

An analytical foundation of the ratio-dependent predator-prey model

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Abstract

Predator-prey models of the Lotka-Volterra type and their refinements describe predator-prey interactions taking populations as basic units of analysis. In contrast to these macro models we *derive* interdependent population growth functions of a predator and a prey species from a micro ecosystem model whose basic entities are representative prey and predator organisms which behave as if they maximize their net offspring under constraints. In the short-run periods prices (scarcity indicators) coordinate and determine all biomass transactions and net offspring which directly translates into population growth and thus constitutes the dynamics of the predator-prey relations. For a specific parametric version our model offers a theoretical foundation of the ratio-dependent predator-prey model with Michaelis-Menten type functional response.

Keywords: predator, prey, ratio-dependence

1 The Problem

Since the pioneering work of Lotka (1925) and Volterra (1926) the literature on two-species predator-prey models has rapidly grown and is now both well-established and diversified. Such models consist of a system of two differential equations, one for each species, linking population changes (or densities) in time to the size of both species' populations. Various different specifications of these differential equations have been suggested in an attempt to improve the match between empirical population dynamics and theoretical predictions.

Over the last decade a particular version of the predator-prey model received increasing attention due to its relatively realistic population dynamics, the so-called ratio-dependent predator-prey model with Michaelis-Menten type functional response¹, defined by

$$x' = ax \cdot \left(1 - \frac{x}{k}\right) - \frac{cxy}{my + x}, \quad (1a)$$

$$y' = y \left(-e + \frac{fx}{my + x}\right), \quad (1b)$$

where the positive constants a , c , e , f , k and m are meant to capture relevant characteristics of the species and their interaction. The common feature of the predator-prey model (1) and its variants is that populations and their changes in time are the models' basic units of analysis and that they rely on lumped parameters set at the species level. Finnoff and Tschirhart (2003) observe that "... the logistic growth functions depend on entire species' populations and as such they take a macro view in which species interactions ... are at an aggregate level. It is a black box approach." This is not to play down the enormous efforts of ecologists and biologists to justify, reject, defend or revise specific versions of the predator-prey model on the grounds of up-to-date biological and physiological knowledge, on the grounds of insights from field and laboratory experiments, and by referring to theoretical arguments like the local law of interaction or to mechanistic models with spatial or temporal heterogeneities. All such theoretical rationales of the specific functional form of the model to be chosen are important and even indispensable to avoid measurement without theory. Yet according to Arino et al. (2004, p. 1103) the main criticism against the ratio-dependent approach (1) is "... that its proponents have made things too easy by providing easy

¹For rigorous analyses of this model's dynamics see Kuang and Beretta (1998), Berezovskaya et al. (2001), Hsu et al. (2001) and Xiao and Ruan (2001). In contrast to other versions of the predator-prey models the ratio-dependent model has been found to be better in line with empirical evidence regarding the so-called 'paradox of enrichment', the 'biological control paradox' and simultaneous extinction of both species (Hsu et al. 2001, Abrams and Ginzburg 2000). It should also be acknowledged, however, that its empirical fit is still controversial (Abrams 1994, Abrams and Ginzburg 2000).

explanations of positive correlations found in nature in an *ad hoc* manner, without having a credible mechanism that could produce ratio-dependence." We share this criticism and even carry it beyond the specification (1) of conventional predator-prey models. In our view it is unsatisfactory that theoretical arguments - be they more or less *ad hoc* in the sense of Arino et al. (2004) - only motivate the choice of functional forms such as (1) without being part of a formal rigorous theory that *derives* rather than *assumes* a specific system of population growth functions. To the extent that theoretical arguments only serve as a motivation for the specification of the predator-prey model without being an explicit and integrated part of the formal model, Finnoff and Tshirhart (2003) are right in characterizing it as a black box approach.

In our view that weakness applies to all predator-prey models whose basic units of analysis are populations. By construction, these macro approaches neglect the processes at the micro level of preying and being preyed upon which ultimately generate the interdependent growth functions (1). In order to *explain* rather than *assume* these growth functions it is necessary to model the predator-prey relationships at the micro level. This is exactly the focus of a rather recent approach based on economic methodology that has been initiated by Hannon (1976) and further developed by Tschirhart (2000, 2002), Pethig and Tschirhart (2001) and Eichner and Pethig (2003). In that literature the basic units of analysis are individual organisms whose behavior leads to the growth of populations. The starting point of these micro approaches is the short-run period in which populations are constant and in which representative individual organisms behave as if they maximize their net energy or net offspring. More specifically, for given (shadow) prices each organism determines its demand for biomass of other species and its supply of own biomass. A short-run ecosystem equilibrium is attained through market-clearing prices, and the equilibrium biomasses determine the rate of reproduction in the short-run period. A sequence of short-run population changes constitutes the predator-prey dynamics.

The present paper sets up a simple two-species ecosystem model of predator-prey interactions at the micro level along the lines of the theoretical approach described in the preceding paragraph. Our main results are

- (i) that this ecosystem model allows us to *derive* (rather than to *assume*) a system of interdependent growth functions for the populations of the prey and predator species;
- (ii) and that one can find a parametric specification of the micro ecosystem model that yields population growth functions which exactly coincide with the ratio-dependent predator-prey model with Michaelis-Menten type functional response.

The rest of the paper is organized as follows: In section 2 the ecosystem model is introduced.

Section 3 specifies and explores a parametric version of that model and contains the main results. Section 4 concludes.

2 The Model

Consider a predator-prey model where the predator feeds on a prey and the prey species feeds on a resource. Following Tschirhart (2000, 2002) and Pethig and Tschirhart (2001) basic units of analysis are representative individual organisms. In the short-run period the representative organism of the prey species generates net offspring, b_x , according to the function $B^x : \mathbb{R}_+ \times [0, \bar{s}_x] \times \mathbb{R}_+ \rightarrow \mathbb{R}$, where

$$b_x = B^x \left(\begin{matrix} d_r, s_x, x \\ +, -, +, 0 \end{matrix} \right). \quad (2)$$

The net offspring of the representative organism of the predator species, b_y , is specified by the function $B^y : \mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}$, where

$$b_y = B^y \left(\begin{matrix} d_x, y \\ +, +, 0 \end{matrix} \right). \quad (3)$$

In (2) and (3), x and y represent the populations of the prey species and the predator species, respectively, that are assumed constant in the short-run period under consideration. Moreover, d_r denotes the prey organism's intake of the resource, d_x denotes the predator organism's intake of prey biomass and s_x denotes the prey organism's loss of own biomass to its predator. The latter is bounded from above by \bar{s}_x , a positive constant. All variables d and s are measured in biomass units (e.g. kilograms). Instead of using the phrases loss and intake of biomass, we interpret d_r [d_x] as the demand of the prey [predator] organism for the resource [for prey biomass] and s_x as the prey organism's supply of own biomass to its predators. This interpretation suggests that biomass transactions are similar to commodities traded on markets. To further specify our 'economic approach' to the ecosystem denote by p_r the price of the resource and by p_x the price of the prey species biomass. The introduction of prices doesn't serve any purpose other than formalizing the notion that organisms have a perception of biomass scarcity. The scarcer their own biomass the lower is the risk of being preyed upon (which doesn't apply to the top predator, of course) and the more successful therefore is their own search for prey. The scarcer the biomass of their prey, the harder it is for the organisms to get hold of it. Moreover, organisms are assumed to be endowed with a positive constant 'income', w_x and w_y , respectively, which will be interpreted below. Prices and these incomes are denominated in virtual units of account. The prey and predator

transactions, respectively, are constrained by

$$w_x + p_x s_x = p_r d_r, \quad (4a)$$

$$w_y = p_x d_x. \quad (4b)$$

Obviously, (4) closely resembles the household's budget constraint that economists use to employ for the consumer's decision problem. According to (4a) the prey organism has two kinds of incomes for buying the resource $p_r d_r$: the exogenous or lumpsum income w_x and an endogenous income equal to the receipts from selling own biomass, $p_x s_x$. The lumpsum income is a parameter reflecting the prey organism's status or power as a predator, i.e. its 'entitlement' to feed on the resource without being forced to sacrifice own biomass to its predators. We therefore interpret w_x as the *predation power* of the prey organism and analogous w_y as the predation power of the predator organism. Note that the amount of riskfree consumption of the resource [prey] 'guaranteed' to the prey [predator] organism through its predation power w_x [w_y] is w_x/p_r and w_y/p_r , respectively: it shrinks with growing scarcity of the resource [prey]. In contrast to the predator organism which in our simple model has no natural enemies the prey organism is able to expand its purchase of the resource beyond $d_r = w_x/p_r$, provided that it is willing to earn some biomass income, $p_x s_x > 0$, to pay for the extra food. Hence the extra purchase of the resource, $p_x s_x/p_r$, needs to be paid by a sacrifice of own biomass s_x which readily reflects what ecologists refer to as the prey organism's *predation risk*, the risk of being preyed upon while preying (Lima and Dill 1990). From the viewpoint of the prey organism p_r/p_x simply conveys the information that after all riskfree preying is carried out, extra food can be obtained only if, on average, p_r/p_x units of own biomass are sacrificed for every unit of extra catch of resource.

To each organism prices are exogenous, i.e. the organism has no control over the price paid for biomass demand and received for biomass supply. However, within the ecosystem the prices are endogenous, being determined in the biomass markets by supply and demand interactions. Recalling that in the short-run the populations x and y are constant, an ecosystem allocation (d_r, d_x, s_x) is said to be feasible if

$$r = x d_r, \quad (5a)$$

$$x s_x = y d_x, \quad (5b)$$

where r denotes the exogenous supply of the basic resource serving as food for the prey species. Equation (5a) [(5b)] equilibrates the total supply, r [$x s_x$], and total demand $x d_r$ [$y d_x$] for the resource [biomass of the prey species].

Having specified the representative organisms' budget constraints we now turn to their decision problems. It is assumed that the organisms behave as if they solve the

maximization problem:

$$\max_{(d_r, s_x)} B^x(d_r, s_x, x) \quad \text{s.t.} \quad w_x + p_x s_x = p_r d_r, \quad (6a)$$

$$\max_{(d_x)} B^y(d_x, y) \quad \text{s.t.} \quad w_y = p_x d_x. \quad (6b)$$

Next consider the coordination of market transactions by prices. A short-run ecosystem equilibrium is said to be constituted by a price vector (p_r, p_x) and transactions (d_r, d_x, s_x) if (5) and (6) are satisfied for given populations x and y .

Assuming that the constrained maximization problems (6) are well-behaved the solution to (6) yields optimal demands and supplies as functions D^r , D^x and S^x of prices and populations:

$$d_r = D^r(p_r, p_x, x), \quad d_x = D^x(p_x, y) \quad \text{and} \quad s_x = S^x(p_r, p_x, x). \quad (7)$$

When these functions are inserted in (5) one obtains the equilibrium prices as functions P^r and P^x of populations:

$$p_r = P^r(x, y) \quad \text{and} \quad p_x = P^x(x, y). \quad (8)$$

Next (8) is plugged into (7) resulting in

$$d_r = \tilde{D}^r(x, y), \quad d_x = \tilde{D}^x(x, y) \quad \text{and} \quad s_x = \tilde{S}^x(x, y). \quad (9)$$

Finally, (9) is inserted into (2) and (3) to yield

$$b_x = \tilde{B}^x(x, y) \quad \text{and} \quad b_y = \tilde{B}^y(x, y). \quad (10)$$

Obviously, with (8), (9) and (10) a short-run ecosystem equilibrium is completely characterized: Supplies and demands, biomass scarcity and reproduction are uniquely determined by the size x and y of populations that prevail during the short-run period under consideration.

Since $\tilde{B}^x(x, y)$ [$\tilde{B}^y(x, y)$] from (10) is the equilibrium net offspring of the representative prey [predator] organism, *aggregate net offspring* of the prey and predator species, respectively, is naturally defined by

$$\frac{dx}{dt} =: x' = x \tilde{B}^x(x, y) \quad \text{and} \quad \frac{dy}{dt} =: y' = y \tilde{B}^y(x, y). \quad (11)$$

Clearly, the aggregate net offspring represents the change in population x' and y' , respectively, from one short-run period to the next. Therefore the equations (11) constitute population update equations that describe the intertemporal interaction of species populations at the aggregate level.

3 A Parametric Version

Even though our model is quite simple it doesn't yield specific information about the characteristics of the short-run equilibrium and predator-prey dynamics unless more structure is placed on the functions B^x and B^y from (2) and (3). The specifications of these functions needs and ought to be guided by exploiting extant ecological knowledge about the relation between predation and preying on the one hand and reproduction at the micro level on the other hand. However, here we pursue a different objective. We wish to answer the question whether there exists a parametric functional form of the functions B^x and B^y such that the population growth functions (11) coincide with (1). The answer will be shown to be in the affirmative for the following parametric specifications of B^x and B^y :

$$B^x(d_r, s_x, x) = x \cdot [\alpha_x \cdot d_r \cdot (\bar{s}_x - s_x) - \beta_x], \quad (12a)$$

$$B^y(d_x, y) = \alpha_y \cdot d_x - \beta_y, \quad (12b)$$

where α_x , α_y , β_x and β_y are positive parameters.

In that case solving (6) yields the biomass demands and supplies

$$D^r(p_r, p_x, x) = \frac{p_x \bar{s}_x + w_x}{2p_r}, \quad D^x(p_x, y) = \frac{w_y}{p_x} \quad \text{and} \quad S^x(p_r, p_x, x) = \frac{p_x \bar{s}_x - w_x}{2p_x}. \quad (13)$$

The properties of these functions conform to our intuition: With respect to own price, biomass demand curves slope down and the biomass supply curve slopes up. Moreover, an increase in an organism's endowment raises its demand for prey biomass but reduces its supply of own biomass.

Repeating the steps leading to the equations (8) and (9) we obtain

Proposition 1. *The short-run ecosystem equilibrium is characterized by*

$$P^r(x, y) = \frac{xw_x + yw_y}{r}, \quad P^x(x, y) = \frac{xw_x + 2yw_y}{x\bar{s}_x}, \quad (14a)$$

$$\tilde{D}^r(x, y) = \frac{r}{x}, \quad \tilde{D}^x(x, y) = \frac{xw_y\bar{s}_x}{xw_x + 2yw_y}, \quad \tilde{S}^x(x, y) = \frac{yw_y\bar{s}_x}{xw_x + 2yw_y}. \quad (14b)$$

The equations (14) demonstrate that with the parametric functions (12) a short-run equilibrium exists and is unique with all equilibrium prices being strictly positive. Observe that the supply of own biomass s_x is positive, too, which means that in equilibrium the prey organism prefers to expand its intake of the resource by sacrificing some own biomass rather than being satisfied with the amount of resource it is able to secure by exclusively relying on its endowment w_x .

Combining (12) and (14b) yields

Proposition 2. *If the functions (2) and (3) of the ecosystem model in section 2 are specified by (12) the ecosystem model of section 2 implies the predator-prey model*

$$x' = x^2 \cdot \left[\alpha_x \cdot \frac{r}{x} \cdot \left(\bar{s}_x - \frac{yw_y \bar{s}_x}{xw_x + 2yw_y} \right) - \beta_x \right], \quad (15a)$$

$$y' = y \cdot \left[\alpha_y \cdot \frac{xw_y \bar{s}_x}{xw_x + 2yw_y} - \beta_y \right], \quad (15b)$$

which is easily seen to coincide with (1) by the assignments $a := \alpha_x r \bar{s}_x$, $c := \alpha_x r \bar{s}_x w_y / w_x$, $e := \beta_y$, $f := \alpha_y \bar{s}_x w_y / w_x$, $k := \alpha_x r \bar{s}_x / \beta_x$ and $m := 2w_y / w_x$.

It is important to emphasize that the population growth functions (15) are rigorously *derived* from the ecosystem model of section 2 when the net offspring functions take the parametric form (12). The parameters a , c , e , f , k , m in the macro system (1) are specified in Proposition 2 by the parameters α_x , α_y , β_x , β_y , \bar{s}_x , r , w_x and w_y of the micro ecosystem model in a rather complex way. Except for $e = \beta_y$ the parameters a , c , f , k and m are *explained* by a set of more basic determinants that describe the ecosystem at the micro level. Two features of the assignment of micro parameters to macro parameters deserve special mention:

- (i) The parameters w_x and w_y have an impact on population growth only through their ratio w_y/w_x , i.e. the population dynamics are affected only by changes of a species' *relative* predation power.
- (ii) Except for β_x and β_y all micro parameters impact on more than one macro parameter. As a consequence, macro parameters cannot be varied independently when the dynamics of (1) are characterized or when sensitivity analyses are carried out in simulation studies.

4 Concluding Remarks

The principal message of the present paper is that it is possible to provide an analytical foundation of the (strict) ratio-dependent predator-prey model with Michaelis-Menten type functional response. This is done by using economic methodology in order to explicitly model, in a stylized way, an ecosystem with biomass transactions and an allocation mechanism that mimics the economic model of perfect competition: representative members of the prey and the predator species perceive scarcities (prices) and maximize their offspring under constraints similar as price-taking consumers maximize their utility. Neither prices nor competitive markets are real, of course, but the phenomena of scarcity, predation power

and predation risk are real and some sort of optimizing on the part of individual members of species is real, too.

As economists we expect to encounter great scepticism or even outright rejection on the part of many ecologists and biologists when an 'economic approach' to the ecosystem and predator-prey models is suggested. We are confident, nonetheless, that our fresh approach to the analytical foundation of predator-prey relationships will eventually be recognized as a powerful tool with great potential. We didn't foresee and hence were fairly surprised that the micro-based ecosystem model of section 2 implies the predator-prey model (1). To the extent that the model (1) can be considered reasonably realistic, the ecosystem model we employed to derive (1) deserves to be credited, too, and ought to be considered as a reliable explanation of the underlying interactions at the micro level. Those who are willing to follow that line of reasoning might want to take a further step and reexamine (12) with respect to its plausibility and compatibility with ecological and biological knowledge (which is beyond the purpose of the present paper). If the functional forms specified in (12) that are crucial for deriving (1) should turn out to have an unsatisfactory ecological foundation one might want to replace them by more suitable specifications. As a consequence the implied predator-prey model will probably deviate from (1). For example, if (12) is replaced by reproduction functions of the Cobb-Douglas type, it is unlikely that the proportionality between prey consumption and predator production brought about by a so-called functional response term will still hold. Rather than considering that a drawback of the analytical foundation suggested here we would tend to look at it as a possibility of searching systematically for improving our understanding of predator-prey dynamics. To be specific, consider for example the simple specifications of the net offspring functions in (12). With tapping on well-founded ecological knowledge, more realistic parametric functions may be employed which then will not lead to the growth functions (15) anymore but offers the chance to derive a predator-prey model that is empirically even more attractive than the model (1).

Another point that deserves attention in the agenda of future research is the concept of basic resource, r , as introduced in (5a). This resource may be interpreted as a third species that serves as food for the prey species at each point in time and its supply r is time-invariant. Technically, an assumption of this kind is needed to close a micro predator-prey model. Another interpretation of r is, however, to think of the prey species as being a herbivore and of the basic resource of being (a composite) of sunlight, water or minerals whose supply increases with the size of land area that serves both species as habitat. If the relation between the basic resource and size of habitat is linear, as e.g. in a simple model suggested by Swanson (1994), r can be taken to represent the size of habitat. As a consequence, it is no longer appropriate to simply equate the notion of population (=

number of individual members of a species) and density (= number of individuals per unit of habitat) as is common in traditional macro predator-prey models.

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