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THE ORIGINS AND EVOLUTION OF PREDATOR–PREY THEORY¹

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Abstract. Predator–prey theory is traced from its origins in the Malthus–Verhulst *logistic* equation, through the Lotka–Volterra equations, *logistic* modifications to both prey and predator equations, incorporation of the Michaelis–Menten–Holling functional response into the predator and prey equations, and the recent development of *ratio*-dependent functional responses and per-capita rate of change functions. Some of the problems of classical predator–prey theory, including the paradoxes of enrichment and biological control, seem to have been caused by the application of the principle of mass action to predator–prey interactions. Predator–prey models that evolved from *logistic* theory or that incorporate *ratio*-dependent functional responses do not have these problems and also seem to be more biologically plausible.

Key words: *logistic; Lotka–Volterra; predator–prey interactions; ratio dependence.*

INTRODUCTION

The dynamical relationship between predators and their prey is one of the dominant themes in ecology. Yet the theory of predator–prey interactions has some notable problems: One is the “paradox of enrichment,” where classical models predict that enriching the system will cause an increase in the equilibrium density of the predator but not in that of the prey (Hairston, Smith, and Slobodkin 1960), and will destabilize the community equilibrium (Rosenzweig 1969). These predictions, however, are not always in line with field observations (Arditi and Ginzburg 1989, Arditi et al. 1991, Ginzburg and Akçakaya 1992). Another is the “biological control paradox” (Luck 1990, Arditi and Berryman 1991), where classical models predict that you cannot have both a very low and a stable pest (prey) equilibrium density, yet there are numerous examples of predator and parasite introductions (classical biological control) that have resulted in exotic pests being maintained at sparse and apparently stable densities (Turnbull and Chant 1961, DeBach 1974, Hagen and Franz 1973).

Recently there has been renewed interest in what is being called *ratio*-dependent predator–prey theory (Arditi and Ginzburg 1989, Berryman 1990). Although *ratio*-dependent predator–prey models are not new, they have not previously occupied a central place in ecological theory. Yet they solve many of the problems of more conventional models, including the paradoxes of enrichment and biological control (Arditi and Ginz-

burg 1989, Arditi and Berryman 1991). In this paper I briefly sketch the origin and evolution of population theory and, in particular, predator–prey models. My objectives are twofold: First, to show how conventional predator–prey models deviated significantly from earlier theory, and how this may have led to some of their problems. Second, to show how *ratio*-dependent predator–prey theory follows logically from basic concepts of single-species population dynamics, and how this viewpoint solves many of the problems and paradoxes of traditional predator–prey theory.

MALTHUS–VERHULST LOGISTIC THEORY

The first definitive theoretical treatment of population dynamics was Thomas Malthus’ (1798) *Essay on the Principle of Population*. Malthus argued that, while populations grow logarithmically, the resources on which they depend remain constant or only increase arithmetically. Thus, the demand for resources must eventually exceed the supply and population growth, being dependent on the resource supply, must then cease. Forty years later, Verhulst (1838) formed Malthus’ “principle of population” into a mathematical model—the *logistic* equation

$$dN/dt = aN(1 - N/K), \quad (1)$$

where N is the biomass density of the population in question, a is its maximum per-capita rate of change, or the intrinsic rate of increase, and K is the equilibrium density, often called the *carrying capacity* of the environment. Although this equation is often criticized for its oversimplicity, it remains the central theoretical

¹ For reprints of this Special Feature, see footnote 1, p. 1529.

construct for single-species population dynamics and, when generalized to account for discrete growth processes, time-delayed and nonlinear density dependence, and multiple domains of attraction, it describes the dynamics of many single-species populations in both laboratory and field (Gause 1934, Allee et al. 1949, Thomas et al. 1980, Berryman and Millstein 1990).

LOTKA-VOLTERRA PREDATOR-PREY THEORY

Lotka's *Elements of Physical Biology* (Lotka 1925) was the next major advance in population dynamics theory. Not only did Lotka derive the *logistic* equation, which he called the "law of population growth," from first principles, but he also proposed the first model of trophic (predator-prey) interactions. However, instead of developing the predator-prey model by extending the *logistic* "law" to two species he, and soon afterwards Volterra (1928, as translated in Chapman 1931), adopted the chemical principle of mass action. In other words, he assumed that the response of the populations would be proportional to the *product* of their biomass densities so that

$$dN/dt = aN - bNP, \quad (2a)$$

$$dP/dt = cNP - dP, \quad (2b)$$

where N and P are the biomass densities of prey and predator, respectively, a and d are their per-capita rates of change in the absence of each other, and b and c are their respective rates of change due to interaction. This application of the principle of mass action seems to have been the point where predator-prey theory deviated from classical (*logistic*) thinking, and where subsequent theorizing may have been misled.

Shortly after publication of the Lotka-Volterra equations, Nicholson and Bailey (1935) proposed a discrete-time model of the interaction between insect parasitoids and their hosts. Although this model was developed from the more mechanistic perspective of parasitoid search behavior, it is identical in concept to the Lotka-Volterra model (Royama 1971).

The zero-growth isoclines of the Lotka-Volterra equations, obtained by setting their left-hand sides to zero, are perpendicular to the axis of the other species (Fig. 1a). Solutions of the differential equations (Eqs. 2) form a series of closed ellipses that depend critically on the initial conditions (neutrally stable limit cycles). In the more reasonable discrete-time (Nicholson-Bailey) form, however, the model has an unstable solution; i.e., the community equilibrium is an unstable focus (similar to the trajectory shown in Fig. 1a). A great deal of theoretical effort has gone into stabilizing the Nicholson-Bailey equations; i.e., by incorporating in-

terference between searching predators, spatial heterogeneities, polyphagy, etc. (Hassell 1978).

INCURSIONS OF LOGISTIC THEORY

In the original Lotka-Volterra equations, the prey population grows infinitely in the absence of predators. To correct this unreasonable assumption, a *logistic* self-limitation term is often added to the prey equation,

$$dN/dt = aN(1 - N/K) - bNP. \quad (3a)$$

This modification produces an isocline structure similar to that shown in Fig. 1b and stabilizes the system (the equilibrium is now a stable focus).

It is interesting that Volterra (1928, as translated in Chapman 1931) and Gause (1934) both used the *logistic* equation as the underlying structure for their two-species competition models, but failed to consider it as a suitable framework for modeling predator-prey interactions. Leslie (1948) seems to have been the first to consider a *logistic* predator equation

$$dP/dt = cP(1 - eP/N), \quad (3b)$$

where e is the density of prey required to maintain a single predator and to replace it with one offspring when it dies. In other words, e is the marginal subsistence demand for prey, $1/e$ is the marginal reproductive value of the resource, and N/e is the carrying capacity of predators when provided with a constant supply of prey. Leslie's equation seems to be the first time that predator/prey *ratios* (P/N) rather than products (NP) are seen in models of trophic relationships. The system of predator-prey equations (Eqs. 3) has an isocline structure similar to that shown in Fig. 1c, with the community equilibrium a stable focus. Notice that the predator isocline is slanting rather than vertical. This new isocline structure seems to be intuitively reasonable because predator equilibrium densities are expected to be dependent on prey abundance (see e.g., Berryman 1981, Arditi and Ginzburg 1989). In addition, the slanting predator isocline solves the paradoxes of enrichment and biological control (Arditi and Ginzburg 1989, Arditi and Berryman 1991).

PREDATOR FUNCTIONAL RESPONSES

The next major contribution to the theory of predator/prey interactions was the addition of a predator functional response. Solomon (1949) and Holling (1959, 1966) argued that, because predators can only handle a finite number of prey in a unit of time, the prey death rate should be a nonlinear function of prey density; i.e.,

$$dN/dt = aN(1 - N/K) - b(N)P, \quad (4a)$$

where $b(N)$ is the functional response of the predator to prey density. Based on a series of elegant behavioral

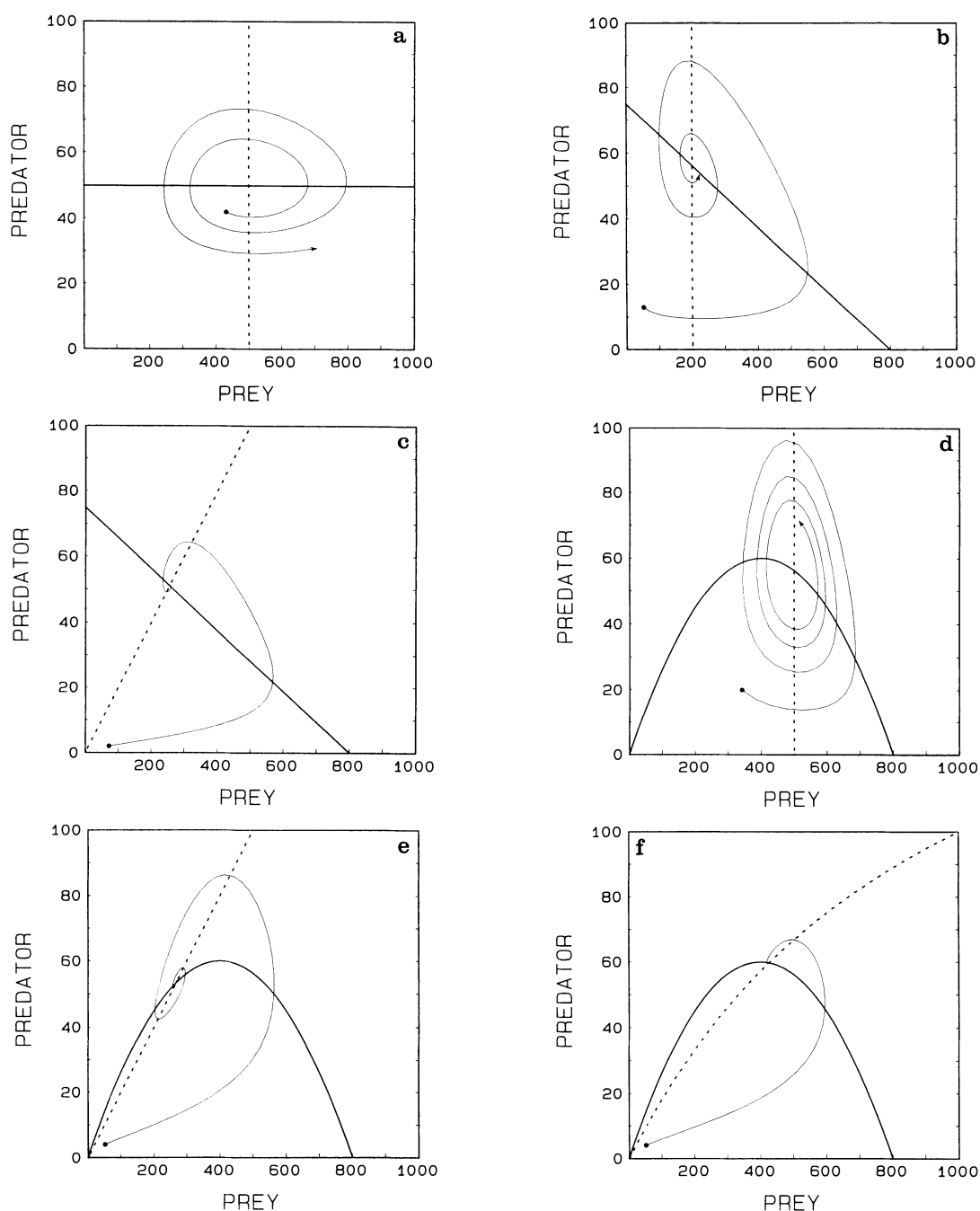


FIG. 1. Zero-growth isoclines for models of interacting prey (—) and predator (---) populations. The thin line is a trajectory predicted by the discrete-time per-capita trophic model, Eqs. 8 and 9 (see Berryman 1990); i.e., $N_{i,t} = N_{i,t-1} \exp\{a_i + b_i N_{i,t-1} + c_i Z_i\}$, where $i = 1$ for prey and $i = 2$ for predator, Z_i is the predator/prey ratio, $N_{2,t-1}/(w_1 + N_{1,t-1})$, in ratio models and $Z_1 = N_{2,t-1}$, $Z_2 = N_{1,t-1}$ in Lotka-Volterra models. (a) Lotka-Volterra-Nicholson-Bailey model: $a_1 = 0.2$, $b_1 = 0$, $c_1 = -0.004$, $a_2 = 0.1$, $b_2 = 0$, $c_2 = 0.0002$. (b) L-V-N-B model with logistic self-limitation on the prey: prey model with parameters the same as (a) except $a_1 = 0.3$ and $b_1 = -0.0004$; predator model the same as (a) except $c_2 = 0.0005$. (c) Logistic-Leslie predator equation: prey model as in (b); ratio predator with $a_2 = 0.2$, $b_2 = 0$, $c_2 = -1$, $w_1 = 0$. (d) Holling-Rosenzweig-MacArthur model: ratio prey model with $a_1 = 0.3$, $b_1 = -0.0004$, $c_1 = -1$, $w_1 = 0$; predator model as in (a), $a_2 = -0.5$, $b_2 = 0$, $c_2 = 0.001$, $w_1 = 0$. (e) Logistic predator-prey model with no predator self-limitation: prey model as in (d); predator model as in (c). (f) Logistic predator-prey model with predator self-limitation: prey model as in (d); predator model as in (c) except $b_2 = -0.001$.

experiments, in which predators (sometimes blindfolded students) searched for different densities of prey (sometimes sandpaper disks), Holling derived his famous "disk" equation which turned out to be identical to the well-known Michaelis-Menten equation of enzyme kinetics (Real 1977); i.e.,

$$b(N) = mN/(w + N), \quad (5)$$

where m is the maximum predator attack rate and w is the prey density where the attack rate is half-saturated. The Michaelis-Menten-Holling equation can be extended to account for general predators that switch from one prey species to another (sigmoid functional responses) (Real 1977). When the functional response is included in the prey equation, we obtain the parabolic (humped) prey isoclines (Rosenzweig 1971) that are characteristic of *ratio*-dependent prey equations (Fig. 1d); note that the functional response introduces *ratio*-dependence into the prey equation because, when w is set to zero as in Fig. 1, the per-capita death rate of the prey becomes mP/N .

On the argument that the prey deaths can be directly translated into predator births, functional responses are often employed in predator equations; i.e.,

$$dP/dt = cP[mN/(w + N)] - dP. \quad (4b)$$

However, this formulation gives rise to the primitive rectilinear Lotka-Volterra predator isocline from which arise the paradoxes of enrichment and biological control (cf. Fig. 1a and d). Nevertheless, the isocline structure shown in Fig. 1d has been employed extensively in the development of modern predator-prey theory (Rosenzweig and MacArthur 1963, MacArthur and Connell 1966).

RATIO-DEPENDENT FUNCTIONAL RESPONSES

Although the inclusion of a functional response in the predator-prey model is intuitively appealing, because it conservatively couples the prey and predator equations, there are some notable problems with this approach. For instance, the functional response describes the behavior of searching predators on a fast (behavioral) time scale (minutes or hours), whereas the population equation, into which it is inserted, often operates on a slower (population dynamical) time scale (days or years). To overcome this problem, Arditi and Ginzburg (1989) suggest that, in cases where the time scales are incongruent, the functional response should be expressed in terms of the *ratio* of prey to predators; e.g., the Holling Type II functional response should be written

$$b(N/P) = m(N/P)/(w + N/P) = mN/(wP + N). \quad (6)$$

A similar feeding equation was proposed previously

by DeAngelis et al. (1975). When inserted into classical predator-prey models, this *ratio*-dependent functional response produces a parabolic prey isocline and right-slanting predator isocline (Fig. 1e), thereby solving the paradoxes of enrichment and biological control (Arditi and Ginzburg 1989, Arditi and Berryman 1991).

THE PER-CAPITA VIEWPOINT

Berryman (1981) and Getz (1984) have argued that, because population dynamics arise from interactions between individual organisms, the equations should be derived as *per-capita* rates of change. For example, we could write the following general *ratio*-dependent per-capita trophic equation,

$$dN_i/N_i dt = R_i = a_i - f_i(N_i/N_{i-1}) - g_i(N_{i+1}/N_i), \quad (7)$$

where N_i is the biomass density of the i^{th} species in a trophic chain, R_i is the per-capita rate of change of that species, a_i is its maximum per-capita rate of change in a given physical environment, f_i defines the interaction between the species and the lower trophic level (its prey) as a function of the predator/prey ratio, and g_i defines its interaction with the higher trophic level (its predator), also as a function of the predator/prey ratio. Using the type II functional response (Eq. 5) for f and g , we can obtain an explicit per-capita trophic equation (see Appendix),

$$R_i = a_i - b_i N_i/(w_{i-1} + N_{i-1}) - c_i N_{i+1}/(w_i + N_i), \quad (8)$$

where b_i defines the effect of *intra*-specific competition for food on the per-capita rate of change (f reduces to the classical *logistic* when $w_{i-1} + N_{i-1} = \text{a constant}$; see Appendix), c_i is a coefficient of vulnerability defining the effect of predation on the per-capita rate of change, and w_i is the biomass density of all other food species in the i^{th} trophic level. Notice that the per-capita viewpoint clarifies the ecological meaning of the functional response parameter w_i , previously called the "half-saturation" point; i.e., it defines the quantity of alternative food available to the predator. Because the denominators of the predator/prey ratios in (Eq. 8) contain all the prey species available to each predator, while the predators utilizing that food are contained in the numerators, it is fairly straightforward to extend this equation to food webs with many species in each trophic level.

It is worth noting that, although simple per-capita equations are nonlinear in respect to their variables, they are linear in their ratios and, therefore, can be fit to data with standard regression techniques (Berryman 1990). In this way, model parameters can be estimated *a posteriori* from time-series data, such as might be obtained from annual surveys or harvest records. For

example, the per-capita rate of change of each species can be estimated from the relationship

$$R_i = 1/N \cdot dN/dt = d \ln N/dt = \ln(N_i/N_{i-1}), \quad (9)$$

and this can be regressed against the predator/prey ratios (Eq. 8). These models can then be used to predict future population trends or to simulate resource or pest management policies (Berryman 1991); i.e., they have practical utility.

CONCLUSIONS

Unlike the theoretical models of *inter*-specific competition and mutualism, which emerged directly from the theory of *logistic* single-species population dynamics, the original Lotka-Volterra predator-prey equations were built around the principle of mass action; i.e., the responses were assumed to be proportional to the *product* rather than the *ratio* of population densities. Predator equations derived in this way have vertical isoclines, leading to the paradoxes of enrichment and biological control.

The inclusion of a predator functional response in the Lotka-Volterra model corrected the unreasonable assumption of unsaturating attack rates. However, the primitive rectilinear predator isocline remained, and so also the paradoxes of enrichment and biological control. This problem was solved by making the functional response depend on prey/predator ratios rather than prey densities alone.

Per-capita predator/prey models evolve naturally from classical *logistic* theory. Such models have slanting predator isoclines, contain implicit functional responses (see Appendix), and solve the paradoxes of enrichment and biological control. In addition, they offer parsimonious descriptions of predator/prey interactions, and can easily be extended to multi-species food webs. It may also be significant that *logistic* models emerge from the reduction and simplification of detailed physiological and behavioral predator-prey models (Rapport and Turner 1975, Gutierrez 1992).

The main criticism that has been levelled at *logistic* (per-capita) predator/prey models is that they may not strictly conform to the laws of conservation (Ginzburg and Akçakaya 1992); i.e., the equations are not explicitly coupled by the biomass of prey killed, as are conventional models. However, it may be overly restrictive to insist that predator/prey models adhere strictly to the laws of conservation. After all, prey death is not always necessary for predator reproduction. For example, true parasites and most organisms that feed on plants do not kill their hosts, but they may reduce fertility, fecundity, and growth rates. Insistence on conformity to the laws of conservation may, therefore, unnecessarily constrain the development of a general theory of predator-prey interactions.

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APPENDIX

The type II functional response (Eq. 5) defines the attack rate per predator supplied with N prey, so for P predators the prey death rate is $mNP/(w + N)$. Dividing by N gives the per-capita death rate $mP/(w + N)$ which, after relabelling, can be substituted for f_i and g_i in Eq. 7 to give Eq. 8. It is important to note that the first per-capita functional response (f_i in Eq. 7) reduces to the classical *logistic* when the lower trophic level is constant; e.g., a constant input of sunlight for plants. Under this condition, $w_{i-1} + N_{i-1}$ is a constant $= E_{i-1}$, and $E_{i-1}/b_i = K_{i-1}$, the equilibrium density or carrying capacity of the environment. Leslie (1948) demonstrated this implicit functional response within the *logistic* equation; e.g., if we write the per-capita logistic predator equation (Eq. 3b)

$$dP/Pdt = c(1 - eP/N),$$

$$R_p = c - bP/N, \quad \text{with } b = ce.$$

For a single predator foraging for prey in an arena, this becomes

$$R_p = c - b/N,$$

which has an identical form to the type II functional response; i.e., $R_p \rightarrow -\infty$ as $N \rightarrow 0$ and $R_p \rightarrow c$ as $N \rightarrow \infty$. Equivalency between the *logistic* equation and the functional response occurs if the per-capita rate of change of the predator is assumed to be directly proportional to the number of prey eaten, a not unreasonable proposition.