

# The Robust Volterra Principle

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## Abstract

Theorizing in ecology and evolution often proceeds via the construction of multiple idealized models. To determine whether a theoretical result actually depends on core features of the models and is not an artifact of simplifying assumptions, theorists have developed the technique of robustness analysis, the examination of multiple models looking for common predictions. A striking example of robustness analysis in ecology is the discovery of the Volterra Principle, which describes the effect of general biocides in predator-prey systems. This paper details the discovery of the Volterra Principle by robustness analysis. It considers the classical ecology literature on robustness and introduces two individual-based models of predation, which are used to further analyze the Volterra Principle. The paper also introduces a distinction between *parameter robustness*, *structural robustness*, and *representational robustness*, and demonstrates that the Volterra Principle exhibits all three kinds of robustness.

## 1 Introduction

Complex biological phenomena rarely admit of single, fully unified theoretical treatments. Instead, biologists often find themselves studying these phenomena using multiple, highly idealized mathematical models. These models may highlight different causal features, may be formulated at different levels of abstraction, or even may employ different mathematical frameworks in their representations of biological systems.

This use of multiple models presents special confirmation-theoretic challenges. Since all of the models employed in these contexts are highly idealized, it is useless to look for which of the models is a true description or is isomorphic to the target system. The theorist knows ahead of time that these relations cannot hold. Further, she is in possession of multiple models

which make incompatible assumptions. Thus the relationship between the theorists' models and target systems is complex and may not be describable in simple confirmation-theoretic terms.

Because the different models are highly idealized, theorists also confront the problem of determining "whether a result depends on the essentials of the model or on the details of the simplifying assumptions." Are the results generated by a set of models reliable, or are they artifacts of the analysis? (Levins, 1966) To address these problems, theorists have developed the technique of *robustness analysis*. This technique involves studying a number of similar, but distinct models of the same phenomenon trying to find common predictions among them. In his famous discussion of robustness analysis, Richard Levins describes what happens when the same prediction is made using multiple models.

[I]f these models, despite their different assumptions, lead to similar results, we have what we can call a robust theorem that is relatively free of the details of the model. Hence, our truth is at the intersection of independent lies. (1966, 20)

There is a small, but growing philosophical literature about robustness analysis. Starting from the pioneering work of Levins (1966) and William Wimsatt (1981), recent discussions have clarified the aims and methods of robustness analysis, discussed whether robustness analysis has a role in confirmation, and exactly what this confirmation-theoretic role consists of. (Orzack & Sober, 1993; Odenbaugh, 2003; Weisberg, forthcoming; Forber, in preparation)

Despite having a schematic for robustness analysis and despite the important discussions of RA's possible confirmation-theoretic role already in the literature, the philosophical literature has few if any detailed discussions of the actual robustness analyses carried out by scientists. Thus the primary purpose of this paper is to explain in detail the discovery of an important biological principle called the *Volterra Principle* by robustness analysis. We will discuss how the Volterra Principle was discovered, why ecologists believe it to be true, and conduct some further robustness analysis by introducing two novel individual-based models of predation. In addition, we will introduce a distinction between *parameter robustness*, *structural robustness*, and *representational robustness* and show that the Volterra Principle exhibits all three kinds of robustness.

## 2 The Lotka-Volterra Model of Predation

Predation is a much studied ecological phenomenon.<sup>1</sup> It is of great interest to ecologists because it often represents a force that keeps populations below their environment's carrying capacities. It is also a factor which can account for oscillation and other periodic dynamics of populations in which there is no external stimulation such as in unchanging environments. (Ricklefs & Miller, 2000) Theoretical ecologists are interested in studying how predation leads to these phenomena. They construct models to study those factors that control the maximum population size as well as the phase, amplitude and frequency of oscillations in populations. Naturally, some of these factors must be determined empirically, but there is also much that can be learned by analyzing clusters of models.

We have chosen to focus our discussion on predation because it provides an especially striking example of a robust theorem called the Volterra Principle. This principle was discovered by Vito Volterra, one of the founders of mathematical biology, and has been subsequently discussed by many key figures in contemporary mathematical ecology including Robert MacArthur (1966), John Maynard-Smith (1974), Joan Roughgarden (1979, 1997), and Robert May (2001). These theorists do not always use Levins' term 'robust theorem,' but their discussions of predation, biological control, and the Volterra Principle make it clear that they believe the principle is robust. Before investigating this principle, we begin by discussing the model from which the principle was first discovered.

Volterra (1926a, 1926b) and Alfred Lotka (1956) independently proposed the first model of predator-prey interactions that we will discuss. This is probably the simplest possible model of predator-prey interactions, but even this simple model already displays rich dynamics as well as the property of greatest interest to us in this project. Volterra was explicit about the grounds for constructing such a simple model. He wrote:

As in any other analogous problem, it is convenient, in order to apply calculus, to start by taking in to account hypotheses which, although deviating from reality, give an approximate image of it. Although, at least in the beginning, the representation is very rough ... it is possible to verify, quantitatively or, pos-

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<sup>1</sup>For a comprehensive review of the classical literature, see T. Royama, 1971. For more contemporary discussions including the history of predator-prey modeling, see Berryman, 1992; Hanski, Henttonen, Korpimäki, Oksanen, & Turchin, 2001; Briggs & Hoopes, 2004; Jurell, 2005.

sibly, qualitatively, whether the results found match the actual statistics, and it is therefore possible to check the correctness of the initial hypothesis, at the same time paving the way for further results. Hence, it is useful, to ease the application of calculus, to schematize the phenomenon by isolating those actions that we intend to examine, supposing that they take place alone, and by neglecting other actions. (Volterra, 1926b, translation G. Sillari)

To understand these remarks and the ways that the Lotka-Volterra model is a very simple way to representing predation, it is useful to think along the lines of a modeler approaching the problem for the first time. We ask: “What are the essential quantities and interactions that our model needs to keep track of in order to represent predation?”

If we are going to treat predation as a population-level phenomenon as Lotka and Volterra did, the primary quantities to keep track of are the size of the predator and prey populations. Alternatively, we can keep track of the population density, a quantity more easily measured empirically. We will refer generically to these measures as *species abundance*.

The next step in thinking about the structure of the model is to describe the intrinsic population dynamics of each species, or how the abundance of each species changes over time. Because the two species interact, their population dynamics are coupled together. This is the essence of the predator-prey interaction: the predators decrease the population of prey by eating them, while the prey increase the population of predators by providing food. Thus, in principle, we have six things to keep track of: the predator growth and death rates, the prey growth and death rates, the effect of predation on the population of prey, and the effect of prey capture on the population of predators. If we set up our model in terms of rates of increase and decrease, we can collapse intrinsic growth and death rates in to a single growth rate for the prey and, a bit less realistically, a single death rate for the predators. This will give us four quantities to keep track of.

Let  $V$  stand for the size of the prey population and  $P$  for the size of the predator population. If we express these basic relationships with coupled differential equations then we get the following basic equations:

$$\frac{dV}{dt} = [\text{prey growth rate}] - [\text{capture rate of prey per predator}]P \quad (1)$$

$$\frac{dP}{dt} = [\text{predator births per capture}]P - [\text{predator death rate}] \quad (2)$$

(after Roughgarden, 1979)

These equations provide a template for a large but tightly linked family of models. Starting from the simple possibilities, the prey growth rate could be linear, exponential, geometric, or logistic. The most typical death rate of the predators in predation models is constant, implying an exponential decay in the absence of prey. More complicated rate expressions are also possible, including functional dependence on environmental parameters and logistic decay when multiple sources of food are present. For the sake of simplicity, we will only consider examples where the predator death rate is constant, but we can modify the form of the intrinsic prey population growth rate.

Of greater biological interest, at least when considering predator-prey interactions, are the second term in equation (1) and the first term in equation (2), called the *functional response* and *numerical response* respectively. (Holling, 1959) As we can see from the equation template, the functional response is a rate, specifically the rate of prey capture per predator. The simplest possible assumption is that the functional response is linear, or that the number of prey capture increases linearly with increasing numbers of prey. This simple assumption may be actually true over some ranges (Korpimäki & Norrdahl, 1991) or when one is considering filter-feeding organisms, but more often than not is simply an approximation. Increasing numbers of prey can create additional ecological interactions, not to mention changing the foraging behaviors of the predators. More realistic assumptions about the functional response have the rate of capture per predator decreasing with increasing number of predators. Even under this assumption, there are several different possibilities. For example, when prey are very abundant, predators will eventually become satiated. Another possibility is even more realistic: With very low numbers of prey, predators will lack the experience to be efficient hunters. With increasing numbers of prey, predators will become more efficient at hunting. Ultimately, there will be a number of prey beyond which the predators simply become satiated. (Tinbergen, 1960; Papaj & Lewis, 1993)

Finally, the numerical response term correlates predator births to the number of prey captured. Because of this, the numerical response is itself a function of the functional response. Specifically, the numerical response

depends on how many prey are in the population, how good the predators are at capturing them, and how much energy from the prey captures can be allocated to the production of new offspring. Naturally, this is a very complex question and will depend on other environmental variables, other stresses on the predator population, the energetic cost of offspring, etc. Ecologists almost always collapse most of this complexity in to a single parameter and represent the numerical response as a constant multiplied by the functional response.

Now that we have considered how the basic template could in principle be filled in, let's return to the Lotka-Volterra (L-V) model itself and to Volterra's justification of it. As we said earlier, the L-V model is probably the simplest way to make a population level predator-prey model because we are going to fill in (1) and (2) with the simplest functions.

In our representation of the L-V model,  $r$  stands for the growth rate of the prey population and  $m$  stands for the death rate of the predators. The functional response is linear, expressed as a constant  $a$  multiplied by  $V$ . Similarly, the numerical response is a linear function of the numerical response so the whole numerical response expression can be written as a parameter  $b$  multiplied by the functional response, or  $b(aV)$ . The L-V model is thus described with the following differential equations:

$$\frac{dV}{dt} = rV - (aV)P \quad (3)$$

$$\frac{dP}{dt} = b(aV)P - mP \quad (4)$$

These equations describe a model which predicts one result: the predator and prey populations will oscillate indefinitely, out of phase with one another. Although for every set of parameter values with species co-existence, there exists one equilibrium where the populations do not oscillate, this equilibrium is unstable and hence the model populations continue to oscillate if it is perturbed even slightly off of these equilibrium values.

Figure 1 plots the result of this oscillation for a set of parameter values and initial conditions. Qualitatively, it can be described as follows: As the prey population increases, the predator population increases as well, lagging behind. However, eventually, the predators begin to overtake the prey by continual feeding, which eventually begins to drive the prey population down in size. This results, in turn, in the predator population being driven down in size, and then the cycle repeats again. This undampened oscillation is the first important property of the L-V model that we will test for robustness in this paper. Before doing so, let us consider several more properties.

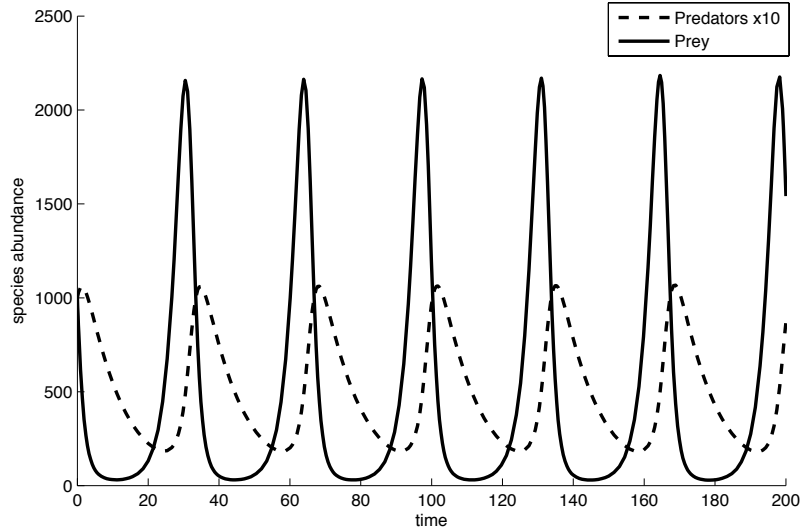


Figure 1: Lotka-Volterra Model's Oscillation

A second important property of the L-V model is neutral stability. The model exhibits neutrally stable oscillations, which means that perturbations away from the current oscillation amplitude will result in a new oscillation beginning from the point to which the oscillation was perturbed. There is no restoring force to bring the population back to the initial amplitude of the oscillations. This can be seen by plotting several trajectories, corresponding to different initial conditions, in the phase space of the model (see figure 2). Each loop is closed, corresponding to a stable oscillation. Perturbation results in the formation of a new loop, corresponding to a new, neutrally stable oscillation.

The third and fourth interesting properties of the L-V model concerns the average number of predators and of prey during one full predator-prey cycle, which corresponds, in this case, to the equilibrium abundances of the species. We can solve for the equilibrium by setting each differential equation to zero. After some algebra, we find that the equilibrium values are:

$$\hat{V} = \frac{m}{ab} \quad (5)$$

$$\hat{P} = \frac{r}{a} \quad (6)$$

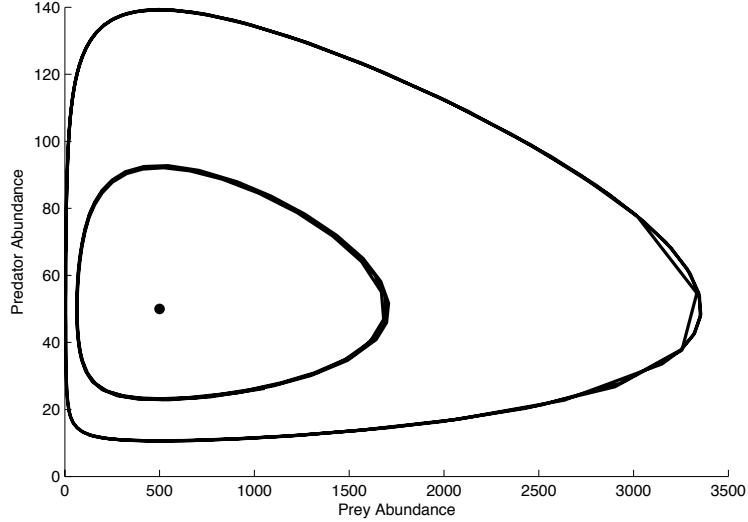


Figure 2: Phase-plot of Lotka-Volterra Model

These equations tell us that the primary factor determining the average abundance of the prey is the death rate of the predators, and the primary factor determining the average abundance of the predator is the growth rate of the prey. The prey's growth rate does not appear to matter for the average size of the prey population. Similarly, the predator's death rate does not matter for the average size of the predator population. This is a surprising result which tells us that the fate of the predator population is more tightly connected to the prey population than it is to its own intrinsic properties. The same is true for the prey population.

Finally, there is a fifth property of the model that is of special concern to us in this paper, what we call the *Volterra property*, which is the key component of the Volterra Principle. The Volterra property states that a general biocide, any substance which has a harmful effect on both predators and prey, will *increase* the relative size of the prey population. We can derive the Volterra property from the L-V model by first expressing the ratio of the average size of the predator population to the average size of the prey population ( $\frac{\bar{P}}{\bar{V}}$ ) as  $\rho$ . Decreases in  $\rho$  will correspond to increases in the relative size of the predator population.

From equations (6) and (5) we can see that



$$\rho = \frac{rb}{m} \quad (7)$$

The next step is to consider how a general biocide affects the model populations. We can represent the introduction of a biocide as corresponding to changes in  $r$  and  $m$ . Specifically, biocides decreases the prey growth rate ( $r$ ) and increases the predator death rate ( $m$ ). Inspecting  $\rho$ , the expression for the ratio of average densities, we can see that  $\rho(\text{biocide}) < \rho(\text{normal})$ . (May, 2001; Roughgarden, 1979, 439) Since smaller values for  $\rho$  mean a larger relative size of the prey population, the population of prey will increase relative to the number of predators when a biocide is applied. This is the Volterra property: the general biocide increases the relative size of the prey population.

The Volterra property is a key component of the Volterra Principle, the ecological theorem being tested for robustness in this paper. The full formulation of the principle can be stated as follows:

*Ceteris paribus*, if the abundance of predators is controlled mostly by the growth of the prey and the abundance of the prey controlled mostly by the death of predators, then a general biocide will increase the abundance of the prey and decrease the abundance of predators.

Note that the Volterra Principle connects the Volterra property (the robust property) with two antecedent conditions (the core structure). These antecedent conditions should be familiar as the third and fourth properties of the L-V model discussed above. As we will see through the various stages of robustness analysis conducted in this paper, the core structure and robust property always come together.

The Volterra Principle has great ecological significance. One very practical consequence of it is that pesticides will often increase unwanted pests, such as the effect DDT had on citrus groves in southern California in the 1950s. When it was used as a treatment against scale insects, orchardists learned that DDT makes the pest problem worse. The cottony cushion scale insect (*Icerya purchasi*) population increased upon the application of DDT because along with the scale insects, the DDT killed the vedalia beetle (*Rodolia cardinalis*), a predator species keeping the scale insect under biological control (Catagirone & Douth, 1989; Elton, 1958).

The principle also has a deeper theoretical significance. It provides a vivid example of how ecologically coupled systems can behave in unexpected,

non-linear ways. Interventions in such systems are difficult and, without due care, can have the opposite effect of what was intended.

These five properties — undampened oscillations, neutral stability, primary dependence of the predator population size on prey growth rate, primary dependence of the prey population size on the predator death rate, and the Volterra property — are very interesting and would be of great ecological relevance if they were generally true of real populations. One way to ask whether these properties hold generally would be direct empirical investigation. We could go out in to the field or design a laboratory experiment and see if these predictions are close to what really happens. But there is another approach to answering the question, one that is often conducted prior to or in conjunction with direct empirical investigation. This approach is robustness analysis. If we investigate related but distinct models, do we continue to see these five properties?

The first step in answering this question is to examine a representative sample of the models described by equations (3) and (4). One does this by evaluating the behavior of the model when the parameters are set to different values with each parameter set corresponding to a complete set of trajectories in the model’s state space, or a single a model. This analysis ensures that there is no special dependence of an interesting result on some particular set of initial conditions. We call this kind of analysis *parameter robustness analysis*, because it shows us whether the model’s behavior is dependent on any particular set of parameters. Although we will not detail the analysis here, all five of the properties are stable under parameter robustness analysis of the L-V model.

A more fundamental forms of robustness analysis is what we call *structural robustness analysis*. In this kind of robustness analysis, the theorist considers changes to the basic structure of the model by analyzing structurally distinct models. In the next section, we describe one kind of structural robustness analysis for predation by considering the density-dependent version of the L-V model. Many other examples could also have been chosen, but this one is both striking and has played an important role in the development of predation theory.

### 3 Predator-prey Model with Density Dependence

While considerations of structural robustness could lead us to add any additional function to the predator-prey equations, a natural ecological addition would be to add a carrying capacity to the growth rate of the prey. If the

predators did not exist, this carrying capacity indicates the maximum size to which the prey can grow, typically limited by resources in the environment. Adding a form of carrying capacity can be accomplished by making the prey population growth density dependent. A logistic growth term of the form  $dV/dt = r(1 - V/K)$  is substituted for the first term in the prey equation. (Leslie, 1948; Roughgarden, 1979; Berryman, 1992), yielding the following equations:

$$\frac{dV}{dt} = r(1 - \frac{V}{K})V - (aV)P \quad (8)$$

$$\frac{dP}{dt} = b(aV)P - mP \quad (9)$$

In the model described by these equations, there are three equilibria, which correspond to the three possible outcomes in the long run. The first equilibrium is extinction of both species. The second equilibrium involves predator extinction, but the prey continues to survive and grow to its carrying capacity. The third equilibrium is of most interest to us and says that both species can coexist. Solving these equations for this third, coexistence equilibrium, we get the following expressions:

$$\hat{V} = \frac{m}{ab} \quad (10)$$

$$\hat{P} = \frac{r}{a}(1 - \frac{m}{abK}) \quad (11)$$

Several things are worth noting about this equilibrium point. First and most importantly, it is a stable equilibrium; there are trajectories leading from the points in the vicinity of this equilibrium to this equilibrium. Once the populations settle on this point, they will not fluctuate in size unless they are perturbed. Population sizes in the vicinity of the other equilibrium values (full extinction or predator extinction) will likewise settle down to their respective equilibrium values.

The stability of this equilibrium can be demonstrated both analytically and graphically. Analytically, we can see that the equilibrium is stable by computing the eigenvalues of the Jacobian matrix. For all parameter sets that bring the population to the third equilibrium, the eigenvalues have a real part and the real part is negative. This corresponds to a stable equilibrium point. (Roughgarden, 1979; May, 2001)

A graphical analysis is shown in figures 3 and 4, which are graphs of the phase space for the density-dependent model with different values of  $K$ . In the figure 3, all of the trajectories can be seen leading in to the

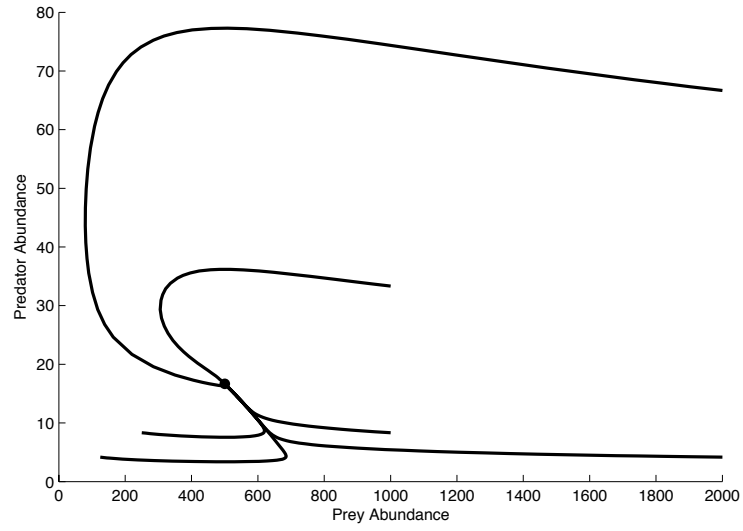


Figure 3: Density-dependent Lotka-Volterra Model with  $K=750$

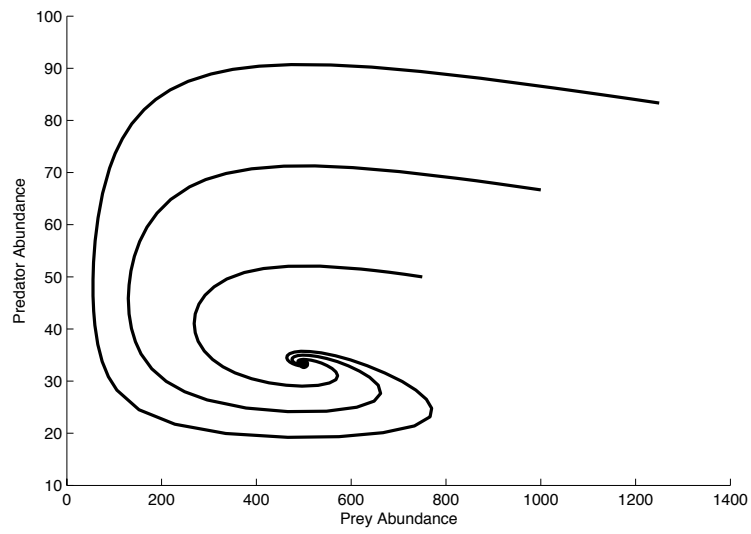


Figure 4: Density-dependent Lotka-Volterra Model with  $K=1500$

equilibrium point. In figure 4, the trajectories spiral in to the point. The difference between these graphs is controlled by the magnitude of  $K$ . For smaller values of  $K$ , there is no oscillatory tendency in the approach to the equilibrium point. When  $K$  is larger, such as in figure 4, the trajectories have an oscillatory tendency as they approach the equilibrium point. The oscillatory tendency increased in magnitude as  $K$  is increased. As  $K \rightarrow \infty$ , the model becomes the simple L-V model and, as we would expect, the oscillations become undamped.

We are now in the position to make two comparisons between the density dependent model and the L-V model. The first property of the L-V model was undamped oscillations. In regions of state space where the density dependent model predicts coexistence, the model shows either no oscillations at all or damped oscillations, all leading to a stable equilibrium. Even an arbitrarily small amount of density dependence will destroy the undamped oscillation. Thus the first property of the L-V model is not structurally robust and cannot be formulated as part of a robust theorem.

Since the first property is not robust, the second property — neutrally stability in the oscillations — cannot be robust either. What about the third and fourth properties of the L-V model? Reexamining equations (10) and (11), we discover a very similar result to the L-V model. The prey equilibrium  $\hat{V}$  is identical to the Lotka-Volterra equilibrium. So the average and in this case equilibrium size of the prey population is primarily dependent on the death rate of the prey. The predator equilibrium  $\hat{P}$  is more complex and depends both on the  $r$  and on  $m$ . However, the primary dependence is on  $r$  and we can conclude that the fourth property is also structurally robust.

Finally, let's consider the most interesting property of the L-V model, the Volterra property. Once again, we express the co-existence equilibrium values as the ratio  $\rho$ , yielding:

$$\rho = \frac{\hat{P}}{\hat{V}} = \frac{r(abK - m)}{aKm} \quad (12)$$

Since  $r$  is in the numerator and  $m$  in the denominator, we can see that the Volterra property, and by extension, the Volterra Principle holds for this model. If we increase the death rate of the predators and decrease the growth rate of the prey, this corresponds to smaller values of  $\rho$ , meaning the relative size of the prey population increases. In fact, in this model the Volterra Principle has an even more direct interpretation. In the L-V model, the equilibrium values corresponded to the average size of each population. However in the density-dependent model, the terms in  $\rho$  are the actual equilibrium sizes (or population densities) of the two populations. Decreasing  $\rho$

will have a direct effect on the equilibrium size of the populations, not the average size over time.

Testing the structural robustness of a theorem is a matter of iteratively varying the basic assumptions of a model to see whether the generalization continues to hold. We could make many other modifications to the density-dependent predator-prey model to test the structural robustness of properties 3-5. For example, we might examine other equations for the functional and numerical responses, examine the effects of population stochasticity, include the possibility of predator satiation, and add terms describing the prey's ability to hide from the predators. These possibilities were explored and shown to be robust in the classical ecology literature about predation. Instead of following those analyses here, we now turn to a different kind of robustness, which varies the representational framework of the model.

When a generalization continues to hold across different representational frameworks, we call this *representational robustness*. One way to vary the representational framework is to move from a model that is *population-based* to one that is *individual-based*. Instead of representing dynamic dependencies between population-level variables, such as the size of the predator or prey populations, individual-based models represent the dynamic dependencies between individual-level variables, such as the states of individual predators or individual prey. In the next sections, we consider two novel individual-based models of predation with which we tested the Volterra Principle for representational robustness.

## 4 Individual-based Predator-prey Models

The models considered so far have treated predation as a population-level phenomenon. These models aggregate the properties of many organisms and represent them using just a handful of population-level state-variables. They contain no explicit representation of individuals or their properties, only the statistical aggregates of those properties. In contrast, individual-based models (IBMs) explicitly represent individuals and their properties. An IBM includes a set of state variables for each individual within the model population. It also includes assumptions about how individuals in the population behave, develop, and interact over time. Since IBMs often contain thousands of variables, their dynamic consequences are usually investigated via computational simulation rather than mathematical analysis.

Population-level models are often more elegant and amenable to mathematical analysis than IBMs, but their very simplicity can be limiting.

Ecological systems have rich structure that is not readily visible from a population-level perspective. Organisms within a population generally differ in their properties and life histories. Interactions between organisms are *local*, involving a few individuals at a particular place and time. IBMs are effective at capturing this individual-level detail because they explicitly represent the properties of each organism in a population, and because individuals can be set up to interact in small numbers on a spatial lattice. When one wants to test whether individual variability or local interactions affect the robustness of a generalization, one can build an IBM.

IBMs are also useful because they integrate our understanding of the different levels in the biological hierarchy. Ecologists gather data about organisms, populations, and communities. IBMs help reconcile these multiple levels of data, because assumptions about organisms and their interactions enter into an IBM, and the population or community consequences of these assumptions result from running IBM simulations. IBMs are thus informed and constrained by ecological data at multiple levels. In contrast, the points of contact between population-level models and data are all at the population-level. Such models include assumptions about populations, but they are either silent or ambiguous concerning assumptions about individuals. This can be a strength when we want to remain agnostic about those assumptions, but it can also be a liability. In many cases, we may want to vary those assumptions and understand their consequences.

In recent years, IBMs have become increasingly common within ecology and among the sciences more generally. (Donalson & Nisbet, 1999; Grimm & Railsback, 2005; DeAngelis & Mooij, 2005) They are not a substitute for population-based models, but they can be used to relax assumptions made by generating population-based models. As such, each of these frameworks may be more or less appropriate depending on the purpose at hand. Indeed, for the purpose of testing the robustness of a generalization, one ought to examine as many representational frameworks as possible.

To test the representational robustness of the five properties of the L-V model, we will translate its variables, parameters, and other assumptions into individual-based terms.<sup>2</sup> In our discussion of the L-V model, we showed how the model makes assumptions about the growth and death rates of the predator and prey populations and about the interaction between these

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<sup>2</sup>The models described using this section and the next were developed in NetLogo v. 3.0.2. (Wilensky, 1999) The source code for the models is available at [journal’s designated repository]. Our models have some similarities to another NetLogo model called ‘Wolf Sheep Predation’ (Wilensky, 1998). For more information on ‘Wolf Sheep Predation,’ see Wilensky & Reisman (2006).

populations in the form of predation. Any individual-based version of this model must reconceive these processes in terms of individuals; it must make assumptions about the births and deaths of discrete predator and prey individuals, and the interactions between these discrete individuals in the form of predation.

In our first IBM version of the L-V model, we assume that individuals move about on a 30x30 lattice composed of 900 cells. Each individual has three variables: a binary variable denoting whether the individual is predator or prey, and two integer variables denoting a vertical and horizontal position on the lattice. Time is discrete; a global clock advances one tick at a time. For each tick of the global clock, all individuals execute a fixed set of rules that determine how they move on the lattice, reproduce, die, and interact with others. The rules for predators are as follows:

**Movement rule:** Move one step in a random direction.

**Predation rule:** Check if there are any prey on the current cell. If so, select one at random, catch it, and pick a random number from 1 to 100. If this number is less than or equal to the parameter *predator-conversion* then reproduce.

**Death rule:** Pick a random number from 1 to 100. If this number is less than or equal to the parameter *predator-death-probability* then reproduce.

These rules, when executed by each predator on the lattice, correspond roughly to assumptions made in the L-V model, but notice that these rules are not determined by that model. To translate any population-based model into individual-based terms, we must make explicit assumptions about individuals that were either implicit or undefined in the population-based version. This means that there is typically no uniquely correct way to carry out the translation from population-based to individual-based models.

The IBM assumes that predators move randomly on a two dimensional lattice. The L-V model, on the other hand, makes no assumption about movement at all. It is consistent with the assumptions that all individuals move, that some individuals move, or even, strictly speaking, that no individuals move. It places no explicit constraints on what intrinsic or environmental factors determine movement or even whether the predator and prey move in a probabilistic or deterministic fashion.

Moreover, the IBM assumes that predators catch prey by randomly selecting one prey individual from all that are located on the same cell. Once



again, this is one of the many possible assumptions we could have made to develop an IBM analogue of the L-V model. We could have represented predation without using a spatial lattice, where predators randomly choose prey individuals from the whole prey population. We could also have used a different predation rule on a lattice. For example, the predation rule could have stated “if a predator is within 1 cell of a prey, then the prey is consumed.” The L-V model does not strictly correspond to any of these particular assumptions. A modeler who wishes to construct an IBM, however, must make an explicit decision about them.

The rules for the prey are as follows:

**Movement rule:** Move one step in a random direction.

**Reproduction rule:** Pick a random number from 1 to 100. If this number is less than or equal to the parameter *prey-reproduction-probability* then reproduce.

**Death rule:** Check if I have been caught by a predator. If so, then die.

Together, the predator and prey rule-sets comprise one possible IBM interpretation of the L-V model. To understand the dynamic consequences of this model, we set up a computational representation of a lattice, place predator and prey individuals on the lattice, iteratively execute the predator or prey rules for each individual, and observe how the system evolves over time. In the initial state used in our simulations, there are  $V$  prey and  $P$  predators positioned randomly on the lattice.

After observing many simulations with differing parameter sets and initial conditions, we concluded that this IBM does not exhibit stable oscillations in the numbers of predators and prey, the first property of the L-V model. There are sets of parameters which initially result in oscillations, but these oscillations are unstable, increasing in amplitude over time until either both species have gone extinct (figure 5), or else the predators have gone extinct and only the prey remain (figure 6). Because this is a probabilistic model, the same parameter set and initial conditions sometimes results in two-species extinction and sometime results in the prey surviving. Figures 5 and 6 correspond to this situation: both used the same parameter set and initial conditions.

Regardless of the parameters, one or both species inevitably goes extinct. Although not conclusive, this result suggests that stable oscillations, or even stable co-existence, is not a representationally robust feature of predator-prey systems. Since the IBM does not exhibit stable oscillations, it clearly will not exhibit property 2 of the L-V model, neutrally stable oscillations.

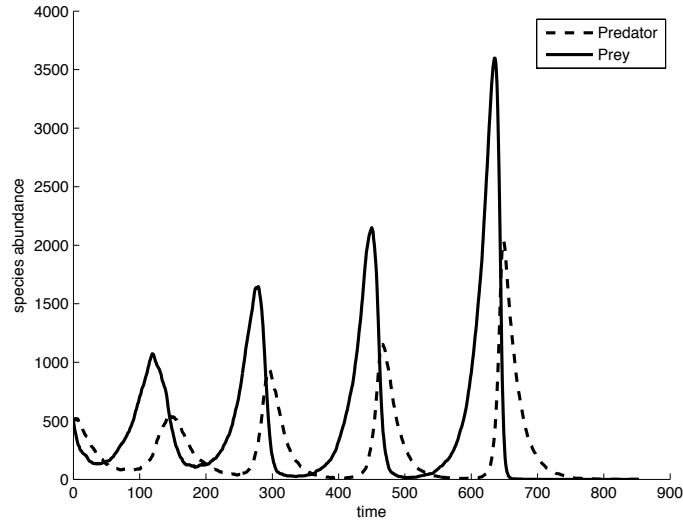


Figure 5: Simple Individual-based Model Corresponding to the Lotka-Volterra Model. In this trial, both species go extinct.

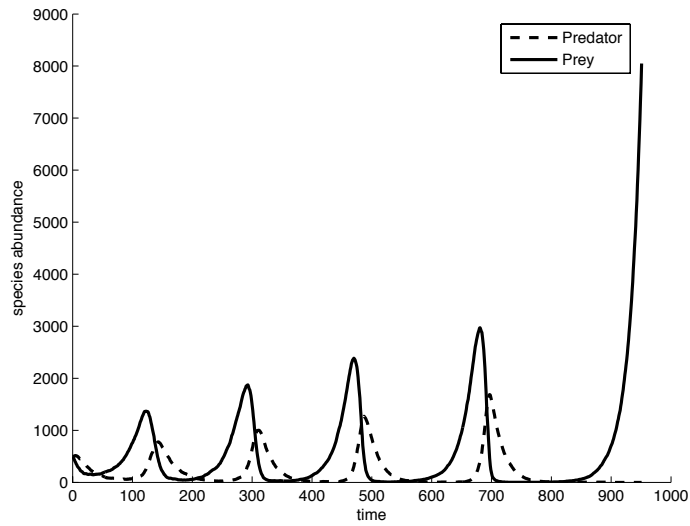


Figure 6: Simple Individual-based Model Corresponding to the Lotka-Volterra Model. In this trial, only the predators go extinct.

This IBM does not exhibit properties 3 and 4 either. According to these properties, the primary factor determining the equilibrium abundance of the prey is the death rate of the predators and the primary factor determining the equilibrium abundance of the predators is the growth rate of the prey. The abundance of predators and prey in the IBM are not controlled in this manner. The predators in the IBM always go extinct, regardless of the parameters controlling prey. The prey in the IBM either go extinct or else they increase in number until they fill the entire lattice, but which of these end-states occurs depends as much on the initial state of the system as it does on the parameters controlling predators.

Finally, since the IBM does not exhibit stable co-existence of species, it does not permit a test of property 5, the Volterra property. Testing this property requires examining the effect of a biocide on average abundances, which are either  $\hat{P} = 0$  and  $\hat{V} = \infty$  or  $\hat{P} = 0$  and  $\hat{V} = 0$ . To test the representational robustness of this property and the Volterra Principle itself, we must begin with a stable predator-prey system, and then check whether it is consistent with properties 3, 4, and 5.

Since we would like to test for the robustness of the Volterra Principle, we need to find an IBM that exhibits stable co-existence of the two species. In the next section, we describe a modification that does stabilize the populations. It achieves this stabilization by adding density-dependence.

## 5 Density Dependence IBM

One source of instability in the previous model is the lack of limits on population growth. The population oscillations tend to become more pronounced with each successive cycle until the population of one or both of the species falls too low and the species goes extinct. This suggests that if we introduce a carrying capacity to limit the upward amplitude of the oscillations in this model, extinction will be less likely.

How can we impose a carrying capacity on the model? The most direct way is to assume a fixed global limit on the number of predators and prey, yet this is not in the spirit of individual-based modeling; it is a top-down assumption about populations, rather than a bottom-up assumption about individuals. A bottom-up alternative is to impose a limited resource into the model, such as space. For example, we might assume that at most one predator can occupy any cell in the lattice at given time.<sup>3</sup> Another type of

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<sup>3</sup>A limitation to this assumption is that carrying capacity would be directly linked to the size of the lattice, so there would be no independent way to vary lattice size and

limited resource is food for the prey population. For example, if the prey are herbivores, the limited availability of edible foliage in the environment imposes a natural carrying capacity on the prey.

In our density-dependent IBM, we assume that the size of the prey population is limited by availability of food in the environment (for convenience, we will call the food “foliage,” but it could represent any naturally available resource). We assume that each cell of the lattice either contains a unit of foliage or not. When eaten by a prey individual, the unit of foliage disappears, and it then has a certain probability (set by the parameter (*foliage-growth-prob*) of reappearing at any subsequent tick. These assumptions suggest a revised rule-set for prey with a new foliage rule and a revised death rule:

**Movement rule:** Move one step in a random direction.

**Foraging rule:** Check if there is foliage on the current cell. If so, eat it, and pick a random number from 1 to 100. If this number is less than or equal to the parameter *prey-conversion-probability* then reproduce.

**Death rule:** Check if I have been caught by a predator. If so, then die.

The rule-set for predators remains the same.

Does this modified IBM, with density-dependence, display any of the five basic properties of the L-V model discussed earlier? After investigating many different initial states and parameter sets, we concluded that there is a wide range of parameter conditions for which this model does exhibit stable oscillations in the numbers of predators and prey. The amplitude of the population oscillations tends to vary stochastically over time, but both species do persist indefinitely. Thus, the density-dependent IBM does exhibit property 1 of the L-V model.

The model does not appear to exhibit property 2, neutrally stable oscillations. Under all the conditions we examined which result in stable oscillations, the average abundance of predators and prey did not depend upon initial conditions or prior population sizes. After perturbing the populations away from their equilibrium temporal average sizes, the populations would always return to their former averages. This suggests that property 2 of the L-V model is not representationally robust.

Does the model exhibit property 3? According to property 3, the average abundance of the prey depends on the death rate of the predators. In this model, predator death is represented as a probability. When the probability of predator deaths is increased, the average number of predators also

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carrying capacity.

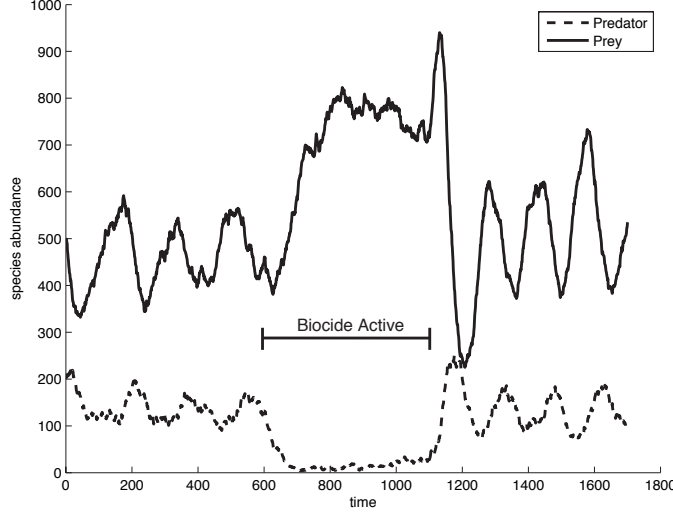


Figure 7: Density-dependent Individual-based Predation Model with Biocide perturbation.

increases. This means that property 3 holds. The same reasoning applies to property 4. Decreases in the predator birth probability correspond to decreasing average sizes for the prey population, so property 4 holds as well.

To check whether the model exhibits property 5, the Volterra property, we must somehow simulate the effect of a general biocide that would elevate the death rate of both the predators and of the prey. Since there are no parameters in the model that correspond directly to these rates, we must manipulate them indirectly. Fortunately, the individual-based framework makes it easy to simulate the dispersion of a general biocide into our model system. We performed the following perturbation: First, initiate a typical simulation of the predator-prey system and wait long enough for the temporal average size of each population to reach a steady state. Next, randomly select some cells on the lattice to become “poisonous”: i.e., any predator or prey that lands on the cell will die. Since movement is random, predators and prey are equally likely to die as a result of landing on poisonous cells and the result is an increase in the death rate of both populations. Finally, wait for the temporal average size of each population to reach a new equilibrium. After performing this perturbation under a variety of parameter settings, we found that introduction of a general biocide tended to increase the average

size of the prey population and to decrease the average size of the predator population (figure 7). In other words, despite moving from a population to an individual-based framework, and despite altering various assumptions of the L-V model, the Volterra Principle still held up. This suggests that the Volterra principle is representationally robust.

The analyses in this paper show that the Volterra Principle exhibits three kinds of robustness. Naturally, the scope of the Volterra Principle’s robustness is not a settled matter. Analysis could continue with different and more realistic models. For example, we might investigate a model where reproduction and death are tied only indirectly to food consumption via the introduction of rudimentary elements of metabolism.<sup>4</sup> In fact, tests for robustness are always an ongoing matter. It is unlikely that a theoretical community will settle the issue of a theorem’s robustness once and for all. Rather, ongoing investigation attempts to demonstrate the scope of a robust theorem.

## 6 Conclusions

Volterra discovered the principle which bears his name in 1926. By constructing a series of models, all similar but differing in some respects, ecologists have shown that the Volterra Principle accurately describes a real ecological phenomenon — the positive effect that a general biocide has on a prey population.

While the Volterra Principle is considered to be well-confirmed by ecologists, its confirmation did not come through standard empirical testing alone. Rather, robustness analysis, or more specifically three kinds of robustness analysis played an important role in generating this confidence. In our discussion of four models of predation, we have outlined three kinds of robustness analysis which correspond to three different levels at which a result’s robustness can be determined in modeling. These are parameter robustness, a result’s surviving changes to the parameter set of a dynamical model; structural robustness, a result’s surviving changes to the mathematical structure of the model; and finally, representational robustness, a result’s surviving changes to the whole representational framework in which the model has been framed.

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<sup>4</sup>We developed such a model and tested it successfully for the Volterra Principle. As with the other individual-based models, it can be found at [URL].

Robustness analyses previously carried out by the ecological community as well as the novel, representational robustness analysis carried out in this paper, has several important results. Stable oscillations are not a robust property of predator-prey models. Some oscillatory tendency does appear in many of the models, but this tendency often leads to stable equilibria. However, as ecologists have shown with aggregate models and as we have shown with two types of individual-based models, the Volterra Principle is a robust property. When two species in a predator-prey relationship coexist, whether they oscillate or not, a general biocide will favor the prey over the predators.

Like all of the most important robust theorems, the Volterra Principle possesses all three kinds of robustness. We believe, however, that representational robustness is the most important. If robustness analysis gives us good reason to believe that a robust theorem is true of real world systems, the theorem should not in any way depend on the mathematical or computational framework used to describe the problem. The Volterra Principle survives a transition between representational frameworks, and is even more dramatically displayed in the individual-based framework. In fact, switching frameworks can, as in this case, enhance robustness analysis because it lets us probe a little deeper to figure out why we see the results that we do.

Levins wrote in 1966 that “our truth is at the intersection of independent lies.” We do not see models, even the highly idealized ones involved in the robustness analysis of the Volterra Principle as ‘lies,’ yet we think Levins’ point is correct. When studying phenomena as complex and hard to measure as predation, scientists often have little choice but to build approximate, idealized models. Finding that some result is robust across these models, however, is an important step in the process of a theorem’s confirmation.

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