

The Modellers' Halting Foray into Ecological Theory: Or, What is This Thing Called 'Growth Rate'?

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Abstract This discussion paper describes the attempt of an imagined group of non-ecologists (“Modellers”) to determine the population growth rate from field data. The Modellers wrestle with the multiple definitions of the growth rate available in the literature and the fact that, in their modelling, it appears to be drastically model-dependent, which seems to throw into question the very concept itself. Specifically, they observe that six representative models used to capture the data produce growth-rate values, which differ significantly. Almost ready to concede that the problem they set for themselves is ill-posed, they arrive at an alternative point of view that not only preserves the identity of the concept of the growth rate, but also helps discriminate between competing models for capturing the data. This is accomplished by assessing how robustly a given model is able to generate growth-rate values from randomized time-series data. This leads to the proposal of an iterative approach to ecological modelling in which the definition of theoretical concepts (such as the growth rate) and model selection complement each other. The paper is based on high-quality field data of mites on apple trees and may be called a “data-driven opinion piece”.

Keywords Population growth rate · Modelling · Field data · Mites

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1 Reader's Guide

Since the reader might find the structure of this note somewhat unusual for a scientific paper, a few introductory remarks are in order. Rather than giving a traditional account of new methods and results obtained by the authors, this paper tells a story; the story of a group of quantitative scientists, newcomers to the field of Ecology, who are trying to determine the population growth rate from field data. Consequently, the paper emphasizes the probing/searching character of scientific practice and an outside view of ecological theory, while dispensing with some of the technical details (which are partially provided in the Appendix in ESM). A substantial amount of well-known ground is revisited, but the paper makes no attempt to be comprehensive. Certain gaps in the discussion and slightly “cavalier” treatments of certain topics are shortcomings that are tolerated as necessary ills to keep the narrative flowing¹. The expert reader is more than welcome to take issue with the presentation; in fact, this is the primary purpose of this paper: to ask questions and stimulate discussion. The authors are therefore pleased and proud that the paper has already generated a substantial amount of discussion in the review process—some of it quite detailed, deep, and even emotional. This paper proposes a “philosophical” approach that the authors feel has the potential of advancing the science (and art) of ecological modelling: basing the definition of ecological quantities (such as the growth rate) on the constructibility and robustness of suitable mathematical models. The in-depth discussion of the growth rate is meant to be an illustration of the general ideas and could be repeated for other ecological phenomena such as density dependence.

2 Introduction

Imagine a group of quantitative scientists, such as statisticians or mathematicians, with only a fleeting knowledge of ecology, who are charged with analyzing a dataset of population counts. Let us call these scientists the “Modellers”. The Modellers feel that, if their analysis is to be relevant to ecologists, it should relate to what they understand to be the most important notion in population ecology, the *population growth rate*. What follows is the story of the Modellers’ journey of discovery, the difficulties they experience, as well as their attempts at overcoming them.

3 What is the Growth Rate?

Canvassing the literature, the Modellers quickly learn that the notion of the growth rate seems to be more multifaceted than they had expected. Not only do they find multiple definitions [(Caughley (1977) lists five on page 109 of his classic book)], but it also remains somewhat unclear to them what rôle the quantity plays in ecological theory. While the Modellers set out to *extract* the growth rate *from* the

¹ One such gap is a thorough discussion of other approaches and areas relevant to the topic of this paper, such as the important and rapidly growing field of bioinformatics.

data by constructing and applying suitable models, McCallum (2008), e.g., seems to suggest that the growth rate is *used in* models as a parameter:

The rate of increase of a population is a parameter basic to a great many ecological models. [...] Perhaps more than any other parameter, the value appropriate for use in a model is context-dependent, varying both with the structure of the model and the model's purpose.

Sufficiently puzzled, they finally find solace in a quote by Berryman (2003) who seems to restore the unity of the concept and even elevates it to a fundamental law of ecology:

The first principle (geometric growth)

Ecologists seem to agree, in general, that geometric (exponential) growth is a good candidate for a law of population ecology. [...] since geometric growth is a fundamental and self-evident property of all populations living under a certain set of conditions (unlimited resources), I prefer to think of it as the first founding principle of population dynamics [...]

We have no intention here to enter the fray of the extensive debate among ecologists about whether Berryman's law (a.k.a. the Malthusian Law) is in fact a Law of Nature and/or whether ecology has any laws at all²; although we admit that the title of O'Hara (2005) spirited article on the subject provided some inspiration for the title of the present paper.

Rather, we imagine the Modellers taking Berryman's law to be the *definition* of the growth rate, according to which it is simply the number r in an exponential-growth expression of the form $N \sim e^{rt}$ (or the discrete-time version thereof³), where $N = N(t)$ denotes the total number of individuals at time t . As a result, the existence of a well-defined growth rate is contingent on populations under the condition of "unlimited resources" following an exponential growth law.

But then, what about the Modellers' data, which are shown in Fig. 1?⁴ This is a plot of field data of mites on apple trees, which, at least at the beginning of the season, do not experience any significant resource limitation. So what are the Modellers to make of the large oscillations? This does not look like a simple exponential e^{rt} at all. The Modellers speculate that these might be oscillations about an "average" exponential growth, which they might have to "filter out" to determine r . However, they put this idea aside for now and start over, looking for the standard definition of the growth rate.

² In addition to the quoted paper by Berryman (2003), interested readers might find contributions such as O'Hara (2005), Ginzburg et al. (2007), Lockwood (2008), Raerinne (2013) useful as potential entry points into the pertinent literature, which also contain older and widely discussed contributions such as Levins (1966) and Turchin (2001).

³ In this paper we use continuous-time models throughout. However, the discussion could equally be applied to discrete-time models.

⁴ This data set is remarkable for its quality and detail, and it has therefore recently attracted renewed interest. While various aspects of the data have been described in the literature (Herbert and Sanford 1969; Herbert 1970; Hardman et al. 1985; Marshall and Pree 1991), some of the raw data have apparently never been analyzed.

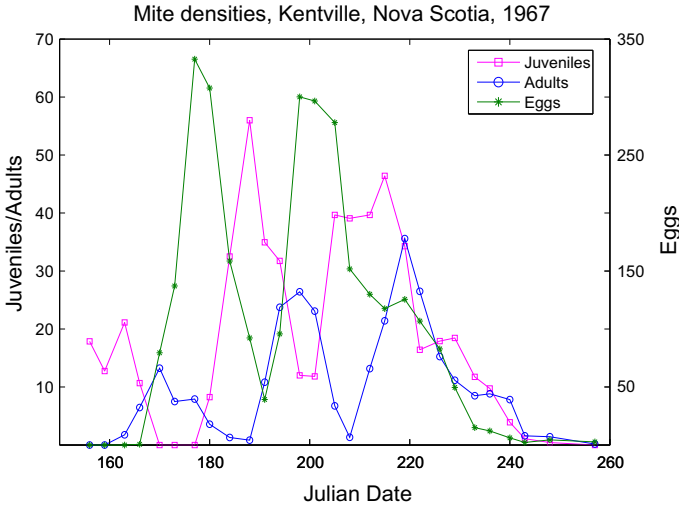


Fig. 1 Mite-population field data (note the different scales for juveniles/adults and eggs)

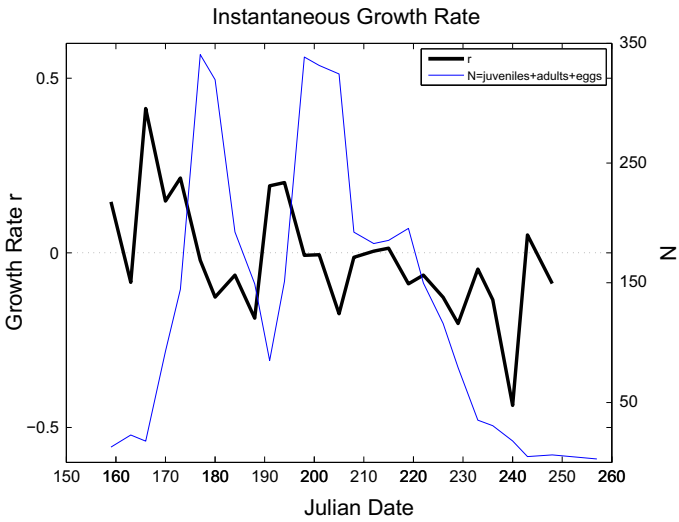


Fig. 2 Instantaneous growth rate $r = \log(N(t + \Delta t)/N(t))$, where $N(t) = E(t) + J(t) + A(t)$ is the total number of individuals

3.1 Census Versus Demographic Growth Rate

In the words of e.g. Sibly and Hone (2002), the standard definition reads

Population growth rate describes the per capita rate of growth of a population, either as the factor by which population size increases per year, conventionally given the symbol $\lambda (= N_{t+1}/N_t)$, or as $r = \log \lambda$.

But when this definition is applied to the data shown in Fig. 1 (*mutatis mutandis*; the relevant time step is obviously not a year) the growth rate “suddenly” fluctuates wildly between positive and negative values (Fig. 2).

Does this mean that a constant growth rate does not exist after all?⁵ Even if the environmental conditions are constant (as they are—at least approximately—during the beginning of the mite season)?

Sibly and Hone continue

In the simplest population model all individuals in the population are assumed equivalent, with the same death rates and birth rates, and there is no migration in or out of the population, so exponential growth occurs; in this model, population growth rate = r = instantaneous birth rate—instantaneous death rate.

The Modellers are intrigued by the appearance of the term “model” in the description of the growth rate, but they just read on for now:

Population growth rate is typically estimated using either census data over time or from demographic (fecundity and survival) data. Census data are analysed by the linear regression of the natural logarithms of abundance over time, and demographic data using the Euler–Lotka equation (Caughley 1977) and population projection matrices (Caswell 2001).

The Modellers, to their dismay, conclude that there are multiple growth rates after all—according to the quote above at least two kinds: one based on “demographic data”, and one based on “census data”. Moreover, the former seems to draw in other quantities (“fecundity and survival”), which seem to have to be known independently/beforehand.

What is more, Sibly and Hone also give two ways of “analysing” census data. In the first quote above, they present the simple formula $r = \log(N_{t+1}/N_t)$; i.e., the formula for the “instantaneous” growth rate (Walthall and Stark 1997). Now they suggest to use “linear regression of the natural logarithms of abundance over time”, which will result in an averaged or smoothed growth quantity. But will the numerical value(s) depend on the time interval(s)? If the Modellers are asked to take averages, how are they going to decide which time interval to use?

3.2 Asymptotic Versus Transient Growth Rate (Population Structure)

Experienced ecologists will readily identify the large oscillations in the data of Fig. 1 as generational waves, and they will argue that in determining the growth rate one must account for the (st)age structure of the population.

The Modellers, obediently, consult e.g. Tenhumberg (2010) who uses the (instantaneous) census-data definition of the growth rate, complete with its fluctuations during the early season (“transient dynamics”), and only offers them the piece of mind of a constant-value growth rate asymptotically.

⁵ We agree with Chester (2012) who argues that, if the growth rate is allowed to depend on time, it loses its meaning and utility.

If nothing else changes, the population eventually reaches the stable stage distribution and the speed at which the population is growing approaches a constant rate (the asymptotic population growth rate).

This, of course, refers to the mathematical fact, discovered by Lotka (1922), that solutions to the appropriate demographic model for structured populations eventually settle on the stable age distribution and grow exponentially with a rate that can be computed from the demographic data (“Lotka’s r ” or “intrinsic rate of increase”). The Modellers are therefore relieved when they realize that the census-data and demographic growth rates of Sibly and Hone are in this sense actually identical.

However, this is still unsatisfactory—at least for anyone ready to accept Berryman’s law: it is, in fact, precisely during the early season that resource limitations are the least likely to occur; so during *this* period the exponential-growth law should work particularly well. Having to wait until the stable age distribution is assumed seems counter-intuitive—as well as unrealistic and impractical, as many species will experience diminished growth due to limited resources before they can even approach the asymptotic state and/or will change their characteristics altogether due to seasonal behaviour etc.⁶ The Modellers’ field data exhibit evidence of both phenomena: the growth of the population slows down and comes to a halt after what appears to be 20–50 days; and during the final part of the season, the population crashes, as the mites switch to laying next-season eggs that will not hatch during the season they are laid (the egg numbers shown in Fig. 1 are for same-season eggs).

It is an interesting fact, which probably deserves to be better known, that classical demography itself offers a resolution of this conundrum. Properly “re-weighting” of the (st)age groups; i.e., considering⁷

$$V(t) := \int_0^\infty v(a)\rho(t, a)da,$$

does indeed result in an exponential-growth law of the form $V(t) \sim e^{rt}$, where r is the “asymptotic growth rate” in the parlance of Tenhumberg (i.e. Lotka’s r). The important point here is that the exponential-growth formula for the aggregate quantity $V(t)$ actually holds *for all* t , not just for large t , as Tenhumberg’s terminology suggests. Demographers know the function $v(a)$ to be Fisher’s (1927) *age-dependent reproductive value*⁸ and $V(t)$ to be the *total* reproductive value. The resolution of the “early-season-versus-asymptotic” conundrum, therefore, lies in the

⁶ Taylor (1979) used life-table data of various insect and mite species to estimate the time for the populations to get within 5% of the stable age distribution (SAD). According to those estimates, it is conceivable for *some* species to approach the SAD within a season.

⁷ In keeping with the the notation used by Lotka and Fisher, we adopt the continuous-time-continuous-age framework, in which $\rho(t, a)$ represents the number of age- a organisms at time t and the time and age variables t and a are allowed to vary continuously in $(0, \infty)$. Our notation is similar to the one in Cushing (1998); see also Webb (1985).

⁸ Although not considered in this note, we mention that in the discrete-time-discrete-age framework of Leslie matrix models, $v(a)$ is given by the dominant left eigenvector of the transition matrix. (The dominant right eigenvector corresponds to the stable age distribution; the logarithm of the dominant

realization that only a very *specific* aggregate population-size quantity (namely $V(t)$) obeys the exponential-growth law stipulated by Berryman. Other quantities, such as the total number of individuals $N(t) = \int \rho(t, a) da$, will generally not grow according to a simple exponential.

As an aside, it is amusing to see that applying a very simple, purely *heuristic* re-weighting formula of the form $W(t) = w_1 E(t) + w_2 J(t) + w_3 A(t)$ can reduce the generational fluctuations in the data significantly, as demonstrated in Fig. 3 (as well as Figures 10 and 11 in E).

Here the weights w_j are computed by taking ratios of life-stage averages (see eq. (6) in Appendix E) and the step function

$$w(a) := \begin{cases} w_1, & a = \text{eggage} \\ w_2, & a = \text{juvenileage} \\ w_3, & a = \text{adultage} \end{cases}$$

serves as a surrogate for $v(a)$.⁹ This observation provides a non-theoretical illustration of the basic “re-weighting” rationale behind the definition of $V(t)$, which is a reflection of the fact that in structured populations not all individuals can be “assumed equivalent”, as is done “in the simplest population model”.

4 The Modellers Go to Work

The Modellers decide that it is high time they finally do some actual modelling. Maybe studying the data will help them clarify some of the theoretical issues with which they have been wrestling. They use six different models to capture the data¹⁰; see Table 1.

The number of parameters ranges from 2 for the simple exponential model $N_0 e^{rt}$ to 12 for the most complex seasonal phenomenological model. The modelling of the data is achieved by standard parameter-fitting methods. The details of the models and the fitting process are not important for this discussion and are therefore omitted. Interested readers may consult the supplementary material of the appendix, which contains some basic information about the models and results. Here it suffices to say that the four seasonal models considered (III–VI in Table 1) are virtually indistinguishable in terms of capturing the data (see Fig. 8 of C). By contrast, the two simple non-seasonal growth models (I and II) are rather crude models of the data (see Fig. 7), as expected from the discussion above.

Footnote 8 continued

eigenvalue to Lotka's r .) For more information on matrix models, as well as structured population models in general, see Caswell (2001).

⁹ Even if the demographic data (fecundity and mortality) as functions of age are piecewise constant, $v(a)$ is not piecewise constant, but piecewise exponential.

¹⁰ All models considered in this paper are continuous in the time variable. Discrete-time models were also tested, but they did not provide any advantage; neither in terms of modelling, nor in terms of fitting the data or determining the growth rate.

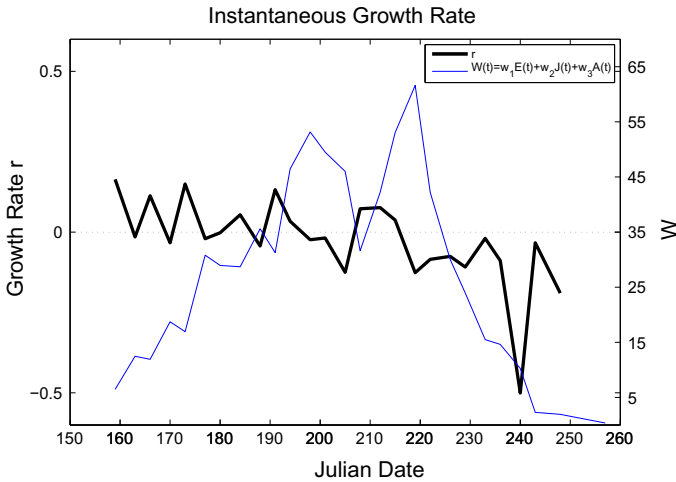


Fig. 3 Instantaneous growth rate derived from the heuristically re-weighted aggregate population $W(t) = w_1E(t) + w_2J(t) + w_3A(t)$ (see text). Compared with Fig. 2, seasonal fluctuations are reduced significantly

Table 1 Models used

	Model	Parameters	Seasonal	Formula (SM)
I	Simple exponential	2	No	(1), $K = \infty$
II	Simple logistic	3	No	(1)
III	Linear phenomenological	11	Yes	(2a)–(2d), $K = \infty$
IV	Nonlinear phenomenological	12	Yes	(2a)–(2d)
V	Linear demographic	10	Yes	(3a)–(3d), $v = 0$
VI	Nonlinear demographic	11	Yes	(3a)–(3d)

For details see B of the Supplementary Material (SM)

The first four models (I–IV) of the table explicitly contain the growth rate as a parameter. The remaining two are demographic models for which the growth rate is computed from the model parameters according to the Euler–Lotka equation (see eq. (4) in B). The results are tabulated below.

Looking at Table 2, it seems inescapable to the Modellers that they have been chasing a chimera: that one and only growth rate they set out to find in the data does not exist. Using 6 models on 3 time intervals each, results in 18 growth rates! (Although some of the values are fairly close and could be interpreted as representing the same quantity.) They draw the conclusion that

the concept of growth rate is *model-dependent*; for any given population, there may be *as many* reasonable answers to the question “what is the population’s growth rate?” *as* there are reasonable models for its dynamics.

Table 2 Growth-rate values derived from various models/ time windows

Model	Time window			
	30 days	50 days	70 days	Full season
I	0.1160	0.0686	0.0329	
II	0.4615	0.4636	0.4789	
III		0.0371	0.0552	0.0419
IV		0.1030	0.0620	0.1255
V		0.0311	0.0210	0.0165
VI		0.0498	0.0445	0.0352

So is this the end of the story? Will the Modellers have to resign themselves to the realization that determining *the* growth rate from population-count data is an ill-posed problem?

5 An Alternate Point of View

Ecologists in the Berryman camp will probably resist the Modellers' move from the enlightened monotheism of one growth rate to the heathen polytheism of many growth rates. They will argue that the Modellers simply confused “estimator” and “estimand” when they interpreted the second Sibly-and-Hone quote above as saying that there are “at least two kinds” of growth rates. These ecologists will probably suggest that the seemingly different growth rates are merely multiple *ways of determining* the growth rate—the implication being that the quantity itself still has a unique “identity”. Similarly, they may conclude that what the Modellers interpreted as model-dependence of the concept, may also be interpreted as multiple ways of computing the same ecological quantity, the growth rate.

The Modellers recognize that this point of view offers, in fact, an intriguing possibility of “turning the table” on the problem: if they were to assume that a well-defined single growth rate does exist after all, could they use this to discriminate between models?

To describe how the Modellers apply this idea to their data, we need to mention that the data actually consist of 24 replicates (see Fig. 5 in A); what was shown above were averaged data. To increase the sample size (which they arbitrarily choose to be 100), the Modellers use a simple resampling technique¹¹. For this larger data set (see Fig. 6), they then repeat the exercise described above; that is, they fit the 6 models to each of the 100 data sets and determine the corresponding growth-rate values. Figure 4 shows the distributions of those values for the various models.

So, which model should one trust? Or, better, *entrust* with determining the “true” growth rate (assuming one believes it exists)? Obviously, the width/narrowness of the distribution would be a factor in making the decision. Given that the data set is derived from measurements of the *same* population, one would expect that the different data sets essentially contain information about the *same* growth

¹¹ Each new data set is the average of 10 randomly selected replicates.

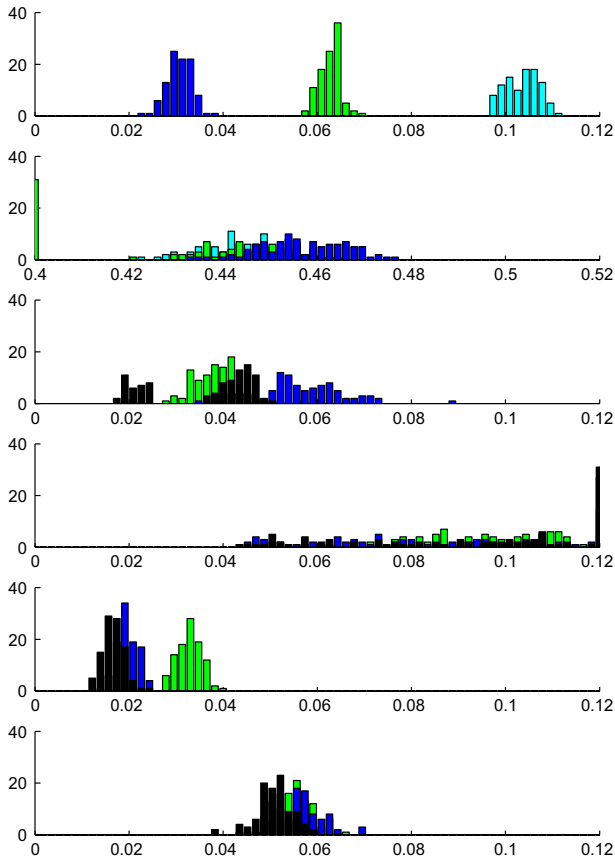


Fig. 4 Growth-rate distributions for models I–VI (rows 1–6) using three different time windows for each model. Colour coding of time windows: turquoise—30 days; green—50 days; blue—70 days; black—full season. (Note the different scale in row 2). (Color figure online)

rate (up to some degree of noise), so one would expect the distribution of r -values to be fairly narrow as well.

This basically eliminates models II and IV, and probably also model III. Perhaps surprisingly, the simplest model (I) has fairly tight distributions, which seems to give it an edge. However, it has a very strong dependence on the time window over which the fitting is performed. This introduces an unacceptable arbitrariness (how would one tell which time window is appropriate?), which rules out this one, too.

The best compromise between narrowness of the distribution and independence of the time window seem to be offered by model VI. So one may be inclined to declare this the “winner”. It is worth noting that the models that perform best in terms of determining the growth rate r (V and VI) are the ones that do not contain r explicitly.

Of course, there are other factors (likely many) to be considered in selecting models in a particular modelling exercise, such as goodness of fit, complexity,

derivability from first principles, purpose etc. (see e.g. Evans et al. 2013 and the literature therein). More importantly, the point here is not to actually find the best model for the particular data set shown above. Rather, what we want to point out is that stipulating the existence (or “reality”) of an ecological parameter such as the growth rate can potentially provide an additional robustness criterion. This turns the apparent *model dependence* of that parameter into a tool for *model selection*¹². Ecologists might want try to identify other ecological quantities that could be utilized in a similar manner.

6 Conclusion

The story of the Modellers presents us with a choice: either abandon the idea of a unique growth rate inherent of a given population and accept that this notion depends on the model used to determine it—or retain the idea of a single growth rate and reject models that are unable to give robust values for it. For instance, McCallum (2008) unceremoniously states that “*there is limited value in estimating r for its own sake*”. On the other hand, in light of Berryman’s Law quoted at the beginning, a sizeable group of ecologists seems to genuinely hold that the growth rate *is* (real and) fundamental. So is it a matter of mere belief—a mode of mind that many scientists probably feel has no place in scientific inquiry¹³—on which side we come down?

Our final argument is that the two alternatives described above may be used in an iterative manner, much like physicists view the genesis of physical theories. That is, we may take the position that an ecological quantity, such as the growth rate, can only reasonably be assumed to have reality/currency if it can be determined robustly; i.e., if at least one model can be found from which consistent and robust values of that quantity can be derived. If the quantity *has* gained this kind of credibility, it may be utilized as a criterion for model selection as described above. If one model emerges as particularly suitable in a modelling exercise, it can be checked again for robustness in providing values for the same and/or other credible and established quantities of interest.

This approach is by its very definition data-based. So we disagree with the sentiment that data cannot be used “to decide between foundational definitions”, which has been expressed in response to an earlier version of this paper. On the contrary, we feel that the discussion of foundational issues should be spurned and guided by empirical facts and data.

As mentioned at the beginning of this story, we feel no urge (and have limited expertise) to enter the philosophical debate surrounding the interrelations of reality (or realism), laws of nature, scientific models etc. and/or the similarities and

¹² In fact, for the data set at hand the Modellers were somewhat unsatisfied with the results of standard model-selection techniques, such as AIC. This motivated them to look for additional criteria such as the ones described in the present paper.

¹³ Philosophers, even philosophers of science, may feel differently about this, however: we note with interest that Nancy Cartwright (1983) uses the word “believe” 15 times in the introductory chapter of her book alone.

differences of ecology and the physical sciences. Nor do we make claims about novelty and originality of the ideas underlying the story of the Modellers. For instance, the critical role of models and the idea of model robustness have been discussed by Cartwright (1999) and Raerinne (2012) (following Levins 1966), respectively, as well as others.

We advocate a pragmatic view, rooted in the simple observation that scientific practice often proceeds (well) without explicit reference to abstract foundational thinking.¹⁴ We, modellers ourselves, view the concept of a data-driven recursive definition of ecological quantities based on the constructibility and robustness of suitable models¹⁵ as such a pragmatic approach.

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¹⁴ For a better-founded account of the utility of philosophy in biology, see Orzack (2012).

¹⁵ which, in reference to Nancy Cartwright's concept of “nomological machines”, we are tempted to call “nomological *mathchines*”

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