*Brit. J. Phil. Sci.* **68** (2017), 1007–1036

# Modelling as Indirect Representation? The Lotka–Volterra Model Revisited

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ABSTRACT

Is there something specific about modelling that distinguishes it from many other theoretical endeavours? We consider Michael Weisberg's ([2007], [2013]) thesis that modelling is a form of indirect representation through a close examination of the historical roots of the Lotka–Volterra model. While Weisberg discusses only Volterra's work, we also study Lotka's very different design of the Lotka–Volterra model. We will argue that while there are elements of indirect representation in both Volterra's and Lotka's modelling approaches, they are largely due to two other features of contemporary model construction processes that Weisberg does not explicitly consider: the methods-drivenness and outcome-orientedness of modelling.




doi:10.1093/bjps/axv055

Advance Access published on March 23, 2016

## 1 Introduction

A substantial and increasing part of scientific practice consists of the construction, development, and investigation of theoretical models. Often this work seems quite separate from empirical investigation, which raises the question of how models are related to real-world phenomena. Is there something specific about model-based theoretical practice that sets it apart from many other theoretical and representational endeavours? This question has been recently addressed by Michael Weisberg ([2007], [2013]) and Peter Godfrey-Smith ([2006]), whose answer is affirmative. Weisberg ([2007]) argues that many standard philosophical accounts approach theory construction as a uniform practice, thus failing to distinguish between modelling and other types of theorizing. Yet the goals, procedures, and representations employed by modellers and other kinds of theorists differ. In particular, Weisberg and Godfrey-Smith distinguish between two types of theorizing: modelling and abstract direct representation. Modellers are engaged in indirect representation, that is, they study real-world phenomena through the detour of creating hypothetical simplified entities, namely, models. In contrast, the theorists practising abstract direct representation strive to represent the data or real-world phenomena directly.

At first sight, the notion of indirect representation seems a somewhat odd choice of term. Any reasoning that makes use of surrogates, such as theoretical representations, to study real-world systems is inevitably indirect. So what is it that the notion of indirect representation is supposed to capture? Weisberg (and Godfrey-Smith) are focusing on the model construction process and the peculiar way models relate to real-world phenomena. The philosophical gist of the idea of indirect representation consists in highlighting the fact that models form a class of theoretical representations that are not constructed by representing as faithfully as possible any real target systems. According to the thesis of indirect representation, the consideration of real-world targets only enters the process of modelling at a later stage. This runs counter to the traditional representational approach to models according to which they are inherently models of some definite real-world systems. In contrast, Weisberg claims that there is no single determinable relationship between a model and the real world. Modelling may be target directed, yet affording many real targets, or none—and the targets of modelling may also be hypothetical or general in nature (Weisberg [2013], Chapters 5 and 7).

There has not, as yet, been much discussion of the thesis of indirect representation, but some reservations have been presented either contesting the distinction between indirect and abstract direct representation (for example, Podnieks [2009]; Scholl and Rätz [2013]) or challenging the implicit supposition that modelling is a uniform practice that can be clearly distinguished from other theoretical representational activities (for example, Toon [2012]; Levy [2013]). Moreover, even when it has been granted that some forms of modelling can indeed be characterized as indirect, such an indirect modelling strategy has been criticized for its tendency to take internal (model-oriented) progress for target-oriented progress (Levy [2011]), or for being a deficient form of theorizing due to its lacking representational accuracy (Scholl and Rätz [2013]).

In the following, we will consider the thesis of modelling as indirect representation through a close examination of the construction of the Lotka–Volterra model by both Alfred Lotka (1880–1949) and Vito Volterra (1860–1940). Weisberg uses the Lotka–Volterra model as one of the prime examples of modelling, but he considers only Volterra's work. We will also take into consideration also Lotka's design of the Lotka–Volterra model, which has not, so far, attracted that much philosophical interest. Although the Lotka–Volterra model is often referred to in philosophical discussion, what has not been recognized is that even though Volterra and Lotka presented models that, from the formal point of view, look identical, they nevertheless adopted different modelling approaches. Thus the seemingly unitary picture that Weisberg depicts of modelling appears to give way to heterogeneous modelling heuristics, exemplified by Volterra and Lotka.

Does this mean that there are different kinds of modellers, or can Lotka's and Volterra's modelling endeavours nevertheless be subsumed under the notion of indirect representation? We argue that there are elements that can be characterized as indirect in both Volterra's and Lotka's work; however, they can be related in an important way to two other features of model construction processes that Weisberg does not explicitly consider, namely, the methods-drivenness and outcome-orientedness of modelling. These two features frequently encountered in actual modelling practices have not, so far, been the target of philosophical analysis; nonetheless, these features become evident when the two designs of the Lotka–Volterra model are compared and contrasted. Interestingly, in such a comparison, it is Lotka more than Volterra that seems to stand out as a modeller in the contemporary sense, anticipating the study of complex systems across different scientific disciplines. What the accounts of Weisberg and Godfrey-Smith overlook, we suggest, is precisely this strong interdisciplinary character of contemporary modelling practices. This is the result (paradoxically perhaps) of being too tied to the representational focus on the model and its target systems. While theirs is an account of modelling or model-based theoretical strategy, it does not really address the actual practices of model construction. In contrast, our account focuses on the tools and other resources that Volterra and Lotka made use of in the construction of their models.

We will first discuss Weisberg's and Godfrey-Smith's accounts of modelling as indirect representation, paying attention to their central philosophical tenets as well as to their critique. In the ensuing sections, we will examine in detail both Volterra's and Lotka's designs of the Lotka–Volterra model. This historical discussion is followed by a philosophical analysis of the extent to which Volterra's and Lotka's modelling approaches accord with the thesis of indirect representation, which finally leads us to consider the methods-driven and outcome-oriented nature of current modelling practices.

## 2 Modelling as Indirect Representation

The important insight of the notion of indirect representation is to redirect the focus from models to the activity of modelling. Weisberg suggests that modelling proceeds in three stages. First, a model is constructed, then, second, the modeller refines, analyses, and articulates its properties and dynamics. It is not until the third stage that the relationship between the model and any target system is assessed, 'if such an assessment is necessary' ([2007], p. 209). This stage might be left aside or implicit, as modellers may go on studying the model systems created without too much explicit attention to their relationship with the world.

The claim that model construction happens before the possible real target systems are considered runs counter to the conventional philosophical understanding of models. More often than not, models are understood as models of some real-world target systems (for example, French and Ladyman [1999]; Morrison and Morgan [1999]; Suárez [1999]; da Costa and French [2000]; Giere [2004]; Bailer-Jones [2009]). This being the case, the burden of proof lies on the shoulders of Weisberg. If models are not representations of some real target systems at the outset, what is represented in them and how is that supposed to happen? In short, what is indirect representation all about?

Interestingly, Weisberg does not try to define indirect representation, but rather reverts to scientific examples. He ([2007]) contrasts Vito Volterra's style of theorizing—which he takes as an example of modelling—with abstract direct representation as exhibited by Dimitri Mendeleev's periodic table. According to Weisberg, Volterra studied the special characteristics of post-World War I fish populations in the Adriatic Sea by imagining a simple biological system composed of one population of predators and one population of prey ([2007], p. 208), to which he attributed only a few properties, writing down a couple of differential equations to describe their mutual dynamics. Weisberg stresses the fact that Volterra did not arrive at these model populations by abstracting away properties of real fish, but rather constructed them by stipulating certain of their properties ([2007], p. 210). Unlike Volterra, Weisberg claims, Mendeleev built his periodic table through abstractions from data in an attempt to identify the key factors of chemical behaviour. Thus, in contrast to modellers such as Volterra, he was trying to 'represent trends in real chemical reactivity, and not trends in a model system' ([2007], p. 215, Footnote 4).[1]

Weisberg ([2013]) also includes concrete models such as the San Francisco Bay model in the category of indirect modelling (in addition to computational models such as Schelling's ([1978]) segregation model. This inclusion seems somewhat awkward, since the construction of a concrete scale model, such as the San Francisco Bay model, appears more obviously directly related to an actual target system (for example, San Francisco Bay) than the Lotka–Volterra model is to any possible predator and prey populations. But we do not want to press further this particular issue, concentrating instead on mathematical modelling.

Godfrey-Smith ([2006]) likewise distinguishes between indirect representation and abstract direct representation, and also invokes examples in trying to account for the difference between them. Godfrey-Smith's examples are more recent: Leo W. Buss's ([1987]) *The Evolution of Individuality* and Maynard Smith and Szathmáry's ([1995]) *The Major Transitions in Evolution*. For Godfrey-Smith, these two influential books on evolutionary theory represent an ideal example of the contrast between abstract direct representation and indirect representation being written about at the same time and on partly overlapping topics. Whereas Buss examines the '*actual* relations between cellular reproduction and whole-organism reproduction in known organisms' (Godfrey-Smith [2006], p. 731), Maynard Smith and Szathmáry describe 'idealized, schematic causal mechanisms'. Rather than studying actual systems, they engage in modelling, that is, they examine, as Godfrey-Smith ([2006], p. 732) puts it, 'tightly constrained "how-possibly" explanations'.[2]

Consequently, the crucial difference between abstract direct representation and indirect representation, according to Weisberg and Godfrey-Smith, does not concern whether one abstracts or approximates, selects or even idealizes. Scientific representation involves all these modes, but in engaging in indirect representation modellers do not seek to represent any specific real system, but proceed instead by describing another simpler hypothetical system. Consequently, models should be considered independent objects in the sense of being independent from some determinable real target systems. Other authors have also recently suggested that models could be conceived of as independent objects, although by this they mean different things. Morrison and

[1] Weisberg ([2013]) no longer contrasts Volterra with Mendeleev. Eric Scerri ([2012]), the author of *The Periodic Table* (Scerri [2007]), argues that Weisberg is mistaken in considering the periodic table as an instance of theorizing.

[2] The notion of indirect representation has been related to the idea of models as fictions (for example, Frigg [2010]; Godfrey-Smith [2006], [2009]), but neither of them implies the other.

Morgan ([1999]) consider models as partly autonomous from theory and data. Knuuttila ([2005]) treats them as independent things in the sense of loosening them from any predetermined representational relationships to real target systems. Although the idea of models as independent entities is not, in itself, novel, the distinction between indirect representation and abstract direct representation provides an additional twist by spelling it out in terms of what kind of strategy guides model building.

Critics have not been convinced by the distinction between direct and indirect representation, nor by the idea that it is indirect representation that characterizes modelling as a distinct endeavour. To be sure, there is a trade-off between powerful philosophical claims involving some degree of reconstruction and stylization, and descriptive match with actual scientific practices. For this reason, the objection that not all forms of modelling are instances of indirect representation does not seem too grave an objection. It is the task of further philosophical discussion to find out the proper scope of the thesis of indirect representation. The doubts concerning the very distinction between indirect and abstract direct representation are potentially more damaging. Podnieks ([2009]) thinks that this distinction is untenable, because abstract direct representation is not all that direct either. He points out that Mendeleev also made use of theory (and data) that 'were produced during a highly non-trivial history' (p. 4). However, as Weisberg and Godfrey-Smith also see abstract direct representation as a form of theorizing, there is no reason why they could not accommodate this observation.

Perhaps the most problematic critique of the thesis of indirect representation so far has been presented by Scholl and Rätz ([2013]) who argue, on the basis of a detailed historical study of both Volterra and Darwin, that indirect representation and abstract direct representation cannot be kept separate. Darwin's model of the origin and distribution of coral reefs and atolls in the Pacific Ocean was used as another example of abstract direct representation by Weisberg ([2007]). Scholl and Rätz question the distinction between indirect representation and direct representation by arguing that both Volterra, with his co-author D'Ancona (Volterra and D'Ancona [1935]), and Darwin were engaged in modelling. In both cases, the authors were struggling with the problem of insufficient epistemic access to the target system, the crucial difference being only that Darwin was successful in delivering a 'how-actually' model in contrast to Volterra's (and D'Ancona's) 'how-possibly' models. Scholl and Rätz's critique ultimately boils down to a critique of what Volterra accomplished, and is related to yet another kind of challenge to the thesis of indirect representation. Namely, it has been suggested that indirect modelling strategies can be deficient with respect to more direct ones, in that their development may not lead to any genuine understanding of real-life targets (Levy [2011]).

Is there, then, anything special about modelling that could be characterized in terms of indirect representation, and if so, what might the motivations or benefits (as opposed to deficits) of this approach be? Since indirect representation is supposedly related to the tightly constrained, hypothetical nature of modelling, the question is why one should be engaged in constructing merely hypothetical systems in the first place. Both Weisberg and Godfrey-Smith indicate that this effort is made due to the complexity of the systems under study, while Scholl and Rätz attribute such effort to the problem of insufficient epistemic access. Undoubtedly, our access to complex systems is more often than not incomplete, but there is more to the problem of complexity than this—as we hope to show with the cases of Lotka and Volterra.

In the following two sections, we will examine how Volterra and Lotka constructed their respective models. As we will argue, Volterra does not actually qualify as the best example of a modeller in the sense of Weisberg, since he aimed to isolate the essential or sufficient components of the real predator–prey system in sea fisheries. Although what he eventually accomplished suits the thesis of indirect representation to some extent, his original intentions were different. Lotka provides a more pure-bred example of a (mathematical) modeller in contemporary terms, but for reasons that are not discussed by Weisberg. Lotka started from a systems theoretical perspective, developing a general model template, which he applied to the analysis of biological and chemical systems. This kind of approach is now becoming prevalent in modelling complex systems. It does not start from imagining simplified hypothetical systems (still somehow connected to some particular real-world systems), but from applying cross-disciplinary computational templates and methods to various subject matters (cf. Humphreys [2004]). Such an approach points to the methods-driven and outcome-oriented nature of modelling.

## 3 The Design of the Lotka–Volterra Model by Volterra

Weisberg begins his story of the origin of the Lotka–Volterra model from the problem presented by Umberto D'Ancona to the world-renowned mathematical physicist Vito Volterra (1860–1940) in 1925. D'Ancona, a marine biologist and Volterra's son-in-law, had made a statistical study of the Adriatic fisheries over the period 1905–23. The data showed an unusual increase in predators towards the end of the First World War, when warfare was hindering fishing. D'Ancona's aim was to get mathematical support for the thesis that cessation of fishing was favourable for predator fish. Thus Volterra set out to 'mathematically explain' D'Ancona's data on 'temporal variations in the composition of species' (Volterra [1927a], p. 68). He had no prior experience of fisheries; but the study of this problem sparked his long-term research programme on the inter-species dynamics (Volterra [1931]; Volterra and D'Ancona [1935]).

Although fisheries were a new field for Volterra, the way he went about modelling the predator–prey system can be traced further back in time (Knuuttila and Loettgers [2012]). Already decades before the formulation of the Lotka–Volterra model, Volterra was interested in the mathematization of biology and social sciences as attested by his inaugural address at the University of Rome (Volterra [1901]). Such mathematization, according to Volterra, would involve transforming qualitative elements into quantitative ones, representing them with differential calculus,[3] and forming hypotheses in the same fashion as in mechanics. Idealization and abstraction were crucial in this process as the goal was to identify the 'fundamental parameters' governing the 'change in the corresponding variable elements of the phenomena' (Volterra [1901], p. 255). Volterra did not speak in favour of 'giving a mechanical explanation of the universe' (Volterra [1901], p. 255), but he advocated in particular for the use of mathematical analogies.

Yet there seems to be something contradictory about the idea of transferring the modelling methods and concepts of mechanics to other entirely different areas of study by using mathematical analogies and, at the same time, striving to capture the fundamental factors behind the phenomena in question. This problem is aggravated by the complexity of the social and biological phenomena in question. Thus the transfer of the mechanical approach to biology led Volterra not to identifying the fundamental parameters, but to resorting to 'the method of hypothesis'.

## 3.1 Volterra's method of hypothesis

In his attempt to account for D'Ancona's statistical data, Volterra originally embarked on '*isolating* those factors one wishes to examine, assuming they act alone, and by neglecting others' (Volterra [1927a], p. 67, emphasis added). Accordingly, he began by distinguishing between 'external' and 'internal' causes. External causes were such 'periodic circumstances relating to the environment' that would 'produce oscillations of an external character in the number of the individuals of the various species' (Volterra [1928], p. 5). What Volterra wanted to focus on instead were internal causes that have 'periods of their own which add their action to these external causes and would exist even if these were withdrawn' (Volterra [1928], p. 5). However, this was just a starting point for him. He went on to model more complicated cases and also some effects of the environment. The Lotka–Volterra model was for

[3] Volterra started his scientific career as a mathematician and made important contributions to the theory of calculus (Volterra [1930]).

Volterra merely one of the basic models of biological associations with which he referred to stable associations that 'are established by many species which live in the same environment' (Volterra [1928], p. 4). In the paper in which he presents the Lotka–Volterra model for the first time (Volterra [1926a], [1928]),[4] he begins by considering one species alone and then adds other species. The first association he models is that between two species that contend for the same food. First after this case, he formulates the Lotka–Volterra model on two species, one of which feeds upon the other.

Although Volterra strove to separate the external and internal causes, it seemed problematic since they are usually interrelated in complex ways. Interacting species in a variable environment, such as the sea, constitute a more complex system than those studied in classical mechanics. The mathematical methods and techniques developed in mechanics could not be directly applied to the study of predator–prey dynamics. Even if the variations observed in populations living in the same environment showed some well-known characteristics observed in many mechanical systems, such as oscillatory behaviour, it was unclear which were the components of the system and in which ways they interacted. Consequently, in applying the methods of mechanics to population dynamics, Volterra faced two problems: On the one hand, the complexity of the system had to be rendered manageable, enabling the use of certain mathematical tools. On the other hand, the available mathematical tools and methods exhibited a serious constraint on the kinds of structures and processes that could be studied. Volterra reflected on this situation in the following way:

> [...] on account of its extreme complexity the question might not lend itself to a mathematical treatment, and that on the contrary mathematical methods, being too delicate, might emphasize some peculiarities and obscure some essentials of the question. To guard against this danger *we must start from the hypotheses*, even though they be rough and simple, and give some scheme for the phenomenon. (Volterra [1928], p. 5, emphasis added)

Consequently, with the help of certain assumptions Volterra constructed a hypothetical system consisting solely of '*the intrinsic phenomena* due to the voracity and fertility of the co-existing species' (Volterra [1927a]). Some of these assumptions were directly due to the application of differential calculus to the problem of predation, as for instance the assumption that species increase or decrease in a continuous way that makes them describable with differential equations. Moreover, Volterra assumed that the individuals of each species are homogeneous, and the birth and death rates are proportional

[4] (Volterra [1928]) is a partial English translation of the Italian original (Volterra [1926a]); thus in the following, references are made to the 1928 translation.

to the number of living individuals of the species. This strategy of formulating a simplified hypothetical system allowed Volterra to make use of well-known mathematical tools and methods, and to explore their applicability to the study of biological associations.

### 3.2 The construction of the Lotka–Volterra model by Volterra

Volterra began to model biological associations from the situation in which each of the species is alone. In such situation, the prey would grow exponentially and the predator in turn would decrease exponentially (due to the lack of food resources). The rates of growth of prey and predator populations can be described by the following two differential equations:

$$\frac{dN_1}{dt} = \varepsilon_1 N_1, \quad \frac{dN_2}{dt} = -\varepsilon_2 N_2.$$

To allow for the interaction between prey and predator populations, Volterra introduced a coupling term in each equation, arriving at the following set of differential equations:

$$\frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2) N_1,$$

$$\frac{dN_2}{dt} = (-\varepsilon_2 + \gamma_2 N_1) N_2.$$

The interaction between predators and preys is described by the product $N_1 N_2$, which introduces non-linearity into the system in addition to coupling the two differential equations. The proportionality constant $\gamma_1$ links the prey mortality to the number of prey and predators, and $\gamma_2$ links the increase in predators to the number of prey and predators. One of the possible solutions to these coupled non-linear differential equations is oscillations in the number of predators and prey. Volterra noted that because of the non-linearity of the equations, the 'study of fluctuations or oscillations of the number of individuals of species living together [. . .] falls outside the ordinary study of oscillations' because the classical study of the theory of oscillations involves linear equations (Volterra [1928], p. 23).

The mathematical analysis of the resulting equations gave Volterra some important results, including a solution to D'Ancona's observation concerning the relative abundance of predatory fish during the war years. Volterra summarized his results in what he called the 'three fundamental laws of the fluctuations of the two species living together' (Volterra [1928], p. 20). The third law states that if an attempt were made to destroy the individuals of the predator and prey species uniformly and in proportion to their number, the average number of the prey would increase and the average number of the predator would decrease.[5] Weisberg ([2007]) writes as if this finding was novel, but it was anticipated by D'Ancona and, in fact, also by E. Ray Lankester ([1884]).[6] Volterra himself located the third law already in Darwin's writings (Volterra [1926b], p. 559; see Darwin [1882], p. 53–4), conceiving his long-term research on 'biological associations' as a contribution to the Darwinian theory of struggle for existence (see Volterra [1931]; Volterra and D'Ancona [1935]).[7]

To appreciate the importance of mechanical analogies in the construction of Volterra's model, one can, first, consider the way he treated predation. He drew an analogy to mechanics by using the so-called 'method of encounters', according to which the number of collisions between the particles of two gases is proportional to the product of their densities.[8] Thus Volterra assumed that the rate of predation upon the prey is proportional to the product of the numbers of the two species. The method of encounters has been criticized by biologists for not taking into account, among other things, the adaptations of predators to become more efficient.

Second, in generalizing his account to take into consideration the different kinds of interactions and multiple species, Volterra utilized mechanical analogies in various ways (for example, Volterra [1926b], [1927a], [1931]). For instance, making use of the concept of friction in mechanics, he made a distinction between two types of biological associations, conservative and dissipative (Volterra [1926b], [1927a]). Conservative systems are analogous to frictionless systems in mechanics. In conservative associations, the oscillations produced by the interactions of the species remain constant, as in the Lotka–Volterra model. In dissipative associations, the fluctuations of the species are damped due to the friction caused by the interaction between individuals of the same species (which takes into account the effects of a population's size on its own growth). These cases display a parallel to the cases of harmonic oscillator and damped oscillator in mechanics. Although conservative associations have very appealing mathematical properties, Volterra thought that dissipative associations are more realistic approximations of the natural situation. In particular, he found it disturbing that in *n* number associations, a stationary state could exist only for an even number of species, which is due to the nonlinearity of the equations in question. In his opinion, the 'conservative biological associations are probably ideals, which can only approximate the conditions effective in nature' ([1928], p. 47).

[5] For this so-called Volterra principle, see (Weisberg and Reisman [2008]).

[6] Lankester suggested that to protect edible prey-fish, their enemies should be destroyed in the same proportion as the adult prey fish were 'removed' ([1884], p. 416).

[7] On Volterra's Darwinism, see (Scudo [1992]).

[8] Volterra also made use of the method of encounters in his study of the demographic evolution of a single species; there, he applied the method of encounters to mating.

The tension between applying the concepts and mathematical techniques suggested by classical mechanics and the aim of constructing more realistic models marked Volterra's long research programme on biological associations. He spent the rest of his life—more than a decade—formulating more elaborated models and taking into account different kinds of associations and situations, making extensive use of modelling methods borrowed from mechanics. As early as (Volterra [1926a]), he also considered the cases of species that were competing for the same food or that formed a predatorprey relationship. One year after the publication of the original Italian article, Volterra also introduced integro-differential equations in an attempt to take into account the delayed effects of feeding on reproduction (Volterra [1927a]).[9] Finally, in a group of papers published in 1936 and 1937, Volterra made use of the calculus of variations in an attempt to provide a synthesis of his theory of biological associations along the lines of analytical mechanics. This is how he explains his agenda:

> *Everybody knows the importance of Hamilton's principle in mechanics* and in all the domains of physical science. An analogous variation principle can be found in biology, and from it one can deduce the fluctuation equations in the canonical Hamiltonian form and also in the form of a Jacobian partial differential equation [...] Hamilton's principle leads to the principle of least action (Maupertuis). *There exists also in biology a closely related principle, which may be called the principle of least vital action*. (Volterra [1937a], p. 35, emphasis added)[10]

Apart from applying the tools of mathematical physics to biology, Volterra was also interested in testing his theories on empirical data.[11] Soon after the publication of his first articles on the biological associations (Volterra [1926a], [1926b], [1927a]), Volterra made an intense effort at the international level to make his results known to the scientific community. This involved works addressed to the general public and correspondence with biologists, in order to find out to what extent his theoretical results matched empirical findings (Israel and Gasca [2002]).[12] The biologists presented Volterra with different kinds of cases, including parasitism and various kinds of interactions between various species. Although might get a certain impression from reading his

[9] Today Volterra is mostly known for the Lotka–Volterra equation. For a discussion on how Volterra's various models anticipated several theoretical advances in theoretical ecology, see Scudo ([1971]).

[10] A partial English translation of this article can be found from Scudo and Ziegler ([1978]).

[11] For example in (Volterra [1936], [1937b]) he discusses the connections between his theories and biological data.

[12] The biologists with whom Volterra corresponded included Georgii F. Gause, R. N. Chapman, Jean Régnier, Raymond Pearl, Karl Pearson, D'Arcy W. Thompson, William R. Thompson, Alfred J. Lotka, and Vladimir A. Kostitzin.

initial mathematical papers on biological associations, which are of a very technical character, in his in his later works, Volterra ([1931]; Volterra and D'Ancona [1935]) paid increasing attention to the mathematical and quantitative studies on the causes of fluctuations in animal populations (see also Scholl and Rätz [2013]).

Volterra's preference of grounding hypotheses in empirical research is also displayed in his reply to Lotka ([1927]), who had claimed priority for the Lotka–Volterra model on the basis of his ([1925]). While Volterra acknowledged Lotka's priority, he pointed out that what he had formulated were principles concerning 'sea-fisheries' (Volterra [1927b]). Lotka has derived his version of the Lotka–Volterra model in a different way than Volterra, making use of another kind of modelling heuristic.

## 4 The Design of the Lotka–Volterra Model by Lotka

Alfred Lotka (1880–1949) was a veritable polymath. Apart from being a mathematician and statistician, he had background in physics, physical chemistry, and biology. Moreover, he was also a renowned demographer and is regarded as the founder of mathematical demography (Coale [1972]). In his work, Lotka integrated concepts, methods, and techniques from those various fields, developing a modelling approach that could be characterized as a precursor for a systems approach. Lotka's eclectic methods did not get recognition from his contemporaries; but decades later, the developers of general systems theory, like Ludwig von Bertalanffy ([1968]) and Norbert Wiener ([1948]), elaborated upon Lotka's work, especially his book *Elements of Physical Biology* (Lotka [1925]). Lotka's design of the Lotka–Volterra model proceeded in the opposite direction to that of Volterra's. Instead of starting from simple cases and generalizing from them, he developed a highly abstract and general model template that could be applied in modelling various kinds of systems.

### 4.1 Physical biology according to Lotka

Lotka was sceptical of applying the most idealized cases of mechanics to biological systems, whose behaviour he considered irreversible. This property of the irreversibility of systems behaviour became the cornerstone of Lotka's modelling approach and his perception of systems in general. In *Elements of Physical Biology*, Lotka explained in detail the irreversibility of biological sytems behaviour, which grounded his more comprehensive programme of developing a 'physical biology' through the employment of 'physical principles and methods in the contemplation of biological *systems*' (Lotka [1925], p. viii). Lotka's main focus was on the evolution of biological systems, which he defined as follows: 'Evolution is the history of a system undergoing irreversible changes' (Lotka [1925], p. 49). This definition does not exclude reversible processes, although Lotka argued that all real processes are irreversible. Reversible processes were for him idealizations. The evolution of a system in time is characterized, according to Lotka, by an increase in entropy. Physical biology was in turn 'a branch of the greater discipline of the general mechanics of evolution' (Lotka [1925], p. 49).

Another important impulse for Lotka's programme of physical biology came from the success of physical chemistry, which had been introduced by the end of the nineteenth century (Servos [1990]). Physical chemistry functioned as a model science for Lotka ([1925], p. 39), in much the same way as mechanics did for Volterra. Based on the conviction 'that the principles of thermodynamics or of statistical mechanics do actually control the processes occurring in systems in the course of organic evolution', Lotka set out to apply the methods, techniques, and concepts from thermodynamics and statistical physics to the study of the evolution of biological systems. He realized, however, that biological systems are too complex to allow any straightforward application of thermodynamics. Lotka attempted to overcome this problem by introducing a generalized approach, which can be best understood as a kind of systems approach. The model later dubbed as the Lotka–Volterra model was just one application of Lotka's systems approach.

Apart from mechanics and physical chemistry, the field of energetics had an impact on Lotka's theorizing. Energetics as a specific theoretical field originated in the nineteenth century in the works of, for instance, Georg Helm ([1898]) and Wilhelm Ostwald ([1892]). It aimed at the development of a generalized theory based on the concept of energy, and the movement can be understood more broadly as a reaction against the mechanistic world-view. Interestingly, in addition to being one of the main spokesmen of energetics, Ostwald ([1893]) was also one of the founding fathers of physical chemistry. Drawing an analogy from energetics and heat engines, Lotka conceptualized the components of systems as energy transformers (energy transformers could be organisms, chemical elements, and so on).

Energy transformers and the processes linked to them constituted what Lotka called the 'micro-mechanics' of a system. 'Macro-mechanics', on the other hand, encompassed the redistribution of mass between the components of the system. This distinction is similar to thermodynamics and statistical mechanics where, according to Lotka ([1925], p. 50), macro-mechanics examines the 'phenomena displayed by the component aggregates in bulk', and the micro-mechanics is 'centered primarily upon the phenomena displayed by the individuals of which the aggregates are composed'. Thus Lotka attempted simultaneously to apply thermodynamics and statistical mechanics to biology, and to formulate a general approach that could overcome the problems inherent in drawing direct analogies between different disciplines—as Volterra had done.

## 4.2 Lotka's systems approach and the Lotka–Volterra model

In his version of the Lotka–Volterra model, Lotka did not make use of energetics; the Lotka–Volterra model was a result of his macro-level considerations. In order to describe the general dynamics in the macro level, Lotka started out from the law of mass action used in chemistry to describe the behaviour of solutions. Lotka introduced the law in his book by using the example of a system consisting of 4 gram-molecules of hydrogen, 2 gram-molecules of oxygen, and 100 gram-molecules of steam, at 1 atmosphere pressure, and 1800°C. The equation describing the evolution of the system is of the following form:

$$\frac{1}{v}\frac{dm_1}{dt} = k_1\frac{m_2^2 m_3}{v^3} - k_2\frac{m_1^2}{v^2},$$

where $v$ is the volume, $m_1$ is the mass of steam, $m_2$ the mass of the hydrogen, and $m_3$ the mass of oxygen. The constants $k_1$ and $k_2$ are characteristic constants of the reaction, such as temperature and pressure. Lotka was not interested in this particular equation, but in the more general statement included in the equation, according to which, 'the rate of increase in mass, the velocity of growth of one component, steam (mass $m_1$), is a function of the masses $m_2$ and $m_3$, as well as of the mass $m_1$ itself, and of the parameters $v$ (volume) and $T$ (temperature)' (Lotka [1925], p. 42). He then went on to write the equation in a more general form:

$$\frac{dX_i}{dt} = F_i(X_1, X_2, \ldots, X_n; P, Q).$$

The equation describes evolution as a process of redistribution of matter among the several components, $X_i$, of the system. Lotka called this equation the 'fundamental equation of kinetics', where function $F$ describes the physical interdependence of the several components; $P$ and $Q$ are parameters of the system; $Q$ defines, in the case of biological systems, the characters of the species variable in time; and $P$ the geometrical constraints of the system, such as volume, area, and extension in space.

Interestingly, Lotka had introduced this general approach in two articles five years before *Elements of Physical Biology* was published. In both of these articles, there appears a pair of equations that have the same form as those Volterra arrived at independently some years later. In the first of the papers (Lotka [1920a]), the equations are applied to the analysis of a biological system, and in the second paper (Lotka [1920b]), they are applied to a chemical system.[13] The title of the second paper refers explicitly to the law of mass action. In contrast to Volterra, who started from simple models of interaction and then generalized the results to any number of species, Lotka started out from very general considerations and only after he had formulated his general equation did he turn to specific cases, such as the Lotka–Volterra model.

Further important elements in Lotka's design of the Lotka–Volterra model were the methods he introduced to analyse and calculate the dynamic behaviour of the systems he had described. Having formulated the fundamental equation of kinetics, Lotka showed that without knowing the precise form of the function $F_i$, describing the interaction between the components, the properties related to the steady states of the system can still be studied. Lotka began by making the assumption that both the environment and the genetic constitutions are constant. By the means of a Taylor series expansion, Lotka then calculated the possible steady states of the system. He was able to show that, in general, the system will exhibit one of the following three behaviours over time: the system asymptotically approaches an equilibrium; it performs irregular oscillations around an equilibrium; or it performs regular oscillations around the equilibrium. He then applied the fundamental equation and his general method for analysing its steady states to the case of two species, one of which preys on the other (the Lotka–Volterra model). The equations he formulated were:

$$\frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2)N_1,$$

$$\frac{dN_2}{dt} = (-\varepsilon_2 + \gamma_2 N_1)N_2.$$

The pair of equations is of the same form as Volterra's equations. They constitute a set of non-linear coupled differential equations, which cannot be solved analytically; thus Lotka's general method of calculating the steady states became a valuable tool for dealing with such sets of coupled differential equations. As already mentioned, although Lotka had formulated the Lotka–Volterra equations in his 1920 articles, he claimed priority for the model on the basis of his ([1925]). The reason for this might be that in (Lotka [1920a]), he draws the Lotka–Volterra equations from his general equation inspired by chemical dynamics, without any discussion of empirical biological systems. In his ([1925]), he applies the equations to the study of a host–parasite system, citing W. R. Thomson ([1922]) and L. O. Howard ([1897]) on this topic. In the

[13] Lotka dealt with the rhythmic effects of chemical reactions already in his earlier writings; see, for example, (Lotka [1910]).

third part of the book, the fundamental kinetic equation is also used to study various other cases, such as the spreading of malaria.

## 5 Philosophical Discussion: Strategies and Tools of Modelling

In the previous two sections, we have examined the construction of what became known later as the Lotka–Volterra model by its authors, Vito Volterra and Alfred Lotka. The purpose of our historical examination was to determine the extent to which the thesis of indirect representation really conforms to the actual construction heuristics and motivations of Lotka and Volterra, given that the thesis of indirect representation is a claim concerning the nature of modelling, that is, model construction. We argue in the subsequent sections that Weisberg's (and Godfrey-Smith's) version of modelling as indirect representation suits Volterra's model design, but only partially. And in Lotka's case, we see a novel modelling approach taking shape that is characteristic of the contemporary study of complex systems. This approach can certainly be seen as at least partially indirect, although largely due to reasons that are not addressed by Weisberg or Godfrey-Smith. One feature, we suggest, that is crucial for contemporary modelling practice is its methods-drivenness. This aspect of modelling is shared by Volterra's and Lotka's otherwise rather different approaches, since both of them used methods, tools, and concepts derived from other disciplines. While we do agree that much of the (mathematical) modelling practice proceeds as if theorists were constructing imagined or hypothetical systems, the question is to what extent this is due to the cross-disciplinary nature of modelling. Moreover, this method-driven nature of modelling is closely linked to an additional feature that guides model construction: its outcome-orientedness. By 'outcome-orientedness', we mean the way models are constructed, keeping an eye on the behaviour they are supposed to exhibit and the results they are expected to produce.

### 5.1 Volterra's path from the method of isolation to the method of hypothesis

The crucial question with respect to indirect representation is why should modellers proceed through the detour of constructing simpler hypothetical systems in the first place? Weisberg's answer is this: 'The strategy employed by Volterra is a common one found in scientific disciplines that face the difficulty of describing, explaining, and making predictions about *complex phenomena*' ([2007], p. 208; see also, for example, Godfrey-Smith [2006], p. 726). But is there something more to be said about why the study of complex phenomena should call for an indirect approach? We suggest that Volterra's path from the method of isolation to the method of hypothesis proves illuminating in this respect.

According to Weisberg, Volterra did not arrive at his model by abstracting away properties of real fish; he constructed it by stipulating certain of their properties ([2007], p. 210). However, what Volterra initially attempted to do, or what was his outspoken goal at least, was to reduce the complexity of the problem by trying to set apart those components of the complex system that could be neglected. His goal was thus to 'isolate' such 'fundamental parameters' and their interactions that supposedly contributed to the variations in the number of individuals in the respective species.

Volterra's methodological views and his point of departure can be fruitfully compared with the philosophical discussion on the method of isolation (for example, Cartwright [1999]; Mäki [2009]). Mäki characterizes the method of isolation in terms of 'sealing off' some causal factors from the influence of other factors. In similar vein, Cartwright relates the method of isolation to the idea of studying how a causal factor (or some factors) operate on their own, unimpeded by other causal factors, which are neutralized by the specific assumptions made in modelling. This characterization fits well with Volterra's methodological views, but this was not the actual modelling heuristic he followed. He did not isolate any causal factors and their interactions from the rest of the factors and interactions, nor claimed that they were the primary ones. Instead, he started right away from the hypothesis that the oscillations in the fishery data could be produced solely by the interaction of the predator and prey species.[14] Herein lies, we think, the important insight of the thesis of indirect representation: from the perspective of actual model construction, there is a difference between the case that abstracts away many aspects of a real system, and the case that departs instead from a few fundamental assumptions. This distinction is often glossed over, although Volterra himself became acutely aware of it once he set out on the course of modelling biological associations.

Thus, somewhat paradoxically, Volterra appears as a modeller in the sense of Weisberg, even though his pronounced methodological views do not accord with Weisberg's account of indirect representation. Apart from envisaging the method of isolation as an ideal form of theorizing, he also considered the empirical verification of theory to be very important. Volterra rejected the idea of formulating mathematical models that could not be tested empirically and he insisted that all the theory's basic magnitudes should be

[14] One might, of course, insist that in starting from certain factors right away, Volterra had already, mentally, isolated these factors from the rest. The problem with this line of thought is that it abstracts away from the difficulties of modelling complex systems: it is as if the causal factors and their interactions are laid bare there for the theorist to choose from; see also Section 5.3.

measurable. This eventually led him into a disagreement with D'Ancona, who was sceptical of the requirement for empirical validation of a theory, but thought instead that Volterra's models were rather to be understood as interesting theoretical working hypotheses, able to stand on their own (see Israel [1991], [1993], p. 504). It is important to pay attention to the fact that Volterra set out to explain empirical statistical observations. His whole modelling endeavour was motivated by the goal of reproducing the kind of oscillating behaviour that was observed empirically in fishery statistics. Thus his approach does not seem to be in line with the three-stage modelling strategy, in which the empirical assessment takes place only in the third stage, if at all. In retrospect, it was Lotka whose methodological approach was more in line with contemporary modelling of complex systems.

### 5.2 The template-based approach of Lotka

Volterra and Lotka dealt with the problem of complexity in nearly opposite ways. Volterra started from the simplest imaginable systems and went on to diversify and generalize his basic models, thus taking into account various possibilities. Lotka, on the other hand, devised a general template that was to be applied and adjusted to different cases. The fundamental equation of kinetics describes the mode of physical interdependence of several species and their environment. In this general equation, the components as well as the interactions between them are not further specified. This has to be done separately for each specific system studied using Lotka's systems approach. Predator–prey dynamics was just one concrete case to which his general approach could be applied. In defining systems in such a general way, Lotka freed his approach from any specific scientific discipline or theory—much the way Ludwig von Bertalanffy ([1968]) did later with his general systems theory.

Lotka's approach anticipates the systems approach and complexity theory, which have led to powerful general methods for studying complex phenomena in various disciplines. This approach highlights one central feature of contemporary modelling that has not so far been adequately targeted by philosophical analysis, namely, modellers typically recycle equations and modelling methods across disciplinary boundaries. Paul Humphreys has recently paid attention to this phenomenon, noting 'the enormous importance of a relatively small number of computational templates' in contemporary computational science (Humphreys [2004], pp. 64, 68). By 'computational template', Humphreys is referring to genuinely cross-disciplinary computational devices, such as functions, sets of equations, and computational methods, which can be applied to different problems in various domains. Examples of computational templates include the Poisson distribution, the Ising model (Hughes [1999]), different agent-based models, and the Lotka–Volterra model.

Lotka's set of general coupled differential equations (the fundamental equation of kinetics) can be considered as a kind of generalized template, from which more specific templates like the Lotka–Volterra model can be drawn. Although a computational template such as the Lotka–Volterra model can be devised in view of a particular empirical system, which is what Volterra did, it can also be viewed as a mere formal system, specifying a general form of interaction between some components. This comes closer to Lotka's approach. Such a formal template describing a certain form of interaction can be applied to different kinds of systems displaying similar behaviour. This is what Lotka did in his papers published in 1920, where he applied the Lotka–Volterra equations to the analysis of a biological system and then to a chemical system (Lotka [1920a], [1920b]). Thus Lotka considered the Lotka–Volterra equations first as a theoretical possibility applicable to different subject matters. Only subsequently did he apply it to the question of predator–prey dynamics, which he treated analogously to host–parasite dynamics (Lotka [1925]).

The subsequent history of the Lotka–Volterra model bears witness to the importance of template-based model construction. It has been extended from the study of populations to the exploration of basic biological mechanisms, such as genetic and metabolic circuits (see Goodwin [1963]; Loettgers [2007]), and it has also been used in disciplines beyond the biological sciences, for instance, in the social sciences (Epstein [1997]). In crossing the borders of its original area of application, it has become a genuine computational template in terms of Humphreys ([2002], [2004]).

Apart from Weisberg and Godfrey-Smith, the importance of such a template-based modelling approach has been largely unnoticed by their critics. For example, Scholl and Rätz ([2013])—following Weisberg—distinguish between dynamical fidelity and representational fidelity, and regard dynamical fidelity as deficient to representational fidelity, whereby 'the model faithfully mirrors the actual causal structure of the target system' (p. 122). Yet, the templates provided by the complex systems theory are precisely used to study the dynamics of the systems of interest. Typically, such complex systems are characterized in terms of various kinds of feedback loops, making their dynamics non-linear. The study of the dynamics of systems with non-linear features is one of the main goals of mathematical modelling in biology, as well as other sciences studying complex phenomena (see, for example, Bechtel [2011]). When the focus is on the patterns created by the complex interactions of the components, the abstractness of mathematical models may also offer an advantage (see Levy and Bechtel [2013]). Levy ([2014]) argues that the abstractness of such models may be in line with the explanatory progress. We agree, but would also like to point out that the mathematical challenges inherent in modelling non-linear systems constitute another reason why these models are often so abstract. This difficulty of modelling complex systems explains why successful equation forms and computational methods become templates that are used across the disciplines. In fact, the continuing importance of the Lotka–Volterra model is partly due to its role as a basic template for the study of non-linear dynamics that became apparent in the 1970s due to the advancements of computer technologies (May [1974]).[15]

### 5.3 Modelling: methods-driven and outcome-oriented

Looking at modelling practices from the perspective of the cross-disciplinary computational templates that modellers utilize partially explains why modellers proceed through the detour of building hypothetical systems. But it simultaneously highlights what Weisberg's (and Godfrey-Smith's) account of modelling leaves unrecognized: 'To judge whether or not a particular theorist is a modeller', argues Weisberg ([2007], p. 222), '[. . .] we will actually need to know something about how the theory was developed and how the modeller set about trying to represent the world'. Accordingly, then, the theory construction process is crucial for deciding whether a theorist is a modeller. Weisberg ([2007], p. 222) then goes on to give an account for how Volterra developed his model:

> Volterra began his investigation of Adriatic fish not by looking directly at these fish or even the statistics gathered from the fish markets, but by constructing a model. This is characteristic of the first stage of modeling. *He imagined a population of predators and a population of prey, each with only two properties*. Setting this idea to paper, *he wrote down equations specifying the model that he had imagined*. (emphasis added)

But if we look at the modelling practices of both Volterra and Lotka, a different picture emerges. Recall that Volterra had to resort to the method of hypothesis in part due to the theoretical difficulties involved in decomposing the problem of the fisheries and deciding which of the possible components and interactions were relevant for the problem. One important dimension of the problem Volterra faced concerned the difficulty of mathematically representing the predator–prey system. The idealizations he made were not introduced primarily in order to 'seal off' the effects of the other causal factors, but to introduce the infinitesimal calculus—based on the abstract concept of 'limits' and the use of continuous magnitudes.

[15] Computer simulation is an invaluable tool in studying non-linear differential equations because of the impossibility of finding analytical solutions for them. Although both Lotka and Volterra introduced methods to study the mathematical properties of their model, nowadays this work is done by computer simulation.

Consequently, it was Volterra's attempt to render the problem into a mathematical form rather than any methodological decision to set aside empirical considerations until some later stage—as suggested by Weisberg—that resulted in his separating the rational phase of theory construction from its empirical validation. Volterra and D'Ancona ([1935], pp. 37-8) reflect on this in the following way:

> [. . .] one does not need to be too concerned if ideal elements are conceived and if one places oneself in ideal conditions which do not correspond entirely to the natural elements or conditions. This is a necessity and it is sufficient to recall the applications of mathematics to mechanics and physics, which led to such important and even practical results [. . .] mathematical calculus, developed in this way, allows us to formulate laws and perceive relations that can be verified.

For Volterra, the success of the mechanistic style of modelling in physics justified the use of this method in modelling biological systems. Indeed, what is striking about the way that both Volterra and Lotka went about their modelling endeavours was how they transferred some existing mathematical forms, modelling methods, and theoretical concepts from one discipline to another. Although what they created was essentially a new kind of computational template—a template for further modelling in ecology and other disciplines—it resulted from an attempt to apply to a new field some modelling methods and techniques taken from (for them) exemplary and more fundamental disciplines. Such transfer of modelling methods from other more mathematically and computationally advanced fields, notably from physics and engineering, has played an important part in the mathematization of biology (for example, Kingsland [1985]) and economics (Mirowski [1989]), for example. Neuroscience, as well as systems and synthetic biology, provide some of the latest examples of this kind of modelling approach (Knuuttila and Loettgers [2013], [2014]).

Given the pervasiveness of this interdisciplinary transfer of methods and templates within modelling practices, the question is why the use of already-established modelling methods and computational templates is so important for modellers. There seems to be two reasons for this. First, mathematical tools are not a perfectly malleable and transparent means of representation. In rendering a problem into a mathematical form, more often than not, one makes use of the already established ways of modelling some other problems in more mathematically developed fields. While Weisberg gives the impression that Volterra first imagined the hypothetical predator–prey system and then cast it in mathematical terms, the contrary seems to be the case: the available mathematical representational tools and the way they were used in mechanics guided him in imagining and describing the predator–prey system in a particular way. Thus some already-established mathematical tools and modelling methods functioned as scaffolding for Volterra's (and Lotka's) scientific imagination.[16]

The other reason, more specific to modelling, is due to a particular property of modelling that is closely related to Humphreys's insight concerning the central role of cross-disciplinary computational templates in modelling: what is typical for modelling is its outcome-orientedness, insofar as starting point of modelling is often provided by the results the models are supposed to produce. Instead of directly trying to represent some selected aspects of a given target system—as is conventionally assumed—modellers proceed in a roundabout way, seeking to build hypothetical systems in the light of their anticipated results or of certain general features of the phenomena they are supposed to exhibit.[17] In the case of Volterra, for example, he succeeded in showing mathematically that the periodic fluctuations in fish populations could be produced by the mere fact of the interaction between the predator and prey. This was a novel result. Ecologists of his time were acquainted with fluctuations, but they tended to seek explanations from some external cause (for example, Whittaker [1941]).

We suggest that largely because of the outcome-orientedness of modelling, modellers use well-known and tractable representational tools and computational methods whose behaviour and outcomes they are familiar with. This goal of achieving certain kinds of results leads to the element of opportunism inherent in modelling. The mathematical forms and modelling methods that have proven successful elsewhere are applied to new fields, often based on some vague similarities between the different phenomena—for example, observed oscillations in biological, chemical, and physical phenomena. If a model succeeds in producing the expected results, or in replicating some features of the phenomenon, it provides an interesting starting point for further model building, whose typical aim is to correct and adjust the template to better suit the domain to which it is applied. Although the outcome-oriented nature of modelling partially explains its hypothetical and indirect characteristics, at the same time it shows that modelling is more rooted in empirical research than it may seem at the outset. Weisberg claims that the assessment of

[16] Weisberg's and Godfrey-Smith's accounts can no doubt be made to accommodate the constraining nature of available mathematical means, but they do not pay explicit attention to them in relation to the thesis of indirect representation. The reason for this might be that they make a distinction between a model and a model description (for example, a set of equations), and for them a model is an abstract or imaginary object. Weisberg ([2013]) notes what he calls the 'borrowing' of templates, but we think that something more creative is happening in cross-disciplinary template transfer.

[17] By 'results', we refer not only to the output of a model, but also to those results that can be derived from it, or otherwise inferred from it. Our point about the outcome-orientedness agrees with the generally accepted idea that modelling is intended to fit with empirical findings. What is at stake, however, is how this happens. Modellers do not first attempt to construct a faithful representation of a target system (that is, ADR in Weisberg's terms), but instead use general model templates on the basis of the characteristics and the behaviour they are known to exhibit.

the relationship between the model and real-world systems, if it happens at all, happens first in the third stage of modelling. But if one approaches modelling as an outcome-oriented activity, it becomes apparent that empirically motivated questions or findings are often built into a model right from the start.

Volterra's case exhibits the outcome-orientedness of modelling very well because his model was supposed to produce oscillations and hence potentially account for the empirical findings concerning variations in fish populations. Although the model was not constructed by abstracting the features of some particular spatio-temporal real target system, its construction was stimulated by certain empirical findings. Volterra's consequent correspondence with the biologists and bio-mathematicians provides another example (see Section 3.2). We agree with Weisberg that Volterra's modelling endeavour was motivated by D'Ancona's empirically grounded question.[18] However, Weisberg considers Volterra's work as an exemplary case of modelling, in which the consideration of the model in terms of its real-world target happens only at the later stage of analysis. This was not how Volterra himself understood what he was doing, as we have sought to show (see also Scholl and Rätz [2013]).

Our suggestion is that the seeming indirectness of Volterra's approach was due to his methods-driven and outcome-oriented attempt to apply the mathematical methods of mechanics to a biological problem, in view of getting the model to exhibit some features of the observed phenomena. This is not to say that we do not appreciate the rationale for the thesis of indirect representation. In our view, it singles out an important characteristic of many current modelling practices, largely overlooked by those philosophical accounts that expect mathematical models to be constructed by faithfully representing the real mechanism producing some phenomena (for example, Craver [2006]). But from our perspective, the indirect characteristics of many modelling practices are largely due to their (often imported) mathematical tools and the uses they are put to. Another point worth considering is the extent to which the seeming indirectness of modelling is due to the division of labour in contemporary science, where modellers and experimentalists frequently participate in different communities.

It is of interest that Weisberg ([2013]) discusses the many kinds of targets models can have—real, hypothetical, general, or none—and presents Volterra's modelling endeavour as directed towards a real-world target. We welcome the care with which Weisberg studies the different kinds of targets

[18] The story about Volterra embarking on an explanation of D'Ancona's findings may very well be just a story. It is more likely that what the variations in fisheries statistics provided for Volterra, a world-renowned mathematical physicist, was an interesting case in which to apply tools from physics. We owe this comment to Tim Rätz. Moreover, we suppose that it is not any coincidence that Volterra and Lotka developed the same equations independently, and at the same time; likewise, Van der Pol developed his oscillator with non-linear damping around the same time too (for example, Van der Pol [1926]).

models can have—a point that has largely been neglected in the recent discussion on modelling. Somewhat surprisingly, however, Weisberg does not explicitly consider the consequences this work might have for the thesis of indirect representation. It seems to us that the different kinds of targets discussed by Weisberg may point to different kinds of modelling practices.

## 6 Conclusion

We have studied the design of the Lotka–Volterra model by both Lotka and Volterra in order to examine the degree to which the notion of indirect representation put forth by Weisberg ([2007], [2013]) and Godfrey-Smith ([2006]) fits modelling. While Volterra is used by Weisberg as an exemplary case of a modeller, Volterra's approach only partially suits Weisberg's three-stage schema. In contrast, Lotka stands out as a more self-conscious modeller, by current standards, but for reasons that Weisberg's and Godfrey-Smith's account does not recognize. In our view, many mathematical modelling practices may seem to be only indirectly representing the phenomena, and to some extent this is the case. But this apparent indirectness is largely due to the methods-driven and outcome-oriented nature of modelling. Both of these crucial features of many contemporary modelling practices are already clearly present in the cases of Volterra and Lotka, who made use of modelling methods, concepts, and mathematical forms of some other sciences in their effort to apply mathematical tools to the analysis of biological systems. While Weisberg's and Godfrey-Smith's account of the actual model construction process relies on scientists' imagination, we have, in contrast, focused on the tools and methods of modelling. Such an approach, we believe, makes more visible the intricacies of actual model construction, and the cross-disciplinary tools utilized. The focus on practices of model construction is in line with the models-as-mediators account (Morrison and Morgan [1999]) and its stress on the various ingredients with which models are made (Boumans [1999]). What our analysis brings to this discussion is the emphasis on the interdisciplinary nature of contemporary modelling practices and their outcome-oriented nature.

Finally, our study concerning the different designs of the Lotka–Volterra model also bears witness to the fact that modelling is no unitary theoretical strategy. Whereas Volterra set out to causally explain real mechanisms, Lotka's approach was to apply a general cross-disciplinary template to specific cases. This is reflected in the different assumptions of the two designs of the Lotka–Volterra model. Lotka's formulation recognizes the implausibility of completely specifying the full functional forms of the equations governing an ecological system. Within a local neighbourhood of an equilibrium, the full equations are approximated by the Taylor series expansion. Volterra, in turn, presented his equations as the fully specified equations governing the dynamics of the system in question. This approach enables, on the one hand, the ecological interpretation of the coefficients; on the other hand, it makes a gross simplification of the biological reality (see Haydon and Lloyd [1999], pp. 205–6). It seems to us that this contrast between Volterra's and Lotka's approaches characterizes model-based theorizing more generally. Both the attempt to capture the basic causal mechanisms underlying a certain specific phenomenon and the use of general templates to model vastly different phenomena co-exist in contemporary modelling practice in such a manner that does not escape certain, subtle tensions.

## Acknowledgements

We wish to thank Paul Humphreys for the numerous inspiring discussions we have had with him over the years, and three anonymous referees for this journal for their constructive and helpful comments.

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