

Population Ecology

(for S. Sarkar and A. Plutynski (eds.), *A Companion to the Philosophy of Biology*, Blackwell, forthcoming.)

1. Introduction.

A population is a collection of individuals of the same species that live together in a region. *Population ecology* is the study of populations (especially population abundance) and how they change over time. Crucial to this study are the various interactions between a population and its resources. A population can decline because it lacks resources or it can decline because it is prey to another species that is increasing in numbers.

Populations are limited by their resources in their capacity to grow; the maximum population abundance (for a given species) an environment can sustain is called the *carrying capacity*. As a population approaches its carrying capacity, overcrowding means that there are less resources for the individuals in the population and this results in a reduction in the birth rate. A population with these features is said to be *density dependent*. Of course most populations are density dependent to some extent, but some grow (almost) exponentially and these are, in effect, density independent. Ecological models that focus on a single species and the relevant carrying capacity are *single species models*. Alternatively, multi-species or community models focus on the interactions of specific species.

The discipline of population ecology holds a great deal of philosophical interest. For a start, we find all the usual problems in philosophy of science, often with new and interesting twists, as well as other problems that seem peculiar to ecology. Some of the former, familiar problems from philosophy of science include the nature of explanation and its relationship to laws, and whether higher-level sciences (like ecology) are reducible to lower-level sciences (like biochemistry). Some of the philosophical problems that arise from within population ecology include whether there is a balance of nature and how the uneasy relationship between the mathematical and empirical sides of the

discipline might be understood. As we shall see, many of these questions are intricately linked, and providing satisfactory answers is no easy matter. But there is no doubt that there are important lessons for philosophy of science to be gleaned from the study of population ecology.

In what follows I will focus on some of the central questions that are prominent in the recent philosophy of population ecology literature. There are, of course, other questions and problems, some of which the interested reader may pursue in the works listed in the references and further reading. But despite this admittedly less than comprehensive treatment of the philosophical issues in population ecology, those I address will give a sense of the flavor of the philosophical issues that arise in population ecology.

It is worth mentioning that many of the philosophical problems in population ecology are of great importance to working ecologists. For example, the issue of whether there are laws in ecology is seen by many ecologists as an important internal question to their discipline and one that has immediate methodological implications. (If there are no laws, ecologists might settle for a more pragmatic and even pluralist attitude towards their models.) Philosophers have been a little slow to turn their attention to ecology and so working ecologists have had to tackle many of the philosophical issues themselves. As a result a great deal of the philosophical ground work has been carried out (for the most part, with a high degree of philosophical sophistication) by working ecologists. (See, for example, Ginzburg, 1986; Pimm, 1991; and Turchin, 2001) But the philosophical problems in population ecology are important in another way. Population ecology itself has a great deal of social and political significance. Conservation management strategies often depend on predictions of population ecology. Where population ecology meets conservation management we find that philosophy of science meets ethics. Typically a great deal more than scientific or philosophical curiosity hangs on the answers to the philosophical and scientific problems faced by population ecology. For example, scientific issues about burden of proof in hypothesis testing have a distinctly ethical dimension. I will say more about such matters in section 6.

2. Laws in Ecology

It has been claimed that ecology is not law governed (Murray, 1999; O'Hara, 2005) The reasons for denying the existence of laws in ecology is not always clear. Often appeals are made to lack of generality and lack of predictive success, but the complicated nature of ecology seems to feature especially prominently in this debate. We need to be careful not to set the bar too high for lawhood though. Consider the claim that ecology is too complex to submit to general laws. This may well be true but it is not obviously true, and it is certainly not something we can determine *a priori*. After all, we take celestial mechanics to be law governed, even though every massive body in the universe interacts gravitationally with every other massive object. It does not get much more complicated than that! While it is true that populations are affected by a great deal around them—the weather, predators, parasites, resources, fertility, and so on—considerations elsewhere in science show that complexity alone does not disqualify a discipline from being law governed. The complexity might “wash out”, (Strevens, 2003), or much of the complexity might be properly ignored in many situations (as we can properly ignore the gravitational influence of Sirius on the earth when we consider the Earth's orbit around the sun).

A case can be made for accepting that ecology has laws, albeit laws with exceptions. There is a very natural way to think of a highly simplistic and idealized equation like Malthus's equation, $N(t) = N_0 e^{rt}$ (where, N is the population abundance, t is time, N_0 is the initial abundance, and r is the population growth rate), as a fundamental law of ecology. After all, this equation can be thought of as analogous to Newton's first law. Each describes what the respective system does in the absence of disturbing influences. In the ecological case, Malthus's law tells us that populations tend to grow exponentially unless interfered with. Interference can come in the form of density dependence, predators, and so on. Of course there always are disturbing influences, so no population grows exponentially for any significant period of time. But why should this disqualify Malthus's equation from being a law? After all, no massive body in the universe moves with uniform motion, but this does not disqualify Newton's first law. If it is good enough for celestial mechanics, it is good enough for ecology. Malthus's equation can be thought of as a fundamental law of population growth—it describes the default case from which departures are to be explained. Moreover, like Newton's first law,

Malthus's equation has considerable empirical support (e.g., the approximate exponential growth of microbial populations in laboratory situations). If we do treat Malthus's equation as a law, analogous to Newton's first law, we are then faced with the project of identifying the "ecological forces" that result in such departures from exponential growth (Ginzburg and Colyvan, 2004).

What of explanation in ecology? On traditional accounts of explanation (e.g., Hempel, 1965), laws are required for explanation. So if ecology does not have laws, there can be no ecological explanation. One response is to deny the traditional account of explanation: ecology has explanations but not laws (Cooper, 2003). Though if what I have suggested above is correct and ecology does have laws, then even on the traditional account of explanation there can be genuinely ecological explanations. Let us focus on the latter response. That is, let us assume that ecology does have laws and ask after the nature of the explanations delivered. There is still a problem for ecological explanation. The laws we are talking about are population-level laws; they are not about the individuals that constitute the populations in question. Consider Malthus's law. It has only initial abundance and the growth rate as parameters, and these both concern properties of the population, not the *individual*. But now here's the problem. Surely the *real* explanation for why a population has the abundance it does will be about births, deaths, immigrations, and emigrations of *individual members*. The law seems to ignore the individual events and the latter are what are causally relevant. How can such a law be genuinely explanatory?

I think this argument against ecological laws being explanatory fails. First, note that the argument is very general and, as stated, it would tell against any macro-level explanations of micro-level phenomenon. For example, the ideal gas law has only macro-level parameters—the individual properties of gas molecules do not feature in this law—so it would seem that the ideal gas law also falls foul of this line of attack on ecological laws. But, any statistical law—by its very nature—is at the level of ensembles not of individuals. It would seem that all statistical laws stand or fall together: the ideal gas law, ecological laws and many others. Surely the argument against ecological laws being explanatory is misguided. I will return to the issue of explanation in ecology in the next section, when I look at mathematical models in ecology.

3. Mathematical Models

Despite being a highly mathematical discipline, ecology has an uneasy relationship with the mathematics it employs. We have already seen that ecology is about assemblages of living organisms and a population grows or declines by adding or subtracting individuals. The details of the population growth or decline will depend entirely on what happens to the individuals that constitute the population in question. But the typical mathematical models of a population ignore the details of individuals. Or rather, all the details about the individuals are packed into a few population-level parameters such as growth rate, carrying capacity and the like.

In order to focus the discussion, let us consider a couple of simple mathematical models. Recall *Malthus's law* from the previous section. This states that the rate of change of population abundance, with respect to time, is proportional to population abundance. Represented mathematically, this becomes the following simple first-order differential equation:

$$dN/dt = rN,$$

where r is the population growth rate, t is time, and N is the population abundance. Solving this equation yields the familiar exponential growth equation (which we also refer to as Malthus's law):

$$N(t) = N_0 e^{rt},$$

where N_0 is the initial population abundance. Of course populations do not grow exponentially for long (if at all)—eventually their growth is limited by resources. Introducing such considerations into the mathematical model yields the logistic equation:

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

where r , t , and N are the same as before, and K is the carrying capacity for the population in question. The logistic equation is, arguably, the simplest useful model in population ecology. Despite a number of idealizations (such as ignoring age structure and genetic variation in the population, and treating that carrying capacity as constant) it is a very good description of many populations. Of course there are other refinements one can make but we won't bother here. The logistic equation will serve as our canonical example of a mathematical model in population ecology.

Now let us turn to the question of the use of mathematical models of population growth. These models are put to at least two different purposes: prediction and explanation. I will return to explanation shortly but for now let us focus on prediction. Most mathematical models are notoriously poor predictors. Of course they can be made to match existing data by suitably adjusting free parameters, but this gives one little confidence in the predictive accuracy of such models. Indeed, models whose parameters are too finely tuned are treated with considerable suspicion. Such models are (pejoratively) called “over fitted” and are thought to be unrealistically complicated and thus unreliable predictors. So an important question about the predictive reliability of models needs to be addressed: what means are available for guaranteeing that the model will give us the right answers? Or failing such guarantees, how do we go about specifying the degree of confidence in the model?

The kind of uncertainty we are dealing with here is called “model uncertainty” and is notoriously difficult to quantify (Regan *et al.*, 2002). But while a mathematical model may not predict the details, it may preserve gross trends. So, for example, we might find that under any reasonable value of the free parameters (or less commonly, under any reasonable model design) the model gives more or less the same answer. The model thus exhibits a certain robustness, and testing models in this way is called *sensitivity analysis* (Levins, 1966; Morgan and Henrion, 1990, pp.39–40; Wimsatt, 1987). Of course, a great deal hangs on how “reasonable values of the free parameters” is understood, but in practice, and in at least some cases, ecological theory provides guidance.

One interesting feature of sensitivity analysis, is that it gives rise to a supervenient logic (admittedly, under a non-standard epistemic interpretation of the

logic in question). If the population p is deemed to have property Q on all reasonable values of the parameters, then we are confident that p has Q . If p fails to have Q on all reasonable values of the parameters, then we are confident that p does not have Q . But what of the indeterminate cases, where on some reasonable values of the parameters p has Q , while on others p does not have Q ? Here it would seem that the right thing to say is that we are neither confident that p has Q nor are we confident that p does not have Q . In short, we assert that p has Q if and only if p has Q on all valuations. The resulting logic is a supervaluational logic and is familiar in the philosophical logic literature as the tool of choice in dealing with vagueness. This logic has interesting features such as being non-bivalent while preserving the classical law of excluded middle (van Fraassen, 1966; Beall and van Fraassen 2003). (Strictly speaking we are talking about the logic of the modal operator “confident that ...” but I will not explore such complications here.)

Validation studies are another way to test a model. Here, one uses part of a data set to construct the model, including the fixing of all free parameters, while withholding another part of the data set. The second, withheld part of the data set is then used to test the model. If the model predicts the withheld data, the model is said to be validated. The problem with such an approach is that it requires large data sets—typically long time series data of a population—and such data is rarely available. Indeed, the absence of such data is often the motivation for constructing a model in the first place.

The problems concerning model uncertainty are deep and philosophically rich. For a start, such uncertainty does not readily submit to probabilistic treatment (Regan *et al.*, 2002). After all, it is very often impossible to assign values to the probability that the model is correct in every detail. Or at least on standard methods of assigning such probabilities, they will come out to be zero. New methods for dealing with such uncertainty are required. One such approach is non-classical logic. For in the face of serious uncertainty, it is necessary to entertain at least three categories: definitely true, definitely false, and indeterminate. Multi-valued and modal logics may prove fruitful in dealing with uncertainty that resists probabilistic treatment (Regan *et al.*, 2002). There are various questions about the relationship between simplicity and predictive success of models. Can we be more confident in a simple model? This is an old chestnut in the philosophy of science. On the one hand, there are good pragmatic arguments for insisting

on simplicity in the models or laws of ecology; thus formulated, the relevant theory will be easier to work with, and generally more tractable. But, on the other hand, what do pragmatic virtues of a theory have to do with truth or even predictive success? Put another way, what is so bad about complex (or overfitted models)? Interesting work on this problem has been carried out by Forster and Sober (1994). Forster and Sober use a theorem due to Akaike to forge a link between simplicity and predictive success. Mikkelsen (2001) applies these ideas specifically to ecology. (See also Colyvan and Ginzburg, 2003 for discussion of possible limitations of this approach to simplicity.)

Thus far, I have been focusing on the typical population models that employ population-level properties like carrying capacity, growth rate, and the like. There are extensions that relax some of the assumptions of single aggregated population dynamics. Age- and stage-based models (also known as matrix models; Caswell, 2001) are models in which organisms are differentiated based on their age or morphological features such as size. Each age or stage class then has its own population growth equation that is coupled with other age or stage classes in the model. Meta-population models incorporate space through a population of sub-populations which are separated by a distance (Gotelli, 2001).

These are all population-level models, though, and it is worth saying a little about another kind of model: individual-based models. The latter are models that focus on the properties and behavior of the individuals of a population. The global population-level properties are then derived from the local interactions. Unlike the global population-level models, individual-based models keep track of individual properties and behaviors (DeAngelis and Rose, 1992). They incorporate diversity amongst individuals by representing each individual separately and explicitly specifying attributes such as the individual's age, size, spatial location, gender, energy reserves etc. Sometimes individual-based models are used to estimate or model population-level parameters (McCauley *et al.*, 1990 and Gurney *et al.*, 1990). In a sense, such individual-based models take a bottom-up approach to determining global population-level properties. A familiar example of an individual-based approach is found in various simulations such as “the game of life” and spatialized prisoner's dilemmas. In such simulations, individuals are located in an environment consisting of cells. Individuals are able to take one of a

number of states and there are rules about the interactions between neighboring cells (or individuals). Such approaches have been put to good use in shedding light on altruism in populations (Sober and Wilson, 1998) and the evolution of various social structures (Skyrms, 2004).

In population ecology, individual-based models are becoming more widely used. Typically such models are *spatially explicit*. That is, they associate a spatial location with each individual. Such spatially-explicit individual-based models are especially useful in modeling species that aren't terribly mobile—otherwise movement rules need to be included and these present serious difficulties. But if the species in question is reasonably sedentary, each individual in the population can be associated with a particular fixed spatial region. These models are particularly suited to plant populations (see, for example, Regan *et al.*, 2003). But with some additional complications individual-based models are also able to be used for animal populations where individuals are allowed to roam over more than one spatial region. Individual-based models are often employed when information about the structure of the population is required. So, for example, spatially-explicit individual-based models are very useful for determining forestation patterns—not just the number of individual trees (Deutschman *et al.*, 1997). To some extent at least, individual based models and the more traditional population-level models are not direct competitors. Very often they are used to answer different questions (Regan, 2002).

Some ecologists take individual-based models to be less problematic than the usual population-level models. For example, individual-based models cannot be accused of ignoring the properties and behavior of the individual members of a population while focusing only on averaged population-level properties. There are still idealizations though. The behavior and properties of the individuals in individual-based models will be highly idealized and often reduced to one of a small number of states. Moreover, the individuals will be restricted to a small number of possible actions. As with other models, the devil is in the details. There is nothing inherently wrong with such idealizations; the question is whether the idealizations at issue are theoretically well motivated and whether they are useful. These are important questions for ecology but they are not, it would seem, questions that will submit to general answers; they must be answered on a case-by-

case basis. And it would seem that these questions must be answered for both individual-based models and population-level models.

Another application of mathematical models is to provide understanding and explanation of certain features of the population in question. Here there is less emphasis on getting detailed predictions and instead the focus is on gaining insights into general population trends and the reasons behind them. Such models are rather controversial in ecology. It is thought by some that mathematical models cannot be explanatory, for they either obscure the underlying biological mechanisms or, worse still, they *ignore* the biological mechanisms. After all, if a population is exhibiting periodic behavior, say, the reason for this behavior must have something to do with births, deaths, immigration, and emigration of individual members of the population. The mathematical model, however, typically employs population-level parameters like carrying capacity and growth rate. A mathematical model thus cannot provide explanation because it is not couched in the right terms (or so the argument goes).

The first thing to stress here is that very often the mathematics is just representing the biological facts in a mathematical way. Properly understood, the mathematics neither ignores nor obscures the underlying biological causal mechanisms. Instead of listing all the individuals in a population at different times, for instance, we can summarize this information in terms of equations for the population abundance. The individual organisms might seem to have dropped out of the picture but they have not. All that is relevant about them is represented mathematically in the equation of growth. Consider another example. The constant K in the logistic equation is not just an uninterpreted constant introduced purely for mathematical convenience. As I have already pointed out, K has a very natural *ecological* interpretation as the carrying capacity. (Though, it might be argued that this interpretation is rather abstract and it is mathematically convenient in that the constant K is just a crude summary of the interactions of a population with its environment.)

Next I note that some explanations are more readily drawn from the model than from the biology. For example, the mathematical model may focus attention away from confusing local-level causal interactions and towards higher-level population trends. We see this in the mathematical explanation of why certain populations undergo specific

abundance cycles. The explanation in terms of the periodic solutions of coupled differential equations is much clearer than any detailed tracking of specific individual-level interactions.

Finally (and most controversially), it may be that some explanations are best looked upon as essentially mathematical rather than biological. For example, the question of why certain populations are so unstable can be best understood in terms of facts about the instability of the relevant differential equations (May, 1973). Of course this is not to say that there is no biological component to the explanation—just that the mathematics is doing most of the explanatory work. The thought is that the biological system in question is represented by a mathematical model, and there are certain (mathematical or logical) limitations on the way the model can behave. In so far as the mathematical model accurately represents the biological system, then those limitations apply to the biological system as well. The crucial point here is that in many such cases (such as the example above) one cannot reconstruct the explanation in biological terms. No system, biological or otherwise, can violate the laws of mathematics. And sometimes that is all the explanation that is required. (See Colyvan, 2001, chapter 3, for more on non-causal, mathematical explanations.)

The claim (mentioned several paragraphs back) that individual-based models are preferable to population-level models is sometimes turned into an argument for the explanatory superiority of individual-based models. The idea behind this line of thought is that although both kinds of models are typically couched in mathematical language, it is only the basic features of the individual-based models that correspond to non-relational properties of the individual members of the population. While there is no doubt that population-level properties like growth rate and the like, supervene on properties of individuals, it is clear that the growth rate is fully determined by births, deaths, immigration and emigration of individual members of the population in question. It is only individual-based models that respect the priority of these basic biological events (or so the argument goes). But as I have already suggested, I think it is a mistake to think of population-level models as ignoring these fundamental biological events. The logistic equation, for instance, does not ignore individual births and deaths, it just incorporates all the relevant information about births and deaths into the growth rate. (Of course, in the

logistic model, there is the assumption that the growth rate is constant, but that is a different worry.) Moreover, individual-based models cannot claim to have cornered the market on the biologically relevant facts. We can, for example, ask why a particular individual died. Typically, individual-based models need to incorporate probabilities of death in various circumstances, but then these probabilities are just standing proxy for deeper biochemical and ultimately physical causes. If we take this line of reasoning all the way, we might conclude that only physics is explanatory. In which case, providing explanations in ecology might mean performing the reduction of ecology to biology, biology to biochemistry, and biochemistry to physics. Surely something has gone wrong here. Surely there are biological and ecological explanations. The question of ecological explanation will arise again in the next section when we consider a particular ecological phenomenon in need of explanation. For the moment, I just note that the argument against population-level explanations being genuine explanations is unconvincing.

I should mention one final use of mathematical models that I have not yet covered. Ecological models are often used for decision making and ecologists sometimes distinguish such models from both predictive and explanatory models. For example, a decision model might give you insights into the best fire-management policy for a piece of bushland (Richards *et al.*, 1999) by indicating general trends one would expect to find under different management strategies. While such management applications of models are in some ways different from those discussed above, it might be argued that they are properly thought of as a kind of hybrid of the predictive and explanatory models. In these decision models, while exact predictions are not required, ball-park predictions *are* required (for otherwise the model would be of no use for decision making). And while these models may not provide anything so rich as a full explanation of the phenomenon in question, they do need to provide some understanding of the basic relationships spelled out in the model. In any case, I will not discuss these decision models further, although the use of these models (and operations research techniques, more generally) in conservation biology is a very interesting and a relatively new development that deserves further philosophical attention.

4. What is the Reason for Population Cycles?

Population cycles are periodic fluctuations in a population's abundance. Although stable population cycles are relatively rare in nature, they are very important for a number of reasons. First, from an ecological point of view, they are important test cases for various theories of population growth. Very often in science it is useful to turn one's attention to rare cases for insights. (Consider, for example, the importance of understanding the rather rare solar eclipses for our theory of celestial mechanics.) In any case, any decent ecological theory must be able to give a satisfying account of population cycles, rare or not. Second, from a philosophical point of view, population cycles provide some interesting insights into the methodology of population ecology and help shed further light on issues concerning ecological explanation.

Classical population ecology holds that stable population cycles are a result of predator-prey interactions, (although some oscillations can be a result of a population overshooting and undershooting carrying capacity). The predator-prey model of population cycles is due to the pioneering work in population ecology by Lotka (1925) and Volterra (1926). This account describes the population of the predator and the prey via two first-order differential equations that explicitly mention the population of the prey (V) and the predator (P), respectively:

$$dV/dt = rV - \alpha VP$$

$$dP/dt = \beta VP - qP$$

where r , q , α , β are constants determined empirically: r is the intrinsic rate of increase in prey population in the absence of predators; q is the per capita death rate of the predator population; α is a measure of *capture efficiency*, which is the effect of a predator on the per capita growth rate of the prey population; and β is a measure of conversion efficiency, which is the ability of the predator to convert prey into per capita predator growth (Gotelli, 2001, pp.126–133).

These equations give rise to a very rich and interesting dynamics. The basic idea of how they produce cycling, though, is rather simple. As the predator population rises there is more predation and so the prey population declines. As the prey population

declines, there is less food for the predators and so the latter's numbers too decline. Once the predator population declines, there is less predation and so the prey population recovers and starts to rise again. The predator population also recovers and on it goes.

There are a number of idealizations made in the standard Lotka-Volterra model. The first is that the predator is a specialist and will starve in the absence of the specific prey in question. It is also assumed that prey population grows exponentially in the absence of predators and that the predators can consume an infinite number of prey. Some of these idealizations can be dropped. For example, functional-response models relax the assumption that individual predators can always increase their prey consumption when the prey population abundance increases (Gotelli, 2001, pp.135–140).

There is little doubt that predator–prey interaction can result in population cycles; the question is whether they are the *only* reason for cycles. The classic example of population cycles due to predator–prey interactions is the Canadian lynx–hare cycles observed by Elton and Nicholson (1942). But there are other examples of population cycles where no known predators exist. But these too can be forced into the predator–prey mould by treating the cycling population as a predator (even if it is a herbivore) and treating the resources (whatever they may be) as prey. So we can think of population–resource models as a generalization of predator–prey models.

There is also another way that cycles might arise. It is a basic assumption (and orthodoxy) throughout population ecology that ecological forces like predation, limitation of resources and so on, affect the growth rate. But if these ecological forces were to result in a second-order change— affect the rate of change of the growth rate— things might look quite different. The idea here is analogous to forces in mechanics. On the Aristotelian view, forces result in velocities, whereas on the Galilean view, forces result in the second-order quantity, acceleration. The traditional population models are Aristotelian whereas the new second-order proposal is Galilean (Ginzburg and Colyvan, 2004). The second-order model has it that the dynamic state is no longer fully described by population abundance. Since the resulting model is a second-order differential equation, both population abundance and the rate of change of the population abundance is required. This second-order model thus has a time lag built into it. But most importantly, for present purposes, this model can give rise to internally-generated

population cycles. That is, the model does not need to rely on population interactions for cycling (although such externally-driven cycles are still possible); the model is capable of producing stable single-species cycles.

An interesting question arises at this point concerning the mechanism for the cycles and the time lag. (In fact, it is really just the time lag that is in need of a mechanism, because in an important sense the internally-generated cycles are just a consequence of the time lag.) It was largely due to the lack of a convincing answer to this question that the second-order theory was given very little attention in the ecological literature until the 1990s. Before I discuss the answer to this question, let me emphasize the importance of providing an answer. After all, you might be tempted to simply dismiss the question. Indeed, this is very close to what happened in the analogous physics case. Why should position depend on both velocity and previous velocities. “That is just the way things are”, is the answer. What is the mechanism for two bodies remote from another to have gravitational influence on one another? Again, that is just the way things are. Why not answer the ecological question along similar lines?

Though this response is tempting, to advance it is, I would suggest, to seriously misunderstand the nature of biology and its relationship to physics. Physics, arguably, is the study of the fundamental laws of nature. We all know that explanation must end somewhere and it seems that physics is the appropriate place for it to end. So while we may accept that some basic laws do not admit of further explanation or justification, any such laws should, it would seem, be reserved for physics.

Fortunately for the second-order theory, there is an account of the time lag. A very plausible reason for such time lags (or *inertia*) in population growth is found in the *maternal effect*. This is the phenomenon of “quality” being transferred from mother to daughter. The idea is that a well nourished and healthy mother produces not only more offspring but also healthier offspring. So, an individual from a healthy mother experiencing a deteriorating environment will do better and be able to continue reproducing longer than individuals in the same environment, not fortunate enough to have a healthy mother. Similarly, an individual from an unhealthy mother will do poorly despite an improving environment. This means that the population abundance at any time

is the product of both the current environment and, to some extent, the environment of the previous generation (Ginzburg and Colyvan, 2004).

The maternal-effect hypothesis provides an elegant answer to the question of the mechanism for the time lags involved in the second-order model of population growth. But other mechanisms are also possible. Predator–prey interactions are still in the mix (though these aren't causes internal to the population). Another possible mechanism is *niche construction*. This is the modification of a population's environment in ways that are beneficial to both the current generation and often to subsequent generations (Sterelny, 2001). A classic example of such niche construction is the building of dams by beavers and the large number of human interventions such as building dwellings that last more than one generation. (In general, niche modifications can last more than one generation and all that is required for the second-order model of cycling to work is a one-generational lag. But time lags of more than one generation can also be accommodated by the theory.) In fact, we can look on the maternal effect as a special case of niche construction.

So what is the cause of population cycles? There may well be more than one cause: predator–prey interactions, maternal effect, and niche construction all seem like plausible candidates—and there may be others. One interesting feature of population cycles is the Calder allometry (Calder, 1984), a correlation between body size of prey and the period of the cycle. Rather surprisingly, the period of the predator–prey cycle does not depend on the size of the predator. This suggests that even in clear cases of predator–prey cycles, the predator might be just along for the ride, with the period of cycling being set by internal (metabolic) properties of the prey. Work continues on the question of the cause of population cycles and the evidence and arguments cited in this work makes for a very interesting case study for philosophers of science.

5. The Balance of Nature Debate

It is often assumed that nature is in balance. The idea is that an ecosystem, if left undisturbed (i.e., without human interference), finds a balance, where all species can coexist. There are many uses of this idea in ecology, conservation biology, and environmental ethics. I will focus on a couple of these.

The first example of the use of this metaphor is in environmental ethics and conservation management: if an ecosystem is in balance and this is seen as desirable and difficult to obtain, then we ought to avoid any human activity that might disrupt the delicate balance. Such interference would result in a less desirable state for the ecosystem. This line of reasoning is often thought to provide support for conservation efforts to leave ecosystems alone. There are some interesting questions here. What does it mean to say that nature is in balance? Is nature really in balance? Why is balance a desirable state for an ecosystem? Let us take each of these questions in turn.

The idea of the balance of nature, no doubt, springs from various unexpected consequences of human interventions in ecosystems. The introduction of foxes into Australia may have seemed innocent enough at the time but it has had a severe impact on small marsupial populations. Nature, we suppose, was in balance but the introduction of foxes disrupted that balance. But what is the notion of balance that is at work here? I take it that the idea is that balance is to be understood in terms of population abundances not straying too far from some equilibrium value (mean growth rates are zero). Presumably, populations can cycle but abundances do not tend to zero nor do they increase without bound. This is certainly one sense of balance. Another might be that nature is in balance in the sense that, once disturbed, the system returns to some equilibrium state. This tendency is often called *stability*. (There are also other closely related notions such as the speed which the system returns to the original state after a disturbance, and the degree to which the system can be changed by perturbances [Pimm, 1993].)

Now, turn to the question of whether nature is in balance. Obviously the answer to this question will depend on how 'balance' is understood. For example, an ecosystem might be in balance in the sense that all the constituent populations have abundances that do not vary greatly, but the ecosystem might still be unstable: a small external interference might result in massive and widespread changes to the ecosystem. On the other hand, an ecosystem might be stable and yet exhibit wild fluctuations in constituent population abundances. Moreover, the time scale is going to be important here. A population abundance that does not change much on one time scale may vary greatly on another. In geological time scales, very few ecosystems can be thought to be balanced in either sense—species become extinct, populations decline and disappear, new species

appear in ecosystems. Some of this is driven by climatic and geological change, some by the contingencies of various ecological factors. So let us suppose that we have fixed the time scale to something appropriate and we have decided on the appropriate sense of 'balance'. Is nature in balance? This is an empirical question and it would be surprising if it submitted to a general answer. It seems plausible that some ecosystems will be in balance while others will not.

Where does this leave us with regard to our final question of why balance is a desirable state for an ecosystem? One (anthropocentric) answer is that we humans require a certain kind of environment for our continuing existence and so we don't want things to change too much from the way they are. Arguably, balance in both senses under discussion is important for this. First consider balance in the sense of population abundance not varying too wildly. Human survival clearly depends on balance in this sense, at least in those environments humans inhabit. For example, if the population abundance of a crucial biotic resources varied wildly it could make human survival in that environment difficult or impossible. (Think of the impacts of droughts on agricultural societies.) Next consider stability. Life in an unstable environment would be rather tenuous. Any disturbance could, potentially, lead to dramatic and irreversible changes. Moreover, such changes, in general, would be to the detriment of human survival. Although it seems that there is a plausible line of argument from the hypothesis that nature is in balance to the conservation of ecosystems, caution needs to be exercised. For a start, we would hardly want this to be the only case for preserving ecosystems, for surely we would like some reason to preserve changing and unstable environments. Indeed, it might well be argued that unstable environments are more in need of protection from human intervention than stable ones.

The second use of the metaphor of nature in balance is in the complexity–stability hypothesis, which is the hypothesis that the greater the complexity in an ecosystem, the greater its stability. It is well known that the disappearance of so-called *keystone species* can result in loss of stability of an ecosystem and great efforts are directed towards saving species considered keystone. But the complexity–stability hypothesis is much more general than this; it is not restricted to key species upon which many others depend. Again there are issues concerning the meaning of key terms here, most notably: stability

and complexity. Do we read complexity in terms of biodiversity, interspecific species interactions, strength of interspecific interactions, or something else? And again there are ethical or conservation management implications: if stability is something to be valued, and a positive feedback between stability and ecological complexity exists, then we ought not reduce the complexity of ecosystems. But there is also considerable ecological importance for this hypothesis. The complexity–stability hypothesis provides a wonderful example of the kind of debate one finds in ecology between the modelers and more empirically-minded ecologists.

On the one hand, modeling work by Robert May (1973), has suggested not only that the complexity–stability hypothesis is false, but that the reverse relationship holds: increased complexity reduces stability. On the other hand, some empirical studies suggest that the complexity–stability hypothesis is true. The shortcomings of the modeling approach we have seen already: the models are idealizations and are quite unlike real ecosystems. Those unsympathetic to modeling are hardly going to reject a plausible piece of ecology, namely the complexity–stability hypothesis, purely as a result of a piece of modeling. But the case for the complexity–stability hypothesis, based on empirical evidence is also less than convincing. After all, the complexity–stability hypothesis is supposed to be a general result, so appealing to a couple of case studies is not going to win the day.

It is worth saying a little about the role of empirical evidence in debates such as this. At the end of the day, empirical evidence is important but it does not, and should not, have the final word. As is well known, it is very difficult (if not impossible) to derive universal generalizations from finite data sets. But even in cases of recalcitrant data, rejecting an hypotheses is no straightforward matter. As Duhem (1954), Lakatos (1970), and Quine (1951), have stressed (in slightly different ways), recalcitrant data does not count against a particular hypothesis. Each hypothesis makes predictions only when combined with a large body of theory (or auxiliary hypotheses). It is the package that is accepted or rejected; a core hypothesis can be protected from recalcitrant data by suitable adjustments elsewhere. The rejection of outliers in data sets is a clear example of such methodology at work. As Robert MacArthur (1972) puts the point:

Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true, as Eddington pointed out, that it is best not to put too much faith in facts until they have been confirmed by theory. (p.253)

Of course such considerations in the philosophy of science do not undermine the evidence-based approach to settling issues such as the complexity–stability hypothesis. After all, there are good reasons to be wary of the modeling approach as well. My point is simply to stress that while having evidence on one’s side is a good thing, one should not take the high moral ground as a result of this. Like most issues in population ecology, there are no easy answers here.

6. Socio-Political Aspects of Population Ecology

An important application of the theory of population ecology is in *population viability analyses* (PVAs). These are studies of populations under various management regimes and are important for conservation and resource management decisions. PVAs thus have great political importance. To take an example from conservation management, the standard International Union for the Conservation of Nature (IUCN) classification of endangered species relies heavily on estimates of current population numbers and predictions of declines in the near future. Examples of resource management include predictions of fish populations for managing fisheries. While such applications, strictly speaking, belong to conservation biology and natural resource management, there is a close relationship between ecology and these more politically-oriented disciplines. Indeed, it can be difficult to disentangle the purely scientific questions about population abundance (which belong to population ecology) from the value-laden decision questions about how best to manage a population (which belong to conservation biology). But there are other ways in which ecology is entangled with socio-political issues. The issue of type I and type II error is perhaps the most striking example.

In standard hypothesis testing in ecology (and elsewhere), one always compares the hypothesis under investigation H with its negation H_0 —the null hypothesis. When making a scientific pronouncement on the matter, there are four possibilities: (i) accepting H when H is false (a false positive or type I error); (ii) failing to reject H_0 when H_0 is false (false negative or type II error); (iii) accepting H when H is true; (iv) failing to

reject H_0 when H_0 is true. In standard hypothesis testing, type I error is considered the more serious error and so to guard against making this type of error, a great deal more is required for the acceptance of H . More specifically, we guard against making type I errors by stipulating that we will not accept H unless the evidence for H is overwhelming. That is, we stipulate that H_0 will win the day unless the probability of H_0 , given the evidence, is very low. The latter probability is the so-called α -level and is somewhat arbitrarily set at 0.05.

The upshot of all this is that standard hypothesis tests in ecology (and elsewhere) are designed to give the benefit of the doubt to H_0 : reject H unless H is proven beyond reasonable doubt. Shrader-Frechette (1994) has argued that there is an ethical dimension to hypothesis testing. One sees this most clearly in legal contexts. The principle of “innocent until proven guilty”, with its subsequent onus of proof on the prosecution is clearly an ethical attitude one takes towards uncertainty in law. But setting the α -level at 0.05 is to take a similar stance in scientific hypothesis testing. The thought behind $\alpha = 0.05$ is that, just as in law, less harm is done if we wrongly deny an effect (or wrongly acquit), but it is bad scientific practice to wrongly accept that there is an effect (or wrongly convict). This is clear enough in the legal setting but, again as Shrader-Frechette (1994) points out, it is hard to defend in all scientific contexts. Ecology, it might be argued, presents us with some interesting problem cases.

Consider an ecological hypothesis that is important for conservation management. Take, for example, the hypothesis that a species will suffer a population decline of such proportions that it will warrant being classified as “critically endangered”. The null hypothesis will thus be that there will not be such a population decline. Which hypothesis deserves the benefit of the doubt here? Well, that will depend to some extent on your attitude towards the species in question, and environmental issues more generally. But there is a good case to be made for reversing the burden of proof in this case so that we will be inclined to accept that the species is undergoing a population decline unless there is rather compelling evidence that it is *not* so declining. That is, we might set the α -level quite high, 0.95, say. Indeed, one might argue that there is a (non-scientific) value judgment about the choice of the α -level and that this reflects the researcher’s attitude towards environmental issues.

There is also a certain amount of arbitrariness about the choice of hypothesis and null hypothesis. If, as in the last example, we take a population decline as *the effect*, the corresponding hypothesis will be that the population is declining, and the null hypothesis will be that there is no decline. As we saw, on standard hypothesis testing (with an α -level of 0.05), it will take some compelling evidence before the null hypothesis is rejected. But what if we were to turn things around and stipulate that the effect is that the population is not declining? Now the hypothesis will be that there is no decline (or if you prefer, that the population is steady or rising) and the null hypothesis will be that the population is declining (or if you prefer, not rising and not steady). Again it will take some compelling evidence before we reject the null hypothesis. But in the absence of any such evidence, in either case we will reject the hypothesis. But what we are accepting will depend on the arbitrariness of how we set up the problem. If you have green sympathies, say, you can set the hypothesis and null hypothesis in such a way that it will be very hard to reject the claim that the population is declining. And similarly, if you do not have such green sympathies you can set the hypothesis and null hypothesis in such a way that it will be very hard to reject the claim that the population is not declining.

It is also worth noting that often in population ecology data is scanty, so α -levels anywhere near the extremes—0.05 or 0.95 might be demanding too much. Setting the α -level at the usual 0.05 (or at the other extreme, 0.95) is in effect to always reject the hypothesis (or respectively, accept it), because there will very rarely be enough evidence to get the probabilities in question below 0.05 (or above 0.95). So to sum up, the poverty of data in much of population ecology and the obvious socio-political implication of many ecological hypotheses suggests that the usual hypothesis tests are inappropriate. What we should do about this is not clear. If we allow one to choose one's α -levels depending on one's attitude to the environment, a rather unpalatable relativism about crucial ecological hypotheses looms. After all, if one ecologist sets her α -level at 0.95 because she is an environmentalist and another sets his at 0.05 because he is not, how do we settle the ensuing debate about whether the species in question is declining in numbers? The question of the decline seems to be a scientific question, but allowing value judgments to enter into the scientific process via the choice of α -level (or the arbitrariness of what counts as the effect) undermines the objectivity of science. This

unwelcome invasion of ethics also seems to blur the distinction between ecology and politically-charged conservation management issues. Be that as it may, the alternative of sticking with the α -level of 0.05 does not solve the problem—it just hides it. Sticking with the traditional α -level of 0.05 is clearly arbitrary, but worse still, such a choice represents a certain bias against the acceptance of any given hypothesis. The result is not objective science; it is just less obviously subjective, because the subjectivity is buried in standard scientific practice.

Issues about uncertainty in population ecology are interesting in their own right, but when one factors in the socio-political importance of a great deal of ecological theory, uncertainty takes on new significance. Indeed, the interaction, on the one hand, of the scientific and statistical questions about uncertainty in ecology and, on the other hand, the various important management decisions that depend on ecological pronouncements gives population ecology (and ecology more generally) a very unusual place amongst the sciences. (See Mayo, forthcoming for more on these issues.)

7. Ecology and Evolution

I will finish by mentioning just a couple of the interesting connections between population ecology and evolutionary theory. Some of these connections go back to the very origins of both disciplines. The first connection is that it is Malthusian growth that drives the struggle for existence, so central to evolutionary theory. After all, populations increase exponentially, yet resources are (eventually) limited. As Charles Darwin (1859) himself pointed out:

As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. (p.78)

But the historical connection between evolution and ecology runs even deeper. Although Darwin showed some interest in giving a general account of this struggle for existence, it was Ernst Haeckel who first identified ecology as “the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence”

(quoted in Cooper, 2003, pp.4–5). More recently, Greg Cooper (2003) has defended this account of ecology and in so doing raises many important issues. Indeed, Cooper argues that many of the issues I have addressed in this chapter (such as the role of models, the question of whether ecology has laws, and whether there is a balance of nature) all arise very naturally in the process of defending the view that ecology is the science of the struggle for existence.

Another related way in which ecology and evolution are connected is via the theory of r - K -selection (Pianka, 1970). Intuitively, there are two reproductive strategies organisms might employ: (i) maximize offspring production and (ii) have only a few offspring but ensure a high survival rate. According to the r - K selection theory, when a population is maintained at a low density the best reproductive strategy is (i) and the population in question is said to be r -selected. On the other hand, populations maintained at high density (i.e., close to carrying capacity) have no advantage in having high offspring reproduction. For these high density populations, the best reproductive strategy is (ii) and such populations are said to be K -selected. The names r -selection and K -selection come from the two parameters in the logistic equation. In r -selection, evolution is supposed to favor early semelparous reproduction (reproduction at a single age), large r , many offspring with poor survivorship, type III survivorship curve (survival probability is low at early ages but high for the later ages) and small adult body size. (Note that *survival probability* for an age x is the probability that an individual of age x will survive to age $x+1$.) Mosquitoes are an example of species that are supposed to have evolved under r -selection. In K -selection, evolution is supposed to favor late, iteroparous reproduction (reproduction at more than one age), small r , few offspring with good survivorship, a type I survivorship curve (survival probability is relatively high for early ages and lower for later ages) and large adult body size. Mammals are examples of species that are supposed to have evolved under K -selection.

The r - K theory, though once popular, now faces serious problems. Some of these problems include: not all species have life history traits that fit the theoretical predictions; attempts to experimentally confirm the theory have failed; and the derivations from the theory did not include age-structured populations (Gotelli, 2001, p.70). One of the more interesting criticisms of the r - K theory is that there can be other factors besides

population density involved in the evolution of life history traits. For example, according to the r - K theory, iteroparous reproduction is supposed to evolve when population density is high and resources are scarce. But such a reproduction strategy might also evolve in volatile environments where there is a risk of losing all offspring, (Murphy, 1968). Having more than one shot at reproduction can certainly have its advantages in such environments. Iteroparous reproduction is a way of spreading the risk.

There is much more that could be said about the relationship between population ecology and evolution. Just as in other areas of population ecology, I think that there will be many interesting philosophical issues to emerge.

Acknowledgements

Some of the material in this chapter has been published previously. I'd like to thank Kluwer Academic Publishers for permission to reproduce portions of 'Models and Explanation in Ecology', originally published in *Metascience* (Vol. 13, December 2004, pp. 334–337) and portions of Colyvan and Ginzburg (2003). Copyright for the material in question remains with Kluwer. I'd also like to thank Lev Ginzburg, Paul Griffiths, Dominic Hyde, Greg Mikkelson, Hugh Possingham, Helen Regan, Sahotra Sarkar, Kim Sterelny, and members of the Ecology Centre at the University of Queensland for fruitful discussions on the issues addressed in this chapter. I'm especially grateful to James Justus Elijah Millgram, and Helen Regan for comments on earlier drafts. I'd also like to thank the Biohumanities Project at the University of Queensland for research support.

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