N. (1983). *How the laws of physics lie.* Oxford, Clarendon Press.

Cartwright, N. (1994). The metaphysics of the disunified world. PSA **2** : 357-364.

Caswell, H. (1988). Theory and models in ecology: a different perspective. Ecological Modelling **43** : 33-44.

Chitty, D. (1996). *Do lemmings commit suicide?* Oxford, Oxford University Press.

Churchland, P. M. (1990). On the nature of theories: a neurocomputational perspective. In: *Scientific theories.* C. W. Savage, (ed.) Minneapolis, University of Minnesota Press: 59-101.

Cole, L. C. (1954). The population consequences of life history phenomena. The quarterly review of biology **29** (2): 103-137.

Collins, J. P. (1986). Evolutionary ecology and the use of natural selection in ecological theory. Journal of the history of biology **19** (2): 257-288.

Considine, D. M. (1995). Equilibrium. In: *Van Nostrand's scientific encyclopedia.* NewYork, Van Nostrand Reinhold.

Cox, D. (1979). Charles Elton and the emergence of modern ecology. Ph.D Thesis: Department of Biology. Saint Louis, Washington University.

Crowcroft, P. (1991). *Elton's ecologists.* Chicago, University of Chicago Press.

Dayton, P. K., M. J. Tegner, et al. (1992). Temporal and spatial patterns of disturbance in a kelp forest community. Ecological Monographs **62** (3): 421-445.

Den Boer, P. J. (1969). Spreading of risk and stabilization of animal numbers. Acta biotheoretica **18** : 165-194.

Den Boer, P. J. and J. Reddingius (1996). *Regulation and stabilization paradigms in population ecology.* London, Chapman &Hall.

Dennis, B. and M. L. Taper (1994). Density dependence in time series observations of natural populations: estimation and testing. Ecological Monographs **64** (2): 205-224.

Dublin, L. L. and A. J. Lotka (1925). On the true rate of natural increase. Journal of the American Statistical Association **20** : 305-339.

Duhem, P. (1954). *The aim and structure of physical theory.* Princeton, Princeton University Press.

Eisenberg (1966). The regulation of density in a natural population of the pond snail, *Lymnea elodes.* Ecology **47** : 889-906.

Elton, C. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. British journal of experimental biology **2** : 119-163.

Elton, C. (1927). *Animal ecology.* New York, The Macmillan Company.

Elton, C. (1930). *Animal ecology and evolution.* Oxford, Oxford University Press.

Elton, C. (1938). Animal numbers and adaptation. In: *Evolution - Essays on the aspects of evolutionary biology.* G. R. Beer, (ed.) Oxford, Clarendon Press: 127-137.

Elton, C. (1942). *Voles, Mice and Lemmings.* Oxford, Clarendon Press.

Elton, C. (1955). Natural control of animal populations. Nature **176** (4479): 419.

Elton, C. (1958). *The ecology of invasions by animals and plants.* London, Methuen and Co.

Elton, C. S. (1949). Population interspersion: an essay on animal community patterns. Journal of Ecology **37** (1): 1-23.

Elton, C. S. (1966). *The pattern of animal communities.* London, Methuen and Co Ltd.

Elton, C. S. and R. S. Miller (1954). The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. Journal of Ecology **42** (2): 460-496.

Elton, C. S. and M. Nicholson (1942). The ten year cycle of the lynx in Canada. Journal of animal ecology **11** (2): 215-244.

Foucault, M. (1976). La politique de la sante au XVIIIe siecle. In: *Les Machines a Guerir.* M. Foucault, B. Barret-Kriegel, A. Thalamy, F. Beguin and B. Fortier, (eds.) Paris, Institut de l'Environment.

Fox, D. R. and J. Ridsdill-Smith (1995). Tests for density dependence revisited. Oecologia **103** : 435-443.

Gaston, K. J. and J. H. Lawton (1987). A test of statistical techniques for detecting density dependence in sequential censuses of animal populations. Oecologia **74** : 404-410.

Giancoli, D., C. (1985). *Physics.* Englewood Cliffs, Prentice Hall Inc.

Giere, R. N. (1984). *Understanding scientific reasoning.* New York, Holt, Rinehart and Winston.

Giere, R. N. (1988). *Explaining Science.* Chicago, University of Chicago Press.

Golley, F. B. (1993). *The history of the ecosystem concept in ecology.* New Haven, Yale University Press.

Gotelli, N. J. (1995). *A primer of ecology.* Sunderland, Sinauer.

Griesemer, J. R. (1992). Niche: historical perspectives. In: *Keywords in evolutionary biology.* E. Fox Keller and E. A. Lloyd, (eds.) Cambridge, Mass., Harvard University Press: 231-240.

Hacking, I. (1983). *Representing and intervening.* Cambridge, Cambridge University Press.

Hagen, J. B. (1992). *An entangled Bank.* New Brunswick, Rutgers University Press.

Hajnal, J. (1957). Mathematical models in demography. *Population studies: animal ecology and demography*, Cold Spring Harbor, Long Island Biological Association: 97-103

Hall, C. S. and J. W. Day (1977). *Ecosystem modeling in theory and practice.* New York, John Wiley & Sons.

Hanski, I. and M. Gilpin (1991). Metapopulation dynamics: brief history and conceptual domain. In: *Metapopulation Dynamics.* I. Hanski and M. Gilpin, (eds.) London, Academic Press: 3-16.

Hanski, I., I. Woiwood, et al. (1993). Density dependence, population persistence, and largely futile arguments. Oecologia **95** : 595-598.

Harding, S. G. (1976). Introduction. In: *Can theories be refuted.* S. G. Harding, (ed.) Dordrecht, D. Reidel: IX-XXI.

Hempel, C. G. (1966). *Philosophy of natural science.* Englewood Cliffs, Prentice-Hall, Inc.

Hempel, C. G. (1993). Empiricism in the Vienna Circle and the Berlin Society For Scientific Philosophy. Recollections and Reflections. In: *Scientific philosophy: origins and development.* F. Stadler, (ed.) Dordrecht, Kluwer Academic Publishers: 1-9.

Hilborn, R. and M. Mangel (1997). *The ecological detective.* Princeton, Princeton University Press.

Huffaker, G. B. and P. S. Messenger (1964). The concept and significance of natural control. In: *Biological control of insect pests and weeds.* P. DeBach, (ed.) London, Chapman and Hall.

Hutchinson, G. E. (1978). *An introduction to population ecology.* New Haven, Yale University Press.

Israel, G. (1993). The emergence of biomathematics and the case of population dynamics. Science in Context **6** (2): 469-509.

Kendall, M. G. and W. R. Buckland (1971). *A dictionary of statistical terms.* Edinburgh, Oliver & Boyd.

Kimler, W. C. (1986). Advantage, adaptiveness, and evolutionary ecology. Journal of the History of Biology **19** (2): 215-233.

Kimura, M. (1992). Neutralism. In: *Keywords in evolutionary biology.* E. Fox Keller and E. A. Lloyd, (eds.) Cambridge, Mass., Harvard University Press: 225-230.

Kingsland, S. (1995). *Modeling nature.* Chicago, University of Chicago Press.

Kitcher, P. (1984). 1953 and all that: a tale of two sciences. Philosophical Review **93** : 335-373.

Krebs, C. J. (1991). The experimental paradigm and long-term population studies. Ibis **133** (Suppl.1): 3-8.

Kuhn, T. S. (1970). *The structure of scientific revolutions.* Chicago, University of Chicago Press.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist **142** (6): 911-927.

Langley, L. L. (1965). *Homeostasis.* New York, Reinhold Publishing Corporation.

Latour, B. (1988). The politics of explanation: an alternative. In: *Knowledge and reflexivity.* S. Woolgar, (ed.) London, SAGE Publications: 155-176.

Laudan, L. (1990). Demystifying underdetermination. In: *Scientific theories.* C. W. Savage, (ed.) Minneapolis, University of Minnesota Press. **XIV**: 267-297.

Leslie, P. H. (1958). A stochastic model for studying the properties of certain biological systems by numerical methods. Biometrika **45** : 16-31.

Levin, S. A., B. Grenfell, et al. (1997). Mathematical and computational challenges in population biology and ecosystems science. Science **275** (17 January 1997): 334-341.

Levins, R. (1966). The strategy of model building in population biology. American Scientist **54** : 421-431.

Lewontin, R. C. (1991). The structure and confirmation of evolutionary theory. Biology and Philosophy **6** : 461-466.

Lindeman, R. L. (1942). The trophic dynamic aspect of ecology. In: *Foundations of Ecology.* L. Real, A. and J. Brown, (eds.) Chicago, University of Chicago Press.

Lloyd, E. A. (1984). A semantic approach to the structure of population genetics. Philosophy of Science **51** : 242-264.

Lotka, A. J. (1925). *Elements of Physical Biology*. Baltimore, Williams & Wilkins Company.

Maelzer, D. A. (1970). The regression of LOG Nn+1 on LOG Nn as a test of density dependence: An exercise with computer constructed density-independent populations. Ecology **51** (5): 810-822.

Malthus, T. R. (1960). *On population*. New York, Random house.

May, R. (1974). *Stability and complexity in model ecosystems*. Princeton, Princeton University Press.

May, R. M. (1976). Simple mathematical models with very complicated dynamics. Nature **261** : 459-467.

Maynard Smith, J. (1974). *Models in ecology*. Cambridge, Cambridge University Press.

McIntosh, R. P. (1985). *The background of ecology*. Cambridge, Cambridge University Press.

McLaren, I. (1971). Introduction. In: *Natural regulation of animal populations*. I. McLaren, (ed.) New York, Atherton Press: 1-21.

Milán Gasca, A. (1996). Mathematical theories versus biological facts: a debate on mathematical population dynamics in the 1930s. Historical Studies in the Physical and Biological Sciences **26** (2): 347-403.

Mitman, G. (1992). *The state of nature*. Chicago, University of Chicago Press.

Morris, R. F. (1959). Single-Factor analysis in population dynamics. Ecology **40** (4): 580-588.

Morris, R. F. (1963 a). The development of predictive equations for the spruce budworm based on the key-factor analysis. Memoirs of the Entomological Society Canada **No. 31** : 117-129.

Morris, R. F. (1963 b). Predictive population equations based on key-factors. Memoirs of the Entomological Society Canada **32** : 16-21.

Murdoch, W. W. (1994). Population regulation in theory and practice. Ecology **75** (2): 271-287.

Murdoch, W. W. and A. Oaten (1975). Predation and population stability. Advances in Ecological Research **9** : 1-131.

Murdoch, W. W. and S. J. Walde (1989). Analysis of insect population dynamics. In: *Toward a more exact ecology.* P. J. Grubb and J. B. Whittaker, (eds.) Oxford, Blackwell Scientific Publications: 113-140.

Murray, B. G. (1994). On density dependence. Oikos **69** (3): 520-523.

Nicholson, A. J. (1927). A new theory of mimicry in insects. Australian Journal of Zoology **5** : 10-104.

Nicholson, A. J. (1933). The balance of animal populations. Journal of Animal Ecology **2** : 132-178.

Nicholson, A. J. (1950). Population oscillations caused by competition for food. Nature **165** (4195): 476-477.

Nicholson, A. J. (1954 a). Compensatory reactions of populations to stresses, and their evolutionary significance. Australian journal of zoology **2** (3): 1-8.

Nicholson, A. J. (1954 b). An outline of the dynamics of animal populations. Australian Journal of Zoology **2** (1): 9-65.

Nicholson, A. J. (1957). The self adjustment of populations to change. In: *Population studies: animal ecology and demography.* Cold Spring Harbor, New York, The biological laboratory, Cold Spring Harbor, N.Y. **XXII:** 153-173.

Nicholson, A. J. (1958). Dynamics of insect populations. Annual Review of Entomology **3** : 107-136.

Nicholson, A. J. (1960). The role of population dynamics in natural selection. In: *The evolution of life.* S. Tax, (ed.) Chicago, The University of Chicago Press. **1:** 477-522.

Nicholson, A. J. and V. A. Bailey (1935). The balance of animal populations -Part I. In: *Foundations of Ecology.* L. Real, A. and J. Brown, (eds.) Chicago, University of Chicago Press.

Nisbet, R. M. and W. S. C. Gurney (1982). *Modelling fluctuating populations.* New York, John Wiley & Sons.

Odum, E. P. (1983). *Basic Ecology.* Philadelphia, Saunders College Publishing.

Palladino, P. (1996). *Entomology, ecology and agriculture*. Amsterdam, Harwood Academic Publishers.

Pankratz, A. (1983). *Forecasting with univariate Box-Jenkins Models*. New York, John Wiley & Sons.

Pianka, E. R. (1978). *Evolutionary ecology*. New York, Harper & Row.

Pickering, A. (1995). *The mangle of practice*. Chicago, The university of Chicago Press.

Pielou, E. C. (1974). *Population and Community ecology*. New York, Gordon and Breach, Science Publishers Inc.

Pollard, E., K. H. Lakhani, et al. (1987). The detection of density dependence from a series of annual censuses. Ecology **68** (6): 2046-2055.

Potvin, C. and D. A. Roff (1993). Distribution-free and robust statistical methods: viable alternatives to parametric statistics. Ecology **74** (6): 1617-1628.

Provine, W. B. (1971). *The origins of theoretical population genetics*. Chicago, Univesity of Chicago Press.

Putnam, H. (1962). What theories are not. In: *Logic, methodology and philosophy of science*. E. Nagel, P. Suppes and A. Tarski, (eds.) Stanford, Stanford University Press: 240-251.

Quine, W. V. (1953). Two dogmas of empiricism. In: *From a logical point of view*. W. V. Quine, (ed.) Cambridge, Harvard University Press.

Reddingius, J. (1971). Gambling for existence. Acta Biotheoretica **20** (Suppl. 1): 1-208.

Robertson, T. B. (1923). *The chemical basis of growth and senescence*. Philadelphia, J. B. Lippincott Company.

Rosenzweig, M. L. and R. H. MacArthur (1963). Graphical representation and stability conditions of predator-prey interactions. The American Naturalist **XCVII** (895): 209-223.

Royama, T. (1977). Population persistence and density dependence. Ecological Monographs **47** : 1-35.

Royama, T. (1992). *Analytical population dynamics.* London, Chapman & Hall.

Salmon, W. C. (1975). *Space, time, and motion.* Encino, Dickenson Publishing.

Scudo, F. M. and J. R. Ziegler (1978). *The golden age of theoretical ecology: 1923-1940.* Berlin, Springer Verlag.

Scudo, F. S. (1971). Vito Volterra and theoretical ecology. Theoretical population biology **2** (1): 1-23.

Sinclair, A. R. E. and R. P. Pech (1996). Density dependence, stochasticity, compensation and predator regulation. Oikos **75** : 164-173.

St. Amant, J. L. (1970). The detection of regulation in animal populations. Ecology **51** (5): 823-828.

Strong, D. R. (1986). Density-vague population change. Trends in Ecology and Evolution **1** (2): 39-42.

Summerhayes, V. S. and C. S. Elton (1923). Contribution to the ecology of Spitsbergen and Bear Island. Journal of Ecology **11** (2): 214-286.

Suppe, F. (1989). *The semantic conception of theories and scientific realism.* Urbana, University of Illinois Press.

Suppes, P. (1957). *Introduction to logic.* Princeton, D. van Nostrand Company.

Suppes, P. (1967). What is a scientific theory? In: *Philosophy of science today.* S. Morgenbesser, (ed.) New York, Basic Books: 55-67.

Thom, C. E. and M. R. Welford (1994). The equilibrium concept in geomorphology. Annals of the Association of American Geographers **84** (4): 666-696.

Thompson, P. (1989). *The structure of biological theories.* New York, State University of New York Press.

Turchin, P. (1990). Rarity of density dependence or population regulation with lags? Nature **344** (April 12 1990): 660-663.

Turchin, P. (1995). Population Regulation: Old Arguments and a New Synthesis. In: *Population Dynamics: New approaches and synthesis.* N. Cappuccino and P. W. Price, (eds.), Academic Press: 19-40.

Underwood, A. J. (1989). The analysis of stress in natural populations. Biological Journal of the Linnean Society **37** : 51-78.

United Nations (1973). The determinants and consequences of population trends. Population Studies **Series A** (50): 33-63.

Van Fraassen, B. C. (1980). *The scientific image.* Oxford, Clarendon Press.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. Nature **118** : 558-560.

Waldram, J. R. (1985). *The theory of thermodynamics.* Cambridge, Cambridge University Press.

Weigend, A. S. (1994). Paradigm change in prediction. Philosophical Transactions of the Royal Society London A **348** : 405-420.

Wiener, N. (1961). *Cybernetics.* Cambridge, MIT Press.

Williams, D. W. and A. M. Liebhold (1995). Detection of delayed density dependence: effects of autocorrelation in an exogenous factor. Ecology **76** (3): 1005-1008.

Wolda, H. and B. Dennis (1993). Density dependence tests, are they? Oecologia **95** : 581-591.

Wolda, H., B. Dennis, et al. (1994). Density dependence tests, and largely futile comments. Oecologia **98** : 229-234.

Wynne-Edwards, V. C. (1962). *Animal dispersion in relation to social behaviour.* Edinburgh, Oliver and Boyd.

Zeng, Z., R. M. Nowierski, et al. (1998). Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. Ecology **79** (6): 2193-2209.