



The Galilean turn in population ecology

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Abstract. The standard mathematical models in population ecology assume that a population's growth rate is a function of its environment. In this paper we investigate an alternative proposal according to which the rate of change of the growth rate is a function of the environment and of environmental change. We focus on the philosophical issues involved in such a fundamental shift in theoretical assumptions, as well as on the explanations the two theories offer for some of the key data such as cyclic populations. We also discuss the relationship between this move in population ecology and a similar move from first-order to second-order differential equations championed by Galileo and Newton in celestial mechanics.

Introduction

Malthus's law of population growth states that, in the absence of disturbances, populations grow exponentially. But how do ecological "forces" impact on this default state? The prevailing view in population ecology is that changes in the environment bring about changes in the population's growth rate. As intuitively plausible as this view may seem, there is good reason to doubt it. Indeed, a very interesting debate has erupted in recent years in population ecology on this very issue.¹ This debate and its philosophical significance is the subject of the present paper.

We will examine the debate initially from a somewhat mathematical and abstract perspective and we will see striking similarities between this debate in population ecology and a similar debate conducted in physics over 300 years ago in the move from Aristotelian physics to Galilean physics. We will also examine some of the evidence presented in the population ecology debate and we will see that it is difficult to reconcile this evidence with the traditional view. Finally, we will discuss some of the reasons for resistance to abandoning traditional theories of population dynamics.

Malthusian law and Lotka-Volterra dynamics

The fundamental law of population ecology is Malthus's law. It can be written a

¹ See Ginzburg (1986), Ginzburg and Colyvan (2004), Turchin (2001, 2003) for some of this debate.

number of different ways. Most commonly it is presented thus: $N(t) = N_0 e^{rt}$, where $N(t)$ is the population size at time t , N_0 is the initial population size and r is the growth rate. For our purposes, however, it will be more convenient to express this law as a second-order differential equation: $\frac{d^2}{dt^2}(\ln N) = 0$. The advantage of this form of the law is that it makes very clear that, according to Malthusian law, the second derivative of the natural logarithm of the population size is zero. That is, the law says that, in the default case, there are no net “accelerations”.

So much for the default case. What of the influence of environmental “forces” such as limitations of resources, predators, or even overpopulation? The central assumption of standard Lotka-Volterra population theory is that population size is a complete descriptor of the dynamic state.² That is: $\frac{1}{N} \frac{dN}{dt} = f(N)$, where, as usual, N is the population size and $f(N)$ is some function of the population size. This equation tells us that the relative growth rate (average number of surviving offspring per parent per unit of time) is a function of the population size. That is, it tells us that changes in population abundance are brought about by changes in the growth rate of the population.³

A couple of comments are appropriate here. First, in order to understand how communities of populations behave, we must write down the relevant equation for each population in the ecosystem. The function f will, typically, be different for each population, since the abundance for one population will depend on the abundances of other populations in the ecosystem. We thus get a very interesting dynamic structure arising from these interactions.⁴ The most famous of such interactions are the predator–prey interactions described by the Lotka-Volterra equations. These equations are simply a pair of coupled differential equations—one for predator and one for prey. Indeed, just two-population interactions lead to very complex behaviour.⁵

We also note that the traditional Lotka-Volterra view is a first-order theory—it describes the dynamics in terms of a first-order differential equation, and the impact of a changing environment is to affect the rate of change of the population abundance. Put somewhat metaphorically, on the traditional view, *ecological forces bring about “velocities”*.

The inertial view of population dynamics

It is clear that changes in environment bring about changes in population abundance.

² We use ‘Lotka-Volterra’ very generally to describe all traditional population theories—not just predator–prey models.

³ See Gotelli (1998) for a good introduction to the basics of population ecology and Kingsland (1985) for a very nice history of the subject.

⁴ See Boyce and DiPrima (1986) and Ginzburg and Golenberg (1985) for elementary mathematical treatments of population interactions.

⁵ The complexity when you consider a real ecosystem is mind-boggling. See May (1974) and May and Oster (1976) for details of some of this complexity.

For instance, if resources dwindle, then any population depending on those resources will founder. Similarly, when resources abound, populations will flourish. The important question, however, concerns the dynamic details of how such changes in abundance come about? Perhaps the simplest picture is that a change in environment brings about changes in the birth rates and death rates so that, overall, the population's growth *rate* is affected by the environment. That's the traditional view and that seems right . . . up to a point. But what if a change in environment affects the *rate of change of the growth rate*? That is, what if ecological forces bring about "accelerations"? This, in essence, is the *inertial view*⁶ of population dynamics.

Now this is a second-order theory,⁷ since the central thesis is about rates of change of rates of change and hence employs a second-order differential equation:⁸ $\frac{d}{dt}\left(\frac{1}{N} \frac{dN}{dt}\right) = f\left(N, \frac{1}{N} \frac{dN}{dt}\right)$. A few points to note in relation to this theory. First, population size is not a complete descriptor of the dynamic state; we need information about both the population size and its rate of change. Thus the disagreement between the inertial theory and the Lotka-Volterra theory is non-trivial. Some of the differences will be discussed in section 5, but for now, we mention one major difference: the second-order, or inertial, character of this theory gives rise to a time lag. According to the inertial view, the rate of change of the population abundance at any time depends on both the population abundance and its rate of change. The fact that this results in a time lag is easiest to see in the discrete presentation of the theory.⁹ The traditional theory, in discrete form, has it that the population abundance N at some time $t + 1$ is a function of the abundance at the previous time step t : $N_{t+1} = N_t F(N_t)$. On the inertial view, the the population abundance at some time $t + 1$ is a function of the abundance at both t and $t - 1$: $N_{t+1} = N_t G(N_t, N_{t-1})$. The dependence of the population abundance at $t + 1$ on N_{t-1} constitutes a time lag that has no counterpart in the traditional Lotka-Volterra theory.

Second, it is interesting to note that the first-order (Lotka-Volterra) equation drops

⁶ The reason for the name will become apparent shortly, along with the other physical analogies used—'velocity', 'acceleration', 'force' and the like. It should be mentioned, though, that the use of the word 'inertia' for internal explanations for population cycles (as opposed to external predator-prey explanations) is not uncommon in the literature. It appears, for example, in a chapter heading of the classic book (Wynne-Edwards 1986) as well as throughout the work of one of the present authors (Ginzburg).

⁷ Second-order theories of population dynamics were first proposed independently by Clark (1971), Ginzburg (1972), and later by Yee (1980). More sophisticated presentations can be found in Ginzburg (1986), Ginzburg and Colyvan (2004).

⁸ We present the theory here in its simplest form, where f is a function of population abundance and the per capita growth rate. This is in order to stress the points of contact with, and departures from, the traditional theory. In the theory's most general form, f is a function of the environment of the population (of which population abundance is part) and the per capita change in the environment (of which per capita growth rate is part). In section 6 of this paper we revert to the more general form of the theory, since the topic of section 6 is most readily seen in this setting. For now, however, we stick with the simpler form.

⁹ And after all, the use of differential equations in population dynamics is clearly an idealisation; populations are discrete and so the appropriate mathematical machinery is really *difference* equations. Differential equations, however, continue to be used, mainly for their convenience.

out as a special case of the inertial view. This is not unlike the way in which Aristotelian physics is a special case of Newtonian physics when friction is high.¹⁰ The analogue of friction in the ecological case is space (or, more generally, resource) constraints. The idea being that when population density is considered (as in the standard first-order logistic equation) these resource constraints act as a kind of friction in the second-order theory.¹¹ When resource constraints are extreme, the growth rate is retarded to such an extent that a “force” is required to sustain the growth rate of the population. Since such severe space or resource constraints are not uncommon, many (but not all) populations behave like first-order systems. This fact is easily accommodated by the inertial theory.

Finally, we point out that this inertial approach allows for much more complex dynamics without requiring population interactions. In effect, this move from a first-order to a second-order model requires more by way of initial conditions but is able to accommodate a greater variety of phenomena. Now there would be little motivation for such a move if the phenomena in question were never observed—the first-order model would thus suffice. In section 5 we will look at some of the crucial phenomena and argue that the inertial view does a better job of accounting for them. For now, we merely wish to draw attention to the important trick of increasing dimensions to produce a more flexible theory. This trick is very common in physics. The idea, in effect, is to delimit the range of questions your theory can address and pass the rest off as uninteresting facts about initial conditions.¹² In the next section we pursue this issue. We discuss a very similar move in physics around the time of Galileo.

Aristotle and Galileo

According to Aristotelian mechanics, the default state is the rest state. That is, a body remains at rest unless acted upon by a force. Moreover, the result of a force acting upon a body is a velocity. This view prevailed for around 2000 years because it was (and is) intuitively plausible and it agreed very well with everyday observations. After all, almost all observed moving bodies slow down and eventually stop unless a force sustains them. But there are a few anomalous cases: most notably, the planets. Planets appear to move continuously and without any obvious force propelling them. How is this possible on the Aristotelian view?

According to the Aristotelian view, there must be some force propelling the planets. Let’s suppose that some Aristotelian physicist were to preempt Newton and suggest that gravity was the force at work here. More specifically, let’s suppose that

¹⁰ For example, in a viscous liquid, particles behave as though governed by Aristotelian physics: forces result in velocities and particles stop almost immediately unless acted upon by a force.

¹¹ This issue is discussed further in Ginzburg (1986).

¹² To solve second-order differential equations you require more by way of initial conditions than a first-order differential equation. The former requires two sets of initial conditions (or boundary conditions), while the latter requires only one.

the imaginary physicist suggested that the result of gravitational force is a velocity, so the gravitational attraction between the planet and the sun resulted in the velocity of the planet circling the sun (or perhaps orbiting the combined centre of mass). As it turns out, this is impossible. If we think of gravitation as a force that results in a first-order quantity, like a velocity, there can be no orbiting planets—all planets would simply hurtle directly towards the sun or spiral into the sun (depending on initial conditions). To get an *orbiting* planet, we require an extra force. Moreover, this extra force must be constantly changing in direction; we require something like “the hand of God” to keep planets orbiting the sun.

The reason for this is a fairly straightforward consequence of the mathematics. To get trajectories as complex as cycles, we require (at least) second-order differential equations.¹³ If gravitation is a force that results in a velocity, the resulting differential equation is only first order.¹⁴ Now this presents a huge problem for anyone proposing a broadly Aristotelian theory of planetary orbits using gravity as the mechanism. The Newtonian theory of gravitation, on the other hand, is the simplest theory that is capable of explaining planetary orbits, without appeal to additional forces. The reason is again straightforward: Newton recognised that forces result in accelerations, not velocities, the resulting mathematical description of the two-body problem is a second-order differential equation and thus it admits periodic solutions such as ellipses.¹⁵

Now there is no question of the superiority of Newtonian theory over Aristotelian theory. What is somewhat surprising then is that the same move from a first-order theory to a second-order theory in population dynamics is receiving a great deal of resistance. Before we examine that debate, let’s return to the inertial model of population growth and briefly consider some of the evidence for it.

Evidence for the inertial view

The first piece of evidence for the inertial view is population cycles. These are populations whose abundance oscillates in a periodic way over time. On the standard, first-order account of population growth, such periodic behaviour must be the result of external ecological forces. These forces might take many forms, but the most common account is in terms of predator–prey interactions. According to this story, whenever we find periodic behaviour there must be (at least) two species interacting in a predator–prey relationship. The idea being that the predator can consume the prey until numbers of the prey decline to such an extent that the predators find it difficult to find prey. The predators then start to starve and thus decline in number. The decline in the predator population allows for a revival in prey numbers, which in turn results in a revival in predator numbers, and so on.

¹³ That is, equations involving second derivatives of the displacement function.

¹⁴ That is, the equation involves only first derivatives of the displacement function.

¹⁵ Of course, it admits other solutions as well, such as paraboli, straight lines and spirals.

Such a system is described by the standard Lotka-Volterra predator–prey equations.¹⁶

According to the inertial model we are proposing here, however, population cycles are possible *without* species interaction. The reason for this is that the theory is second order and thus allows for periodic trajectories—these trajectories are driven by an internal mechanism, to be discussed in the next section. Now since the standard Lotka-Volterra model requires species interaction for cycles, if we were to find a cycling population that was not part of a predator–prey pair, this would count for the inertial view and against the Lotka-Volterra view. Although there are many such populations it is not so easy to dismiss the Lotka-Volterra view. In cases of single-species cycles, the species in question must be using *some* resources, such as grasses, and these resources can be considered the prey. Moreover, this move does not seem in any way *ad hoc* because it is clear that overexploitation–underexploitation cycles should also result with, say, grasses and kangaroos. The existence of (apparently) single-species population cycles is thus not decisive.

The best evidence for the inertial view comes from considering a starving population. Let’s assume that there is no food for a given population. Some organisms respond to the absence of food by shutting down their various metabolic functions. They do not die in the absence of energetic input but rather “sleep” until food is available again. Simple unicellular organisms such as *E. coli* do this. Most other organisms, including mammals and birds, die in the absence of food. It is this death process we wish to consider more closely.

In the 1980s Larry Slobodkin conducted some very interesting experiments on water from the Hudson River. He used the freshwater polyps, brown and green hydra, to determine the quality of the water from various sites in the Hudson system. In particular, he placed five of these animals in a synthetic pond of water from the Hudson. In all, there were over 100 such ponds with water from 51 different locations. He fed the hydra for three weeks prior to the experiment and then stopped feeding them, with the number of individuals in each pond being recorded on a weekly basis.

The experiment was originally conceived of and designed to study how quickly the hydra died in the different Hudson water samples. It turns out, however, that this experiment also tells us something rather important about population dynamics. Since all the hydra populations were without food during the experiment, we have a study of the way in which populations die in the absence of energetic input. According to accepted wisdom in population dynamics, the hydra populations should have died exponentially. That is, if we graph the logarithm of the number of individuals in a given population versus time, we should end up with a straight line with negative slope. What the experiments showed, however, was that the hydra died with acceleration (see Figure 1). That is, the graph of the logarithm of the number of individuals in a given population versus time was a parabola—the shape of the flight of a projectile falling under the influence of gravity.

¹⁶ These equations admit periodic solutions, since coupled first-order equations can be thought of as a single second-order differential equation.

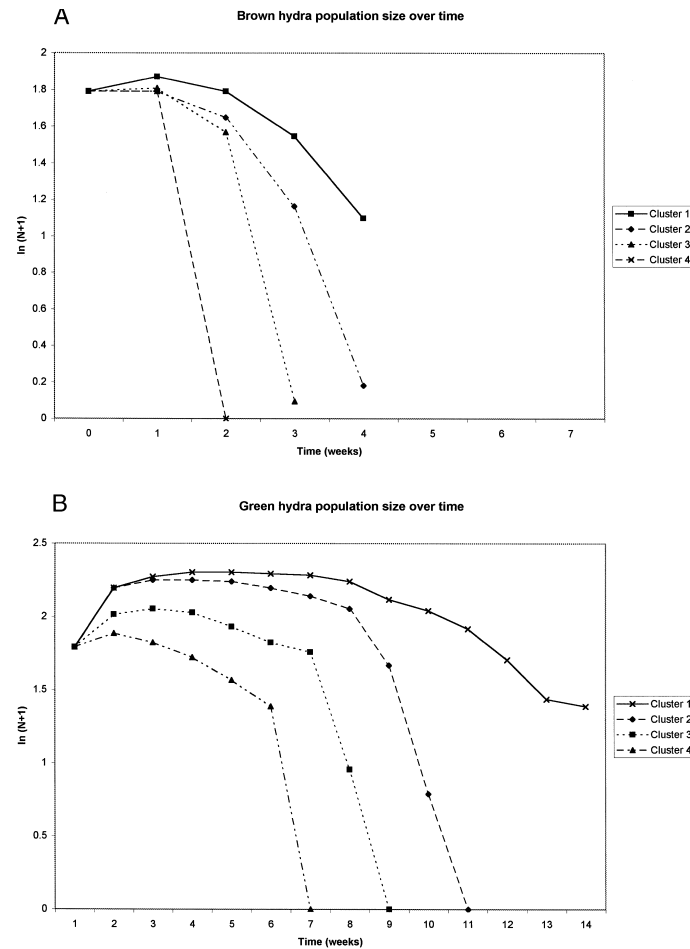


Figure 1. Figure 1 summarises the results of a starvation experiment conducted by Slobodkin on brown and green hydra (Akçakaya et al. 1988). The original purpose of this experiment was to assess the water quality of samples from 51 different sites on the Hudson River. However, the results also demonstrate that the decline of populations under starvation is accelerating rather than constant. Two replicates were run using water from each site, for both brown and green hydra, resulting in 102 populations tested for each. Each population started with 5 individuals and the population size was recorded once a week. A geometric average was taken for the population sizes of the two replicates for each location. The data from five of the 204 total populations were discarded because of insufficient data points (less than 2 non-zero points). For this figure the population data was combined into clusters, with each cluster based on the longevity of the included populations. The natural log of the population sizes is shown; the original data in arithmetic scale can be found in Akçakaya et al. (1988). Since the natural log of 0 does not exist, we added 1 to the population size in order to be able to show the decline to zero abundance.

Now the length of time it took for each of the different populations to die was different, depending on the relevant population's initial growth rate—just as a rock thrown (with the same force) travels further, if thrown at a trajectory of 45 degrees

as opposed to, say, a trajectory of 10 degrees. Also the brown hydra died more quickly than the green, since the green hydra have extra energy input from their symbiosis with green algae (that gives them their colour). The important point, for present purposes, is that all the populations exhibited accelerated death. This is a telling point against the traditional model of population growth. On the other hand, this is exactly what you would expect on the second-order model we're proposing. For if organisms continue to metabolise energy in the absence of food, their internal energy level will decline and their rate of reproduction will follow this decline. Thus we expect the total population abundance to decline with an accelerated, not a constant, exponential death rate. This experiment, though not decisive—no single experiment ever is—presents a serious problem for the standard model of population growth and a telling point in favour of the second-order, inertial proposal.¹⁷

The maternal effect

The essence of the inertial view is that there is a lag in population growth: the rate of change of the growth rate is a function of the environment and of environmental change.¹⁸ Or, put another way, the rate of change of the growth rate is a function of the environment and of previous environments (the environments of previous generations). If this view is correct, the importance of previous environments has not been appreciated thus far in population dynamics. But how can a population respond to past environments, and why should a population respond to the way things *were* rather than simply responding to how things are now? We thus arrive at the first stumbling block for the inertial view. The problem is that thus far we have been concerned with the mathematics of the model—arguing for a second-order model over a first-order model—without regard for how the mathematical model is interpreted in terms of the biological systems being studied. In short, a second-order model is all well and good, but given that this implies a time lag, what is the causal mechanism that underwrites this lag?

This is a very good question, and it was largely due to the lack of a convincing answer to this question that this theory was given very little attention in the ecological literature until the 1990s. Before we discuss our answer to this question, let us emphasize the importance of providing an answer. After all, you might be tempted to simply dismiss the question and trust the mathematics, wherever it should lead. Indeed, this is very close to what happened in the analogous physics story. Why should position depend on both velocity and previous velocities. “That’s just the way things are”, is the answer. What is the mechanism for two bodies

¹⁷ See Akçakaya et al. (1988) for further details of the relevance of the Slobodkin experiments to the debate over first-order versus second-order models of population dynamics.

¹⁸ We discuss the more general form of the theory in this section (recall footnote 8): $\frac{d}{dt} \left(\frac{1}{N} \frac{dN}{dt} \right) = f \left(E, \frac{1}{N} \frac{dE}{dt} \right)$. Here E is the quality of the environment (which includes the abundance of the population in question).

remote from another to have gravitational influence on one another? Again, that's just the way things are. Why not answer the ecological question along similar lines?

This is a very tempting response for the more mathematically oriented scientist, but to advance such a response is, we believe, to seriously misunderstand the nature of biology and its relationship to physics. Physics, by its very nature 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, we suggest, be reserved for physics.¹⁹

Let us be clear about what we are *not* saying. We are not suggesting a commitment to a foundational view of knowledge. On the contrary, we both reject any such foundational assumptions. Our point, although most readily put in foundationalist terms, can be recast in coherentist terms: physics is the more central discipline and so, typically, scientific facts from other scientific disciplines must either reduce to, or supervene upon, physical facts. So, while it is permissible to have primitive physical laws that are unexplained, this is less acceptable in other scientific disciplines. We also wish to point out that we are not suggesting that the relevant reductions can be performed or that the details of the relevant supervenience relations can be spelled out. We are simply suggesting that it would be most implausible for biological facts, for example, *not* to at least supervene upon physical facts. To deny this is to give up on physicalism.²⁰

All we are saying then is that to accept the inertial view, without further ado is effectively to give up on the search for a physical or causal mechanism for the time lag we drew attention to above. Such faith in the mathematics might not be out of place in physics where explanation is nearing an end, but in biology and ecology it is not unreasonable to ask after the reason for the lag. Even a nod in the direction of the mechanism and a promisory note is preferable to no story at all.

Fortunately there is a story to be told here. The primary reason for inertia in population growth, we believe, is the *maternal effect*. This is the phenomenon of "quality" being transferred from mother to daughter. The idea being 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 blessed with 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

¹⁹ Issues concerning the differences in time scales may also be relevant here. Physics is very often concerned with instantaneous change, where the time scale is arbitrarily small; in population ecology, on the other hand, working with *generation time* seems more natural. Perhaps, as a result of this, in ecology there is a tendency to think in terms of cause and effect. Moreover, in ecology there is time to isolate the causes. This is not always the case in physics.

²⁰ This is not an argument, of course, just a commitment to physicalism.

both the current environment and, to some extent, the environment of the previous generation.²¹

The maternal-effect hypothesis provides an elegant answer to the question of the mechanism for the time lags involved in the inertial model of population growth. This, as we've already suggested, loomed as a serious problem for the inertial view. There is, however, another, more general concern about the inertial model. This concern involves the role of mathematics in theory choice and we discuss this issue in the next section.

The role of mathematics in ecology

Now you might think that in our defence of the inertial model of population growth we have put the mathematical cart before the empirical horse. After all, we've followed the mathematics of the second-order model as far as it would take us, driven primarily by analogies in physics, but it was seemingly only an afterthought to propose an ecologically-based mechanism for the theory (in the form of the maternal effect hypothesis). Surely this is the wrong way to go about developing a theory. If an ecological theory is not motivated by *ecological* considerations, it would seem to be resting on shaky ground. Moreover, if an ecological theory is motivated by *mathematical* considerations it would seem to be lacking motivation altogether.

This is a very interesting point and one that raises all sorts of issues about the role mathematics plays in empirical theories. Although to discuss these issues in detail would take us too far afield²² we do need to say something by way of appeasing those sympathetic to the view that ecological theories should be motivated by ecological considerations, not mathematical considerations. The first thing to note is that there are many episodes in the history of science where the mathematics seemed to lead the way.²³ One such case was Maxwell's prediction of electromagnetic radiation. This prediction was a direct result (or so it would seem) of Maxwell being led by the similarities between the mathematical formalism of electromagnetic theory and the mathematical formalism of Newtonian gravitational theory. Our first response then is that if we are guilty of having the mathematical cart before the empirical horse, we are not alone.²⁴ Although this may not seem like an entirely satisfying response, there is something to it. The mystery of the applicability of mathematics has long been a puzzle for physicists, mathematicians and philosophers of mathematics; what we have here is simply one more instance of it.

There is another response though: the "proof is in the pudding" response. Now

²¹ See Rossiter (1996) for a nice survey of the maternal effect and Ginzburg (1998), Ginzburg and Taneyhill (1994) for details of its importance as a cause of inertia in population dynamics.

²² See Colyvan (2001, June-2001), Steiner (1998), Wigner (1960) for more on this very interesting issue.

²³ See, for example, Steiner (1998) for details of many such episodes in physics.

²⁴ Indeed, we are in pretty good company.

we admit that we were led to consider the inertial model of population growth by considering the analogy between population cycles and planetary orbits, and considering the mathematical formalism of each. That was not the end of the story though. Ultimately, the theory has to stand on its own legs, proving itself against its competitors on the usual fronts of empirical adequacy, elegance, consistency and so forth. We claim that the inertial theory performs very well on these fronts; how we came to this theory should have little to do with the theory's acceptance or rejection. The proof, as we say, is in the pudding.²⁵

A related issue concerns the interpretation of the second derivative in the ecological case. Although, second derivatives are well understood *mathematically*, it might be argued that the *ecological* interpretation of $d/dt(1/N dN/dt)$ is puzzling. Moreover, so the objection goes, we understand what the second derivative is in the analogous physical case; d^2s/dt^2 is simply acceleration. But since we don't really understand what $d/dt(1/N dN/dt)$ is, we have no reason to attach physical significance to the second derivative in the ecological case. This is an interesting objection but ultimately misguided. First, consider the case of acceleration in physics. Sure we have a convenient and familiar word for d^2s/dt^2 , but this is because it is important and it is needed. Its physical significance has little to do with whether there is a word for it or not, or whether we have an intuitive understanding of it or not.²⁶ Indeed, the thought that we understand acceleration in terms other than as "a rate of change of a rate of change of displacement" says more about the familiarity of the concept than its physical significance.²⁷

Now to the second derivative in ecology. We've deliberately used the word 'acceleration' for the concept in question so as to both stress the analogy with the physics case and to give a convenient (and familiar) name to what we take to be a significant ecological concept. Ultimately, the second derivative in ecology, like elsewhere, just concerns the rate of change of the rate of change of some quantity. Now that might be clumsy to say but we take it that it's perfectly intelligible.

Finally, let us briefly consider the legitimacy of the move to higher dimensions to gain flexibility in a theory. We've already pointed out that this is a device often used

²⁵ This response can be fleshed out further if we consider the distinction between reasons for entertaining an hypothesis and reasons for accepting it. It should not count against an hypothesis that it was initially the result of a drug-induced dream, say. So long as it stands up well to empirical tests and other desiderata of good theories, surely that's all that counts. Now it is clear that drug-induced dreams are generally not good hypotheses generators but mathematical analogies, it would seem, are. Why this is so (if it is so) is simply a restatement of the problem of the mystery of the applicability of mathematics. This is a problem, we believe, in need of serious attention but it is not, as we've already suggested, a special problem for us here. In any case, the origin of an hypothesis is not a reason for accepting or rejecting it. Hypothesis generation and hypothesis acceptance are two quite distinct exercises, and it would be counterproductive to hold hypothesis generation to the more rigorous standards of hypothesis acceptance.

²⁶ Consider the concept of intrinsic curvature of space-time manifolds in general relativity. It's not clear that anyone has an intuitive (i.e. non-mathematical) understanding of this concept, but there is no denying its significance.

²⁷ No doubt, when Newton first introduced the concept of inertia to physics, it had no intuitive reading.

by physicists. We've seen how Newton increased the order of the differential equation from one to two so as to get gravitational theory to work; Einstein treated time as a space-like dimension to (in effect) raise the dimension of the relevant manifold from three to four; and in the Hilbert-space formalism of quantum mechanics, finite-dimensional matrices are generalised to infinite-dimensional operators. Such moves are always open when a theory is unable to account for all the known phenomena. Once put like this, it does seem like an *ad hoc* trick, despite its illustrious history. The question, then, is: when is this trick legitimate and when is it not? And more pertinent to the point of the present discussion, is the move from the Lotka-Volterra theory to the inertial theory of population growth legitimate or not?

We don't believe that there is a general answer to the former question; we must consider each case of increasing the dimension of a theory on its own merits. As for the latter question, we agree that, all other things being equal, we should prefer theories with lower degrees of freedom. The question really then is whether the inertial theory is the simplest theory that can account for the data. This issue clearly requires further investigation, but we hope that in this paper we have said enough to conclude that the inertial theory of population growth is a good contender to the Lotka-Volterra theory. Only time will tell which is ultimately the preferred theory. And then, and only then, will we know whether the move to a second-order model was justified.

Closing remarks

There are at least two interesting philosophical lessons to be gleaned from this case study. First, we've seen that the role of mathematics may be quite different in different scientific theories. Even though the move from first- to second-order theories in physics was relatively unproblematic, there has been much resistance to this move in ecology. We have suggested that this resistance in ecology was to some extent justified in the absence of a mechanism explaining the time lag. We argued that accepting laws with brute-fact relationships like action at a distance and conservation principles are often appropriate in physics, but in many other sciences like biology and ecology, one would prefer causal explanations. Science may not be the homogeneous body of knowledge with uniform methodology that it is often taken to be.²⁸ Ecology and biology might be quite different from physics with respect to what counts as a satisfying explanation.

Second, this case sheds some light on a type of simplicity that seems rather important in many scientific contexts: the simplicity of lower-dimensional theories. At least some of the resistance to the second-order inertial view is due to the fact that this theory has one more degree of freedom than the competing Lotka-Volterra, first-order theory. The problem of spelling out what simplicity in science amounts to is notoriously difficult, but in this case it is rather straight forward: all other things

²⁸ See Cartwright (1999) for more on this issue.

being equal, prefer the theory with fewer degrees of freedom.²⁹ Obviously, we think that the move to the second-order theory is, in this case, justified, but we resist the move to a third-order theory, for instance. Why? Because we too agree that one ought not multiply dimensions beyond necessity.

We should mention some very interesting recent work on simplicity in the philosophy of science by Forster and Sober (1994). This work invokes a theorem by Akaike (1973) to shed light on the notion of simplicity involved in fitting the simplest curve to data.³⁰ In particular, Akaike's theorem tells us about the trade-off between fit and simplicity in curve fitting problems: it provides a way of balancing the competing goals of fewer parameters, and fit with the data. It turns out that simplicity is important for the predictive power of the model.

There are clearly some points of contact between the simplicity we have in mind—the simplicity of lower dimensional models—and the simplicity addressed by Forster and Sober—the simplicity of fewer parameters. There is, however, at least one major point of dissimilarity; in the application of Akaike's theorem, the dimensionality of the model is fixed in advance. But the dimensionality of the model is precisely the issue that we're interested in. Moreover, there is no obvious way to construe the choice of dimension as a curve-fitting problem, so the Akaike framework does not seem applicable here.³¹ This may mean that the kind of simplicity that Forster and Sober discuss is just one among many. This would not be at all surprising, but the matter certainly deserves further attention. In particular, the relationship between the simplicity of lower dimensions and the simplicity of fewer parameters is an intriguing issue that we hope to pursue elsewhere.³²

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²⁹ Stated thus, this kind of simplicity bears a striking resemblance to Popper's criterion of falsifiability: the fewer degrees of freedom the theory has, the less phenomena the theory is able to account for (and the more falsifiable it would seem to be).

³⁰ See also Mikkelsen (2001) for applications of these ideas to ecology.

³¹ There is also the issue that the goal when invoking Akaike's theorem is that of determining which model will be the more successful at *prediction*. Arguably, the goal when choosing the appropriate dimension of a model is that of finding the space most amenable to providing satisfying *explanations*. (Think of the move from three to four dimensions proposed by special relativity.) Again, there seems to be a substantial difference between these two enterprises. We thank Chris Hitchcock for this point.

³² Earlier versions of this paper were presented at the Australasian Association of History, Philosophy and Social Studies of Science Conference at the University of Melbourne in June 2001 and at the Universidade Federale da Bahia in Salvador, Brazil in August 2001. Work from this paper was also presented at a series of seminars in Stony Brook in 2001. We thank the audiences and participants at all these forums for their many valuable contributions. We would also like to thank Chris Hitchcock and Elliott Sober for useful discussions on the matter of simplicity in modelling. Work for this paper was sponsored jointly by Applied Biomathematics, New York, and by an Australian Research Council Strategic Partnership with Industry, Research and Training Grant to Mark Colyvan.

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