# 1

# How to Ask Meaningful Ecological Questions

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## Summary

I present and discuss four rules for asking good ecological questions:

*Rule No. 1*. Understand the successes and failures from ecological history but do not let this knowledge become a straitjacket.
*Rule No. 2*. Develop and define a series of multiple alternative hypotheses and explicitly state what each hypothesis predicts and what it forbids.
*Rule No. 3*. Seek generality from your hypotheses and experiments but distrust it.
*Rule No. 4*. If your research has policy implications, read the social science literature about how scientific information and policy decisions interface.

Meaningful questions in population ecology address theoretical issues or management questions that demand a solution. The solution should be looked for among a set of multiple working hypotheses. If you have only one hypothesis with no alternatives, there is nothing to do. The classical null hypothesis in a statistical sense is not an alternative hypothesis in which population ecology is interested. Given a question, the possible outcomes of the study should be noted before any field work is carried out, and an interpretation given of what each possible result means in terms of basic theory or applied management. The most useful questions often have multiple dimensions and apply to more than one taxonomic group. Once you have an important question formulated with alternative hypotheses, you must discuss the critical aspects of the experimental design – replication, randomization, treatments, and controls. How many replicates are needed over what landscape units? How long a study is required? How often do you need to sample? Will the confidence limits of any estimates be narrow or wide? If the proposed steps are not followed, it is possible to get lost in the mechanical details of a study without knowing clearly how the outcome will reflect back on the original questions. Serendipity may rescue poorly conceived studies, but the probability of this event may be less than $P < 0.01$. Management and conservation problems demand both good data and effective policy development. Ecologists need to become more proactive in providing solutions to politicians and business leaders who develop policy options with ecological consequences.

## 1.1 What Problems Do Population Ecologists Try to Solve?

Every ecological question comes down to a question of *population ecology*, and hence it is useful to start by asking how one goes about asking meaningful ecological questions in population ecology. Implicitly the starting point must involve answering the flip question of: How does one avoid questions that yield information that do not help in solving an ecological problem? The first and simplest guide is to look at the historical literature in population ecology, which is littered with questions that have led nowhere in terms of increased understanding of ecological dynamics or improving sustainable land management (Hartway and Mills 2012; Walsh et al. 2012). The second guide must be that a historical search is not sufficient, because it will not tell you about future research questions. Thus, it is possible to make a mistake and to spend time exploring alleys that are dead ends. But it is useful to realize that setbacks are not a scientific defeat because these explorations will show the next generation of ecologists what to avoid. So this advice might be coded as the first rule of asking meaningful questions:

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Companion website: www.wiley.com/go/MurrayPopulationEcology

*Rule No. 1. Understand the successes and failures from ecological history but do not let this knowledge become a straitjacket.*

A simple example will illustrate this point. The management of Northern Bobwhites (*Colinus virginianus*) in the USA involved a controversial issue of whether quail populations could be limited by the lack of water and thus would benefit from managers providing free water, such as a pond, in their habitat. Guthery (1999) examined the competing hypotheses about water limitation and showed that even in southern Texas quail did not need free water to survive and thus that water sources were not required as a management tool. Whether this conclusion will hold under climate change is an important issue for managers in the future.

At a general level, philosophers of science provide a set of guidelines on how to develop general theory. Ask general questions rather than particular ones. General questions will apply to a variety of species and habitats, particular questions will involve only one or a few species in a restricted environmental space. Formulate your research questions as *testable hypotheses*, and if possible develop multiple working hypotheses with *alternative predictions* that are mutually exclusive (Platt 1964; Chapter 2; Chamberlin 1897).

The two major questions that population ecologists address involve the *distribution* and *abundance* of organisms. This focus for population ecology was clearly stated by Charles Elton (1927) and rigorously re-stated by Andrewartha and Birch (1954). Knowing the factors that limit the distribution of an organism can assist in analyzing problems with introduced pests (Urban et al. 2007), as well as giving some indication of how organisms might change their distributions in light of climate change or other anthropogenic stressors like habitat loss (Thomas et al. 2006; Flockhart et al. 2015, Chapter 15). Knowing the factors that affect changes in the abundance of an organism can be even more critical if the species is a keystone in the community or if it is endangered and declining in numbers. It is with these kinds of problems that this book grapples, and as methods of approach are continually improved, we ecologists hope to answer pressing questions more rapidly and more accurately.

We must recognize at the start that population ecologists should not pretend to solve every ecological problem or solve every management question. In particular, ecologists try to answer *scientific questions* and not policy issues. If a songbird is declining in abundance, the job of the population ecologist is to find out why it is declining and to recommend what might be done to reverse the observed decline. Our political systems and society at large make the *policy decisions*, for example the decision either to set aside arable grasslands to protect this bird population or to use the grassland area to produce more crops for human consumption. Ecologists will have strong views about the value of *biodiversity conservation*, and will press for policy decisions that favor biodiversity, but their role as scientists is to make estimates of the probable course of events under policy A vs. policy B. So let us begin with a clear understanding that we ecologists do not run the world and do not make policy, but rather we provide evidence-based recommendations from the science we are able to do. The separation of policy options and research questions is central to this approach to global issues to which ecological data on populations are relevant (Sutherland et al. 2010).

Many ecological questions are posed with no clear connection to population ecology. For example, increasing levels of carbon dioxide ($CO_2$) in the atmosphere are affecting the acidity of sea water and potentially affecting the geochemical carbon cycle (Dybas 2006; Ruttimann 2006; Boyd et al. 2010). On the surface the problem appears to be one for chemical ecologists, but quickly the question become exactly which species of phytoplankton are being affected by changes in seawater acidity, and how this disruption of population growth affects predators or competitors in the community that either feed on the particular phytoplankton species or compete with it for nutrients. Problems of this type, once broken down in a reductionist manner, quickly fall into the basket of population dynamics.

There is a temptation to ask questions about community or ecosystem ecology with the implicit belief that we can reach an understanding of the problem, and in particular to be able to recommend policy alternatives to alleviate the problem, without getting buried in population dynamics. Neither *community ecology* nor *ecosystem ecology* have solved ecological problems without delving into the details of population dynamics to sort out mechanisms. *Macroecology* is also useful for recognizing ecological patterns that require explanations at the level of both community and population ecology (Trebilco et al. 2013; Borrelli et al. 2015).

Given the broad questions about distribution and abundance, there are many more steps that have to be decided before one has posed a good ecological question. The first step is to choose the species of interest. Research priorities may be dictated to you by your employer if you work for a wildlife agency, or may be decided by funding options if you are a graduate student. Financial support would seem to be a major constraint for a new scientist, but in fact there are important and interesting questions to be asked for every species. Important questions are either general questions that apply to many species, or conservation questions that have a direct bearing on management decisions. Important questions always have at least two and possibly three or more potential answers which are not presently known. To confirm potential knowledge gaps, you will have to know the literature on your species and closely related species very well.

Studies of single-species populations could be considered ecological stamp-collecting, but this would be an error. Some species can be considered model organisms whose results can be generalized to many species in their group. Studies of single species are necessary to answer broad questions regarding, for example the types of *numerical responses* predicted by predator–prey theory (Sundell et al. 2013; Bowler et al. 2014). Designing single-species studies to test broad ecological models is an essential way to refine *ecological theory* (Chapters 8–10).

Theoretical ecologists put forward many different models of the ecological universe; some of these are useful and important, while others are irrelevant and unanswerable. The theoretical literature in ecology abounds with concepts like density dependence, competitive exclusion, chaos, resilience, and stability that are potentially useful if they can be defined rigorously and are available for empirical measurement. *Resilience*, for example, is a useful word, but its ecological measurement is fraught with problems (Carpenter et al. 2001; Myers-Smith et al. 2012). Even if a theoretical concept can be measured, it may not have much utility, so it pays a young investigator to ask where the concept leads. A key example is the idea of *direct density dependence* in reproductive and survival rates. The concept is clearly presented in every textbook as the foundation for understanding population changes; the means of measuring it are fairly straightforward for many species, but having done so leads one to a dead end. The concept has the illusion of precision but suffers from two problems. It provides no predictability, so the observed density dependence in one population will not allow one to predict quantitatively the relationship in other populations of the same species (Krebs 2002). The second problem is that it does not define mechanisms that can be manipulated for wildlife management or conservation questions. Without mechanisms like predation, food shortage or disease, managers have no potential levers to use to solve the problems they face. Consequently, demonstrating density dependence in population dynamics is useful only as a first step toward the much more difficult goal of finding mechanisms involving births, deaths, and movements that drive density changes (Strong 1986). Birth rates may not automatically increase (or death rates decrease) as a population declines in abundance, and *Allee effects* may doom some populations to local extinction (Courchamp et al. 2008). Too many ecological concepts lead one to unanswerable questions or questions that once answered have no utility for management or conservation (Peters 1991).

Two major empirical processes stare ecologists in the face at this time in history and should demand our attention – *climate change* and *habitat loss*. Both factors are having and will have major impacts on distribution and abundance and when they are both occurring together, they may be difficult to disentangle. These two processes raise general questions that are applicable to many species: how is global warming changing the distribution of species? Are most geographical distributions limited by climatic factors? Will alpine and subalpine species be driven to extinction? How quickly can a species adapt to temperature shifts? Will top-down systems be affected by climate change? Habitat loss is universal in the era of rising human populations, and the effects of habitat loss and habitat fragmentation are key issues that may have general effects or individual species-specific effects (Stephens et al. 2003; Hanski 2011).

Two aspects of these global problems complicate ecological investigations in this century. First, both problems are strongly affected by human actions. While in past decades ecologists could argue that human influences were relatively minor and large ecosystems were relatively intact over much of the globe, now the rapidly growing human population and the need for resources for human consumption have plundered the natural world and set up new situations for organisms. Thus, the justification that one was studying a system in a *steady state* that was at least, in ecological time, unchanging is now gone. Given these new realities, past observed population dynamics are only an approximate guide to future population dynamics for any particular species. Second, the adaptations that organisms have made to their environment may now be antiquated (Conroy et al. 2011). A confronting example is the lack of anti-predator adaptations in native Australian mammals and birds to introduced predators such as the red fox (*Vulpes vulpes*, Short et al. 2002) or toxic cane toads (*Rhinella marina*). Cane toads were introduced into northern Australia, and because they are toxic to predators, initial concerns were that generalist predators would be devastated by this potential prey species. Fortunately, many species have learned to avoid eating cane toads, and to date, the predicted devastation of the predator guild has been minimal for most species (Shine 2010). Both these aspects mean that ecologists must rely more on empirical studies of our current ecosystems than on predictions based on past observations. One alternative is to rely on predictions from studies on *model species*, with the assumption that the dynamics of the chosen model species is general and applies to all similar species. This alternative assumes a generality of mechanistic understanding that is only slowly accumulating in population ecology. An excellent example is the general observation of strong population declines in migratory species of insectivorous birds (Benton et al. 2002). The associated habitat change has been an intensification of agricultural production, with the presumption that the mechanism involved was food shortage on the nesting ground. The hypothesis of food limitation was tested and rejected for Tree Swallows (*Tachycineta bicolor*, Rioux Paquette et al. 2014), with the suggestion that the responsible mechanism might be operating during migration or on over-wintering sites that are yet unstudied. We do not yet know if these general declines in bird populations have many different causes or whether there is a common mechanism which could then provide a common solution.

There has always been a tension in ecology between those who argue that basic studies of population distribution and abundance are the key to progress, versus others who feel that all of ecology is now a crisis discipline and ecologists should study nothing but solutions to practical management and conservation issues (Fleishman et al. 1999). I doubt that this debate is fruitful, since there is no way of knowing the future needs of biodiversity conservation. There is a pressing need to study immediate conservation and management problems, but there is also a pressing need to develop more general understanding of population dynamics, research that can often be done with abundant species of no great economic value or conservation concern.

## 1.2 What Approaches Do Population Ecologists Use?

The factors limiting geographic distributions of organisms have been well dissected for more than 100 years (Chapter 15), but studies of distributional limitations have become important only since the era of climate change was recognized during the 1980s. *Species distributions* can be difficult to map because they are scale-dependent (Forman 1964; Gaston 1991). The scale dependency of studies of distributions has produced a strange literature of limitations that are contradictory. As a simple example, dispersal abilities may limit a species range at a continental scale, but have little relevance to understanding why species X appears in patch Y but not in patch Z only a few meters away (Kroiss and HilleRisLambers 2014). Given that you have mapped a geographic range at an appropriate scale, the two possible approaches you can take are *observational*, "watch and wait, hope something happens," or *experimental* manipulations. Studies of distributional limitation are hampered by the long time frame needed to see changes and the confounding of human actions, climate change, and organismal adaptations to these changes.

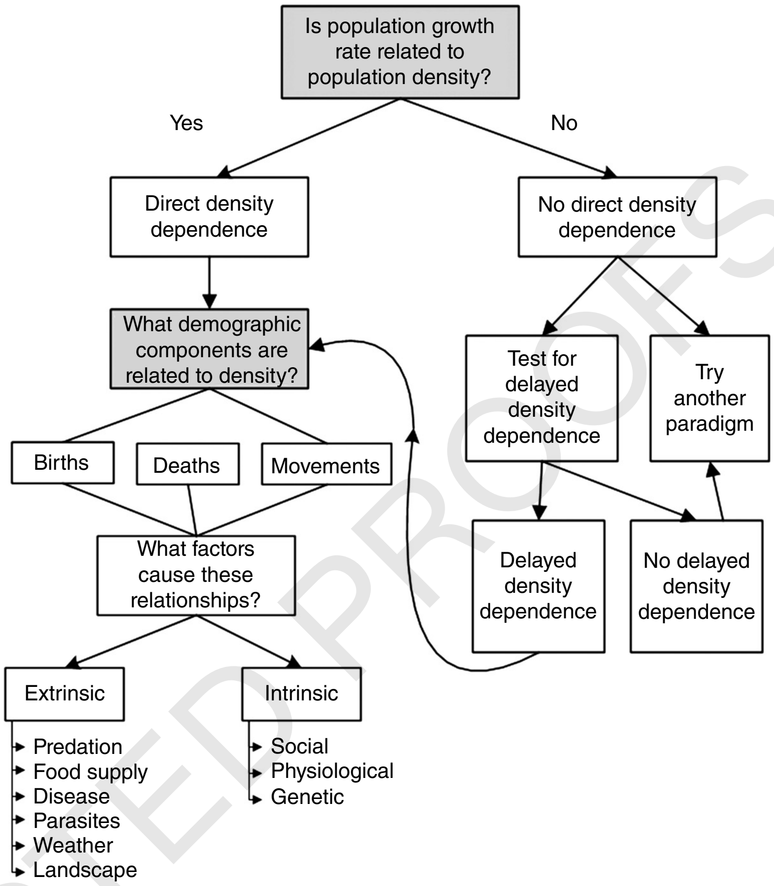
There are more studies of changes in the abundance of particular organisms than studies of distributional limitations. Changes in abundance have been particularly attractive to theoretical ecologists, and we can surmise that the number of models now exceeds the number of empirical studies explicitly designed to test the models (Chapter 5). In general, the theoretical literature has directed population ecologists to two paradigms or two approaches to answering the question of what determines the rate of population growth of species X (Sibly and Hone 2002). I have called these the *density paradigm* and the *mechanistic paradigm* (after Kuhn 1970). If you do not like the word "paradigm" replace it with "approach."

The *density paradigm* instructs us to plot population growth rate against population density. At this point, we should become suspicious because the variables on the X- and the Y-axis are not independent. But we are assured by some biometricians that this is not a problem (Griffiths 1998), so we might forget about this potential problem. If the density data are a time series of one or more plots, much now depends on the trend shown by the data (Chapter 4). If density is monotonically falling (or rising), it will not be possible to estimate an "equilibrium" density, except by assuming independence between points or the use of formal time series methods. If a population does not change much in density, the relationship may well look like a shotgun pattern (Strong 1986). Experimental manipulations of density are needed in many cases.

A *decision tree* illustrates how to proceed (Figure 1.1). If there is a negative relationship between population growth rate and density, the next question is which of the demographic components drive this relationship. Given that data are available to answer this question, the next step is to find out which factors or combinations of factors cause changes in births and deaths, as well as movements if the population is open. All this is what I will call the standard analysis procedure of the *density paradigm*. However, what happens if there is no pattern in the plot of growth rate against density? Does this mean that the population is not subject to density-dependent constraints on growth, or merely that there is too much noise in the data or that there are other factors at play, such as tradeoffs among demographic rates, that obfuscate the relationship?

We are assured by both theoreticians and empiricists that there *must* be a negative relationship between population growth rate and density (Nicholson 1933; Sinclair 1989; Turchin 1999). If this is true, it raises an interesting question of the relationship of theory in ecology to empirical data. If there must be a relationship, the problem of the field ecologist is to describe this relationship in terms of its slope and intercept, and to determine if Allee effects occur at low density. The problem is not to ask if indeed such a relationship exists (Murray 1999, 2000). There is no alternative hypothesis to test.

**Figure 1.1** Decision tree for the density paradigm for explaining changes in population density (after Krebs 2002). The gray boxes indicate the key questions in which the density paradigm differs from the mechanistic paradigm shown in Figure 1.2.



The first strategy that is adopted after finding that there is no relationship between population growth rate and population density is to invoke *delayed density dependence* (Turchin 1990). This is a reasonable strategy because virtually every interaction in population ecology involves some time delays. But this strategy opens Pandora's Box because data analysis begins to take on the form of *data dredging* if we have no a priori way of knowing the duration of the critical time delays. Fortunately, we have independent natural history data for many systems that can set limits for what are biologically reasonable time delays, which permits us to define the limits for time series analyses. There are elegant methods of time series analysis that can be applied to population data to estimate the integrated time lags in a series of density estimates (Stenseth et al. 1998), but it is less clear how to translate these estimated time lags into ecological understanding. Do predators respond to changes in prey abundance quickly via *dispersal movements* (Korpimäki 1994), or more slowly via *recruitment processes* (O'Donoghue et al. 1997; Eberhardt and Peterson 1999)? Data constraints, such as only annual census data, affect our ability to draw biology out of statistics at this point.

If delayed density dependence can be identified in a time series of population densities, we can proceed in the same manner as the standard analysis procedure of the density paradigm, and try to determine what causes these time lags. The remaining problem is what to do with cases in which no direct or delayed density dependence can be identified in a time series. In theory, this situation cannot occur, but it seems to arise frequently enough to cause endless arguments in the literature about the means of testing for direct and delayed density dependence (den Boer and Reddingius 1989; Dennis and Taper 1994). Many ecologists in this situation would not give up studying population regulation, but would switch to the *mechanistic paradigm* discussed by Sibly and Hone (2002).

The *mechanistic paradigm* can be viewed in two different ways. Sibly and Hone (2002) consider it an elaboration of the density paradigm (Figure 1.1), and indicate that one can proceed to this level of analysis for populations that are well studied in a reductionist manner. Note that the key variable in the density paradigm illustrated in Figure 1.1 is always *population density*. Krebs (1995), by contrast, postulated that the key variable should be *population growth rate*, and suggested that the mechanistic paradigm is an alternative to the conventional approach that proceeds via the density paradigm. The mechanistic paradigm

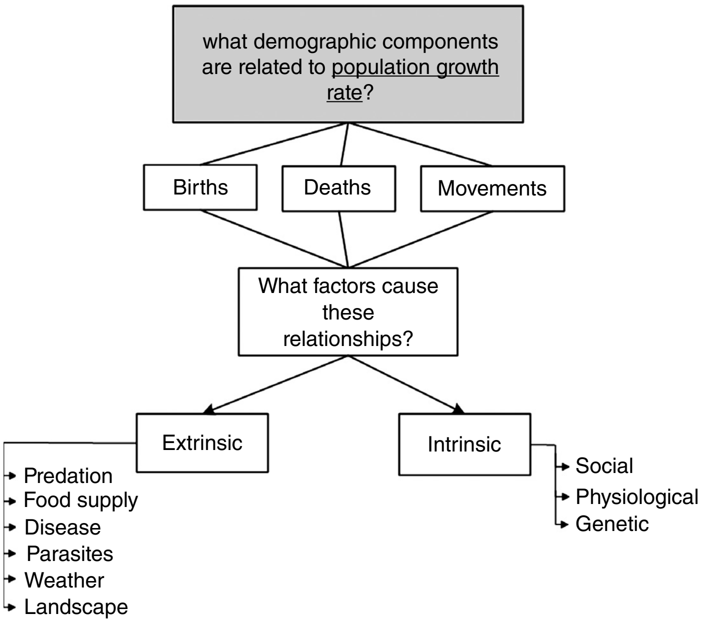


**Figure 1.2** Decision tree for the mechanistic paradigm for explaining population growth rate changes (after Krebs 2002). The gray box indicates the key question in which this paradigm differs from that of the density paradigm shown in Figure 1.1.

short-circuits the search for density dependence on the assumption that no predictive science of population dynamics could be founded on describing relationships between vital rates and population density without specifying the ecological mechanisms driving these rates. Density is not a mechanism but a surrogate for a variety of mechanisms that require study.

The key question seems to be whether or not any density-dependent relationships are repeatable in time or space. I have been able to find few ecologists who have asked this question. For those I have found, none of the studies have shown repeatable patterns in time or space (Krebs 2002) and the explanation for this failure lies in the fact that density is not a mechanism. When density dependence can be found, it is not quantitatively repeatable in space or in time. Both (1998) showed this in his elegant work on populations of Great Tits (*Parus major*) in the Netherlands. Annual mean clutch size in this species declined strongly with density but the regression lines between population density and clutch size differed greatly in his six study areas, probably because of food supplies. The pattern was clear, but the process not. The conclusion I reached was that density-dependent relationships occur often (as most ecologists believe) but are not repeatable (as is rarely tested) and are an unreliable basis for a predictive ecology. Thus, spending valuable research time on showing density dependence is rarely needed and should not be the central focus for solving problem in wildlife management and conservation.

The flow diagram for the mechanistic paradigm (Figure 1.2) is similar to that of the density paradigm (Figure 1.1), but has one significant difference (outlined in gray): instead of asking what demographic components are related to *population density*, it asks which components are related to the *population growth rate*. In cases where density is closely related to population growth rate, there will be no difference between these two approaches. But in every nonequilibrial system, the differences can be large. The critical assumption again depends on whether there is an equilibrium point for the system under study. A mechanistic approach is best adapted to short-term considerations in which questions about ultimate equilibrium states are not particularly relevant or interesting because the world is changing too rapidly. It is closely related to the approach to population dynamics typified by the Leslie matrix (Caswell 2001; Chapter 8), and is particularly well suited to our current ecological situation in which climate change is rewriting many ecological interactions. The mechanistic approach does not concern itself with asymptotic properties, but takes into account the fact that asymptotic properties may not capture transient, short-term dynamics. An example of the use of the mechanistic paradigm is given from our long-term studies of the population cycles of snowshoe hares (*Lepus americanus*) in the Yukon (Box 1.1).

The mechanistic paradigm asks how individual animals are influenced by the factors affecting density, and recognizes that individuals vary in their responses to predators, food supplies, parasites, and weather, as well as in their social standing within the population. Behavioral ecology has made a particularly strong contribution to our understanding of individual differences, and is pushing strongly to utilize this understanding to enrich population dynamics.

Is the mechanistic approach better than the density approach? Both approaches rely on precise estimates of

### Box 1.1 An Example of Hypothesis Development and Testing – The Kluane Project

The Kluane Project began in 1976 as a research program aimed at providing an explanation for the 9–10 year cycles in population numbers of snowshoe hares (*Lepus americanus*) in the boreal forests of Canada. Jamie Smith, Tony Sinclair, and I started the first 10 years of study with the aim of testing the three most likely explanations for the hare cycle – winter food shortage, excess predation pressure, or social interactions. We wanted to test social interactions since this was such an important part of the explanation of the three to four year vole and lemming cycle, and if we could produce a general explanation for both these mammalian cycles, it would be a valuable achievement. Alas it was not to be because we learned very early that snowshoe hares have no social behavior that is of any consequence for population limitation (since they are not territorial and do not commit infanticide), and our hypothesis list was reduced to two likely mechanisms – food shortage and predation mortality. It is critical to note that they was a long history of detailed work on snowshoe hares before we began, particularly by Lloyd Keith and his associates but also by many other ecologists, so we knew much about the natural history of their population fluctuations when we started in 1976. We knew that cycles were regionally (500 km) synchronous, so movements of animals could not be the explanation for increases and declines. Lloyd Keith had shown that hare reproductive rates varied dramatically with the cycle in a delayed density-dependent manner so that the number of litters was reduced from four to two as hares reached peak density and entered the decline and low phase. Everything in the boreal forest eats snowshoe hares – Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), Great-horned Owls (*Bubo virginianus*), and Northern Goshawks (*Accipiter gentilis*) – and if you include the predators of juvenile hares you can add another long list from Gray Jays (*Perisoreus canadensis*), to red squirrels (*Tamiasciurus hudsonicus*) and arctic ground squirrels (*Spermophilus parryii*), and several of the smaller raptors. It was known from the early work of Lloyd Keith, Jerry Wolff, and John Bryant that in some cycles severe overbrowsing of winter shrubs occurred, which could suggest food shortage.

Given all this information, how can one proceed? We first tested the simplest hypothesis of winter food shortage from 1976 to 1985, predicting that if we provided winter food experimentally to specific populations, we could stop the cycle or at least slow it down. We provided commercial rabbit chow to three areas over each winter, and because of a complaint about unnatural high-quality chow for food, we also supplied natural food over three winters by cutting down large trees. We knew from natural history observations that hares devoured white spruce and aspen trees that blew over in wind storms, and spruce needles from tall trees were in fact their favorite winter food in cafeteria tests. The results were unequivocal – adding winter food increased the local hare density by immigration but all the fed grids collapsed at the same time and at the same rate as the control grids with no added food. It took 10 years to establish this, and the suggestion from these results was that we should study predation as a more likely cause of the cycle.

Consequently in 1986 we began the Kluane Boreal Forest Ecosystem Project. The entire project was very much a team effort. In addition to Jamie Smith and Tony Sinclair, we are fortunate to have Rudy Boonstra, Stan Boutin, Susan Hannon, Kathy Martin, Roy Turkington, and Mark Dale on the team, along with many first-class graduate students. We adopted a conventional statistical design of control areas (60 ha) and manipulated areas (100 ha) with the treatments being fertilizer addition (nutrient bottom up), food addition (bottom up), predator reduction (top down) and a combined treatment of simultaneous food addition and predator reduction. Predator reduction involved electric fences around 1 km$^2$ to keep out mammal predators. We attempted to eliminate avian predation with fishing net strung between trees but it was unsuccessful due to snow accumulation. For each treatment we wrote down before the studies were done what the predictions were and what the alternative hypotheses would predict for all the major species in the ecosystem.

The strongest impact on hare densities was achieved by the combined food addition – predator reduction treatment, and we were left after 10 years to try to explain this interaction of food and predation. We had determined by radio telemetry that the immediate cause of death of >90% of all hares was predation, so clearly predation was a critical driver of the mortality component of hare dynamics. But we were puzzled by the interaction with food supplies since food limitation seemed the most likely cause of reproductive curtailment yet at the same time by no other measures could we find evidence of food shortage in hares on control areas.

Rudy Boonstra saved the day by suggesting that reproductive curtailment might arise from stress, with the stressing agent being unsuccessful predator chases. If this was correct, predation could be the cause of both the mortality changes as well as the reproductive changes that occurred to drive the cyclic dynamics. By the 1990s new methods had been developed by physiologists to measure stress levels in individuals by the metabolic breakdown products released in fecal pellets. After much work the stress hypothesis was validated by Michael

Sheriff in 2009 with the important addition that there was a maternal effect of stress – stressed mothers reduced their reproductive rate and also produced stressed offspring, raising the issue of how long stress effects might be passed on from generation to generation by nongenetic means. The end point now is that maternal effects are seen as a potentially critical variable in the population ecology of many vertebrate species.

So all this research over 40 years has validated the hypothesis that predation is the dominant mechanism driving the changes in reproduction and mortality in the snowshoe hare cycle. This abbreviated synopsis is examined in more detail in the book by Krebs et al. (2001) and the publications cited in it. The whole process is neatly summarized in Popper (1963) – conjectures (= hypotheses) and refutations (= testing).

birth, death, and movement rates (Chapters 6, 7, and 13). At present, the bulk of the population literature now favors the density approach, probably because it is simpler to estimate population density with narrow confidence limits than it is to estimate population growth rate. But the question we need to answer is whether or not the density approach has led to a rapid rate of progress in understanding the problems ecologists face, whether of overabundant wildlife or endangered species. Two good examples to investigate the utility of these two paradigms would be the issues of how to conserve polar bears (*Ursus maritimus*; Sahanatien and Derocher 2012), and how to manage overabundant ungulates (Bradford and Hobbs 2008). The mechanistic approach involves much more effort to analyze mechanisms, whether they be predation, disease, food supplies, or weather. I think that we would solve more problems and have less controversy if we adopted the mechanistic approach with clear alternative hypotheses, but only the future will tell if that is correct.

### 1.2.1 Generating and Testing Hypotheses in Population Ecology

Many philosophers of science define science by the *hypothetico-deductive method* (Popper 1963; Mentis 1988; O'Connor 2000). An alternative approach is a completely empirical method often called the *inductive approach*. Induction operates by gathering data and then trying to decipher what they mean. Both the hypothetico-deductive and inductive methods are further discussed in Chapter 2. Hypotheses can be generated after all the data are collected, and further data collection can test these hypotheses. In a sense, all ecologists have been using inductive methods by observing patterns in nature, and certainly one cannot begin any study without some natural history knowledge and some idea of patterns that you wish to investigate. But for many ecological systems the patterns are clear but the explanations are not known. It is at this point that the hypothetico-deductive methods of Popper (1963), Platt (1964), and Chamberlin (1897) become most useful.

Induction is often defended in ecology by the necessity of having information to generate hypotheses. This viewpoint is certainly correct. Without some data or understanding it is impossible to generate hypotheses to explain any ecological problem. Consequently, there is much discussion at cross purposes in ecology about these issues, and the simple advice is: (i) develop a hypothesis, (ii) make some predictions, and (iii) test the predictions. The method of *multiple alternative hypotheses* comes into play here (Chamberlin 1897; Chapter 2). A single hypothesis is quite useless in science and pairing a single hypothesis with the statistical null hypothesis is probably the most common error in ecological science (Anderson et al. 2000). A simple example will illustrate this problem, which appears regularly in graduate student theses. A single hypothesis that a herbivore species is selective in its diet could be tested against the null hypothesis that its diet is completely nonselective. The test would be a complete waste of time since no ecologist on earth would question the idea that all herbivores are selective foragers. But the basic idea could be turned into a set of interesting questions, for example with multiple alternative hypotheses that this species is a generalist or a specialist, that it selects food plants high in protein, or alternatively high in carbohydrates, or alternatively low in feeding deterrents, and whether the diet varies seasonally. The second approach would be informative and predictive of how this herbivore species operates in its foraging universe. And this simple example illustrates how most forage ecologists now operate (Bryant 1981).

*Rule No. 2. Develop and define a series of multiple alternative hypotheses and explicitly state what each hypothesis predicts and what it forbids.*

There are a whole set of assumptions buried in the hypothetico-deductive framework that few ecologists tend to discuss. A list of multiple alternative hypotheses may not include the correct hypothesis or the best fitting statistical model. There is no way to correct for this problem except by having excellent natural history information and knowing the background of studies in your particular field. The optimistic view that ecological science progresses in a linear way toward correct ideas is far from reality. Progress in understanding is slow and

**Box 1.2 Rules of Thumb for Judging Ecological Models**

(1) Compare the number of parameters with the number of data points. When a model uses 10 parameters to fit to a time series of 25 data points, chances are that it can fit almost any 25 data points.

(2) Compare the complexity of the proposed model with the complexity of the phenomenon that it seeks to explain. Often, proposed models turn out to be dramatically more complex than the ecological problems that they seek to solve. If one can state the ecological phenomenon in fewer words than it takes to formulate the model, the theory is probably not useful.

(3) Beware of meaningless caveats confessing oversimplification. Eager for their work to be embraced by ecologists, theoreticians like to conclude that their models are oversimplified. An already complex model that "admits" that there are more mechanisms to be taken into account (read: more parameters) betrays a tendency toward further unjustified complexity

(4) Beware of being given what you expect. As ecologists, we have come to expect that our data will be "messy," and many theoreticians will go out of their way to meet this expectation. One way to make the curves look "less perfect" is to simply add environmental noise and observational error (each variance adding one more parameter). Suspect that rhetoric is at work when models that are fully capable of producing a perfect fit are tweaked to show a more palatable near-perfect fit.

*Source:* Adapted from Ginzburg and Jensen (2004).

shows reverses not infrequently. The most graphic new illustration is the technique of multimodal inference based on *information theory* (AIC [Akaike's Information Criterion] analysis) of alternative statistical models (Anderson et al. 2000; Chapter 2). Anderson and Burnham (2002) discussed four issues that limit the utility of this approach. The four issues include: (i) poor scientific questions, (ii) too many models, (iii) the true model is not in the set evaluated, and (iv) using AIC methods as equivalent to standard statistical tests that use *p*-values. If the number of models exceeds the number of data points, more data are required. We should not think, Anderson and Burnham (2002) argue, that we will find the "true" model or hypothesis but rather one or more models in a set of alternative models that best fit the data. The most important point these authors recognize is to think carefully about the models or hypotheses you wish to test, and define alternative hypotheses as precisely as possible before you gather or analyze data (Chapter 2).

Much controversy in the past has emerged between the view that population ecologists should do *field experiments* versus the view that *observational studies* are equally valid (Diamond 1986). This discussion is of limited use, as the most important item on the agenda is to gather the necessary data that will test a series of hypotheses. In some cases, this can be done only by observational methods; in other cases some experimental manipulation can be carried out. There are many reasons to pick one or the other approach – financial, political, time available – but we must not lose the critical aspect of defining the hypotheses precisely and specifying what data will reject each particular hypothesis.

There is also much discussion in ecology about the value of *simulation models* for testing alternative hypotheses (Aber 1997). Ginzburg and Jensen (2004) pointed out that many mathematical models used in population ecology are overfitted with too many parameters. The authors presented a series of *rules of thumb* for judging ecological models (Box 1.2). Ginzburg et al. (2007) suggest that if a hypothesis (or a model representing that hypothesis) is so general that data cannot be used to test it, the hypothesis or model must be made more specific. Simulation models should contain parameters that can be measured in the real world, and if that restriction is widely accepted, the value of simulation models could be greatly improved (Chapter 10).

## 1.3 Generality in Population Ecology

We search for generality in ecology but are constrained by a series of problems that are not easily resolved. Typically, we assume in our studies some type of spatial and temporal invariance. For example, if nematode intestinal parasites limit density of Red Grouse (*Lagopus lagopus*) in Yorkshire, they should also limit density in Scotland (cf. Redpath et al. 2006; Moss et al. 2010). Moreover, if this idea was correct in 1990, it will also be correct in 2020, or 2120. Ecologists now recognize the role of climate change in affecting populations but tend to avoid discussing all the issues associated with the assumption of spatial and temporal invariance. Because of habitat changes due to agricultural intensification, and habitat loss due to land degradation, the assumption of spatial and temporal invariance is particularly worrisome. This task is further complicated by concerns about how natural selection will affect populations in relation to climate change as well as human land-use change (Henden et al. 2009; Conroy et al. 2011).

*Rule No. 3. Seek generality from your hypotheses and experiments but distrust it.*
For the present, we do not seem to have any recourse for this problem but it has consequences for what population research is to be done. Typically, ecologists do not wish to repeat studies done in the past, which is exactly what we ought to be doing in the face of climate and land-use changes to test the generality of our findings. Funding agencies stress the importance of novel research without acknowledging the value of repetition in space, time, or across study taxa. But in our current situation, ecologists have more questions than we have money or person-power to answer. The answer we have to this problem is to design optimal monitoring programs at a large scale, and there is much discussion of the design of these programs at a regional and national level (Stadt et al. 2006; Lindenmayer et al. 2012). At the level of species distributions, monitoring is clearly effective in detecting spatial and temporal changes (Fujisaki et al. 2008; Snäll et al. 2011; Sullivan et al. 2014, Chapters 12 and 15). Monitoring of cryptic mammals is more difficult and can only rarely be done by citizen groups (Harris and Yalden 2004; Sutherland 2006), although remote networks of camera traps are providing a new approach for achieving monitoring goals (Meek et al. 2014).

*Replication* is an important issue in experimental design, but the conflict here for population studies is that the advice of "use a larger study area" conflicts with the recommendations of statisticians to "take many replicates." If one can take replicates of some experimental study, it is possible to do power analyses to detect what effect sizes can be measured at a given level of replication (Schindler 1998; Johnson 2002; Field et al. 2007), although one must be wary of post-hoc power tests and such assessment is best conducted prior to data collection. In many cases, the ecological needs of a study must trump the statistical needs, and hence the rule "$n = 1$ is better than $n = 0$". In our Kluane Lake experiments (Box 1.1) we could not replicate an experimental treatment that combined an electric fence + food additions because of the financial costs involved. And the standard recommendations to randomize treatments could not always be followed in our project for logistical reasons (Krebs 2010). Replication can be done in space as well as in time.

Meta-analyses are one possible solution to the problems of replication and limited spatial coverage (Stewart 2010). The basic assumption of meta-analyses is that a given hypothesis has been investigated many times by different research groups, and by pooling statistical results we obtain a more precise estimate of the effect size for a given treatment. Problems arise when individual studies utilize different methods of measurement so that the average effect size may be a poor estimate of the correct but unknown effect size. Ecological studies always differ and judgment is required about how similar they must be for pooled effects to be meaningful. Meta-analysis may overestimate effect size because of publication bias due to failure to publish studies with nonsignificant or negative results (Jennions and Møller 2002), or may be biased in favor of the prevalent paradigm (Koricheva 2003). Careful interpretation is required to avoid spuriously precise estimates of effect size (Slavin 1995; Whittaker 2010). Stewart (2010) rejected these criticisms as unwarranted, but Vetter et al. (2013) then evaluated 133 papers that used meta-analyses in biodiversity conservation, and found that few of them were reliable. The authors provided recommendations for improving the use of meta-analyses in ecology. Their warning is still relevant: meta-analyses can be useful if done properly, with the caveat that both the analyses and studies replicated in time are subject to the types of environmental changes that are now under way.

## 1.4 Final Thoughts

Ecological knowledge may be restricted to the scientific literature and read by the academic community, but the implications of findings often are lost when dealing with management issues or the development of policy alternatives (Lawton 2007; Sutherland et al. 2010). As Lawton (2007) has succinctly put it:

> Many scientists hold to the "deficit model" of turning science into policy, the view that if only politicians are told what the science reveals, "correct" policies will automatically follow. Nothing could be further from the truth. Politicians have all kinds of reasons, some valid, some less valid, not to adopt what often seem to us to be common sense policies to protect the environment.

The litany of reasons why ecological information may not be used in policy and management issues is unfortunately long. Possible reasons include poor communication by scientists, an overabundance of information, a lack of public support for the changes required, conflicts with other financial or political interests, and ambiguous science. Another important issue is time scale – ecologists wish to have years to study a problem, but politicians wish to have an answer today so they can decide what to do.

Ecologists should not only identify and research problems in natural resource management, but also suggest solutions.

At different times, national governments of Canada, Australia, and the USA have forbidden government scientists from any discussions of policy. Scientific research in ecology, geological, and medicine often has implicit policy implications, and restrictions would seem to ignore science in favor of political opinions. Fortunately, university scientists are not bound by government rules and are usually able to speak out in matters of science that affect public policy. The implications of science for policy decisions can lead ecologists into the field of social science.

A good example of the clash between ecological understanding and public policy occurs in the management of wolves (*Canis lupus*) in North America and Europe. Wolves are apex predators in many ecosystems (Ripple et al. 2014), and wolf populations have increased in both North America and Europe in recent years after more than a hundred years of decline (Jacobs et al. 2014). In the USA and parts of Canada, governments have conducted lethal control of wolves to benefit livestock producers and to enhance populations of moose (*Alces* spp.), caribou (*Rangifer tarandus*), and other native ungulates. The ecological consequences of large predator reductions are now well known but the problem has rested in public opinion about the utility of wolf control (Bergstrom et al. 2014). Much of wolf management is strongly affected by public opinion, and rather less by ecological information.

*Rule No. 4. If your research has policy implications, read the social science literature about how scientific information and policy decisions interface.*

Linking science to policy decisions is not easy, as illustrated by the global problems of dealing with climate change, or addressing competing interests of industrial development and landscape protection. One important approach is to identify policies for conservation and land management and to map the research needs relevant to each policy option. Sutherland et al. (2010) have completed these tasks for the United Kingdom and have listed 25 policy areas for conservation that affect the UK as well as many other countries in Europe. The key to success is to increase the interactions among ecologists, government, and business policy makers so that mutual understanding and tolerance are well recognized. By focusing on the twin issues of *biodiversity conservation* and *ecosystem services*, ecologists may be able to build public support for measures that require some realignment of our current economic system. Opposition to change will be strong, as it has been in the past (Oreskes and Conway 2010), and consequently ecologists should not be discouraged by a lack of immediate success. Public education is the key.

Particular issues in land management require a balanced approach that extends beyond ecological science to social and political science. Braysher et al. (2012) identified five key principles for successful efforts in pest management, and I have restated these broad principles as a five-point template for conservation researchers:

1) All key stakeholders need to be actively engaged and consulted for effective conservation plans.
2) Land-use management for biodiversity needs to focus on the outcome, not just on effort and dollars expended.
3) A whole ecosystem approach is required for managing conservation programs.
4) Most conservation management occurs in ecosystems in which our knowledge is imperfect.
5) An effective monitoring and evaluation strategy is essential for all management interventions designed to protect biodiversity.

Not all population ecologists will be directly concerned with policy and management for biodiversity, since we need to base all these policies on the best science available. But more and more the public are asking ecologists for information and recommendations on issues of concern, whether the issues involve the protection of threatened whales or the ecological consequences of climatic warming. We need to be ready.

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