



# Ratio-Dependence in Predator-Prey Systems as an Edge and Basic Minimal Model of Predator Interference

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The functional response (trophic function or individual ration) quantifies the average amount of prey consumed per unit of time by a single predator. Since the seminal Lotka-Volterra model, it is a key element of the predation theory. Holling has enhanced the theory by classifying *prey-dependent* functional responses into three types that long remained a generally accepted basis of modeling predator-prey interactions. However, contradictions between the observed dynamics of natural ecosystems and the properties of predator-prey models with Holling-type trophic functions, such as the paradox of enrichment, the paradox of biological control, and the paradoxical enrichment response mediated by trophic cascades, required further improvement of the theory. This led to the idea of the inclusion of predator interference into the trophic function. Various functional responses depending on both prey and predator densities have been suggested and compared in their performance to fit observed data. At the end of the 1980s, Arditi and Ginzburg stimulated a lively debate having a strong impact on predation theory. They proposed the concept of a spectrum of *predator-dependent* trophic functions, with two opposite edges being the *prey-dependent* and the *ratio-dependent* cases, and they suggested revising the theory by using the ratio-dependent edge of the spectrum as a null model of predator interference. Ratio-dependence offers the simplest way of accounting for mutual interference in predator-prey models, resolving the abovementioned contradictions between theory and natural observations. Depending on the practical needs and the availability of observations, the more detailed models can be built on this theoretical basis.

**Keywords:** functional response, trophic function, non-adaptive selection, predator interference, ratio-dependence, predator-dependence, Arditi-Ginzburg functional response

## INTRODUCTION

Since the first predator-prey model (Lotka, 1925; Volterra, 1926), classical trophic functions ignored interactions (i.e., interference) among predators, depending only on prey density,  $g(N)$  (refer to the examples in **Table 1**). Due to this, the Lotka-Volterra (LV)-type models demonstrate either structural instability (Svirezhev and Logofet, 1983; Bazykin, 1989) or large-amplitude oscillations with periodic drops of population abundances to extremely low levels in scenarios when the coexistence of more stable species is expected (Rosenzweig, 1971; Arditi and Ginzburg, 1989; Luck, 1990; Arditi and Berryman, 1991; Berryman, 1999; Sapoukhina et al., 2003). In a stochastic

**TABLE 1** | Examples of trophic functions without and with mutual interference of predators.

Name	Expression	Source
Lotka-Volterra (LV)	$g(N) = aN$	Lotka, 1925; Volterra, 1926
Ivlev-Gause (IG)	$g(N) = R(1 - e^{-\varepsilon N})$	Gause, 1934; Ivlev, 1955, 1961
Holling type I (H-I)	$g(N) = \min\{aN, R\}$	Holling, 1959a; Bazykin, 1985, 1989
Holling type II (H-II)	$g(N) = \frac{aN}{1+ahN}$	Holling, 1959a,b
Holling type III (H-III)	$g(N) = \frac{aN^2}{1+ahN^2}; n > 1$	Holling, 1959a; Real, 1977
Ivlev (IRD)	$g(N/P) = R(1 - e^{-\varepsilon N/P})$	Ivlev, 1947, 1955, 1961
Hassell-Varley (HV)	$g(N, P) = \alpha N/P^m$	Hassell and Varley, 1969
Hassell-Varley-Holling (HVH)	$g(N, P) = \frac{\alpha N/P^m}{1+ahN/P^m}$	Sutherland, 1983; Arditi and Akçakaya, 1990
Beddington-DeAngelis (BDA)	$g(N, P) = \frac{aN}{(1+awP+ahN)}$	Beddington, 1975; DeAngelis et al., 1975
Arditi-Ginzburg donor control (AG-DC)	$g(N/P) = \min\{aN/P, R\}$	Arditi et al., 1978
Arditi-Ginzburg-Contois (AGC)	$g(N/P) = \frac{\alpha N/P}{1+ahN/P} = \frac{\alpha N}{P+ahN}$	Ginzburg et al., 1971; Arditi et al., 1978; Arditi and Ginzburg, 1989
Bazykin-Crowley-Martin (BCM)	$g(N, P) = \frac{\alpha N}{1+ahN} \cdot \frac{1}{1+\beta P}$	Bazykin et al., 1981; Bazykin, 1989; Crowley and Martin, 1989
Bazykin-Harrison (BH)	$g(N, P) = g(N) / (1 + \beta P)$	Bazykin et al., 1981; Harrison, 1995
Trân hybrid model of prey sharing (Tr-Sh)	$g(N, P) = \frac{N}{P} \left[ 1 - (1 - \varepsilon \tau) \frac{P}{N} \right]$	Trân, 2008
Trân hybrid model of prey depletion (Tr-Dp)	$g(N, P) = \frac{N}{P} (1 - e^{-\varepsilon P})$	Trân, 2008
General RD model 1 (GRD-1)	$g(N, P) = \frac{aN}{P/P_0 + e^{-P/P_0} + ahN}$	Tyutyunov et al., 2008
General RD model 2 (GRD-2)	$g(N, P) = \frac{aN}{P/P_0 + 1/(1+P/P_0) + ahN}$	Tyutyunov et al., 2010

environment, such large fluctuations should cause the extinction of the consumer (Arditi et al., 2004; Jensen and Ginzburg, 2005; Hastings et al., 2018). The use of *predator-dependent* trophic functions (Table 1) corrects the models, enabling them to reproduce stable dynamic patterns that more closely approximate nature.

Arditi and Ginzburg (1989) proposed the idea of a spectrum of every possible *predator-dependent* trophic functions, with two opposite edges being the *prey-dependent* and *ratio-dependent* cases:

$$g(N) \leftarrow g(N, P) \rightarrow g(N/P). \quad (1)$$

Spectrum (1) ranks trophic functions from one extreme case of non-sharing to the other extreme case of perfect sharing of food among predators. Having highlighted the contradictions between the observed dynamics of natural ecosystems and the qualitative properties of predator-prey models with prey-dependent trophic functions, Arditi and Ginzburg (1989) suggested revising theoretical models by means of ratio-dependent functions providing the most parsimonious way of accounting for predator interference (Arditi et al., 1992). Their ideas inspired a lively debate stimulating great interest in justifying criteria for realistic functional response. The study by Arditi and Ginzburg (2012) summarizes their view on the current results of the long-lasting debate.

Some theoretical models with variable interference allow a much stronger (*overcompensating*) level of mutual interference than ratio-dependence. The analysis of these models (Arditi et al., 2004) showed that only moderate interference has the stabilizing effect on large oscillations, i.e., both low and strong interference levels increase the risk of predator extinction in a stochastic environment. Thus, the overcompensating interference should be rare in natural trophic systems subjected to non-adaptive selection (Borrelli et al., 2015), although observations reveal the cases of predator interference beyond ratio-dependence (Arditi and Akçakaya, 1990; Arditi and Ginzburg, 2012; Hossie and Murray, 2016; Novak and Stouffer, 2021a). Notably, both low and overcompensating interferences imply imperfect sharing of prey, thus falling inside the domain of spectrum (1). Unfortunately, opponents of the ratio-dependent theory misinterpret the meaning of the spectrum, alleging that it includes only functional responses reducible to ratio-dependence, excluding cases with interference stronger than ratio-dependence (Abrams, 1994, 2015).

The fundamental question of the ratio-dependent theory is which of the two ends of the spectrum (1) better describes predator-prey systems. Seeking for the simplest model providing qualitatively realistic predator-prey dynamics, Arditi and Ginzburg (1989, 2012, 2014) suggested using the ratio-dependent trophic function as a null model of predator interference. The concept of a minimal model that can be a starting point for building a more detailed description of a studied system is highly important. Such basic model is a compact mathematical formulation of theory providing general predictions over a set of different models for specific situations (Ginzburg and Colyvan, 2004; Ginzburg and Jensen, 2008; Batterman and Collin, 2014). Solving particular problems may require more detailed descriptions of a trophic system and elaborating the basic ratio-dependent model into a more general predator-dependent model if necessary.

## TRANSFERRING THE BASIS OF PREDATION THEORY FROM PREY- TO RATIO-DEPENDENCE

### Historical Primacy of Prey-Dependent Models

The LV model, ignoring the intraspecies competition of prey, implies unlimited Malthusian growth of prey in the absence of predator. Being sensitive to initial conditions, the model is structurally unstable (Kostitzin, 1937; Kolmogorov, 1972; Svirezhev and Logofet, 1983; Begon et al., 1986; Bazykin, 1989). Replacing Malthusian prey growth with logistic law stabilizes the model. However, this does not solve the problem of unlimited consumption rates by an individual predator. Such consumption is an unrealistic hypothesis because a predator does not consume all encountered prey (Nicholson, 1933). The fate of prey depends on the satiety of the predator. Making the same assumptions, Gause (1934) has proposed and experimentally validated an exponential trophic function saturating with prey density. This

dependence [Ivlev-Gause (IG), **Table 1**] well describes the individual food ration of fish (Ivlev, 1961) and crustaceans (Sushchenya, 1975).

Holling (1959a,b, 1965) has identified three types of functional responses accounting for two kinds of predator activity, namely, searching for and handling prey. All types of the functional responses of Holling (1959a) are bounded monotonically increasing prey-dependent functions. The Holling type I function increases linearly for small  $N$  and is limited from above for large  $N$ . Although in his illustration, Holling (1959a) smoothly connected the linear growth phase with a horizontal line of the saturation phase, the piecewise-linear function (H-I, **Table 1**) provides a convenient approximation (Svirezhev and Logofet, 1983; Bazykin, 1989; Jeschke et al., 2004). Type I trophic functions are typical for non-selective filter feeders (Jeschke et al., 2004) and for some parasitoids (Kaçar et al., 2017).

The type II functional response is a concave saturating function. Thus, the Ivlev trophic function IG belongs to type II (Holling, 1965). The most popular parameterization of the Holling type II trophic function is the famous “disk-equation” of Holling (1959b) accounting for the handling time  $h$  (H-II, **Table 1**). It coincides with a microbial population growth model by Monod (1949) and with the Michaelis–Menten model of enzyme kinetics (Michaelis and Menten, 1913). Its modification gives the sigmoid Holling type III (H-III, **Table 1**) functional response (Real, 1977).

Contrary to the constant searching efficiency  $a$  in H-II, the searching efficiency in H-III depends on the prey density:  $\tilde{a}(N) = aN^{n-1}$ . The most practical value of  $n$  used in empirical and theoretical studies is  $n = 2$  (Bazykin, 1989; Sarnelle and Wilson, 2008; Svirezhev, 2008; Prokopenko et al., 2017). Sigmoid trophic functions are suitable for predators that increase their searching efficiency with prey density and for polyphagous predators that switch to more abundant alternative prey (Holling, 1959a; Murdoch, 1969; Jeschke et al., 2004). Sarnelle and Wilson (2008) demonstrated evidence of a type III response for *Daphnia*.

## The Fallacies of Conventional Models and Their Correction With Predator-Dependence

With logistic prey growth and constant predator mortality, the considered predator-prey model is a system of differential equations as follows:

$$\begin{cases} \frac{dN}{dt} = N(r - cN) - Pg(\cdot); \\ \frac{dP}{dt} = \epsilon Pg(\cdot) - \mu P, \end{cases} \quad (2)$$

where  $g(\cdot)$  denotes a trophic function with the appropriate argument(s).

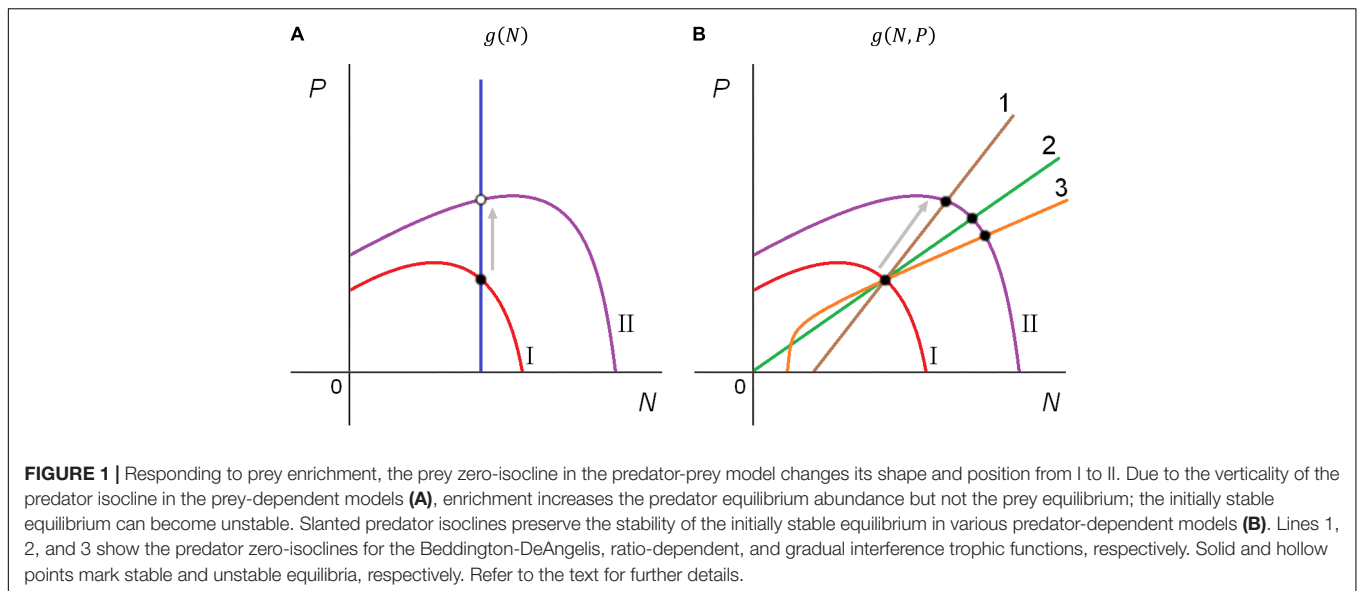
The classical predation theory assumes that predators encounter prey at random and the trophic function depends on prey density only,  $g(\cdot) = g(N)$ . This leads to paradoxical contradiction noted by Arditi and Ginzburg (1989). On the one hand, classical trophic functions fit data collected from the laboratory trophic systems (Gause, 1934; Holling, 1959a,b, 1965; Ivlev, 1961; Veilleux, 1979; Arditi and Saïah, 1992; Bohannan and Lenski, 1997; Jeschke et al., 2004; Tully et al., 2005). On the other

hand, attempts to apply the prey-dependent model (2) to describe the dynamics of large-scale ecosystems often fail. The unrealistic dynamic patterns of conventional models include the *paradox of enrichment* demonstrated by the Rosenzweig–MacArthur predator-prey model [system (2) with trophic function H-II] (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971) and the closely related *paradox of biological control* (Luck, 1990; Arditi and Berryman, 1991; Berryman, 1999; Sapoukhina et al., 2003), as well as the absurd divergently directed reaction of “trophic cascade” levels to bottom-up biomanipulation, called *enrichment response* (Jensen and Ginzburg, 2005; Arditi and Ginzburg, 2012). Jensen and Ginzburg (2005) opine that all known attempts to find natural observations of such dynamics involve either inaccurate processing or erroneous interpretation of the data (Akçakaya et al., 1995). The fundamental cause of the abovementioned contradictions is the verticality of zero-isocline of the predator equation *IsoP* in models with prey-dependent trophic function  $g(N)$  (Arditi and Ginzburg, 1989). The verticality of *IsoP* in **Figure 1A** implies that it is enough to have a constant number of prey to maintain any abundance of a predator population. A hypothesis of mutual interference among the predators is more realistic (Begon et al., 1986): “individual consumption rates decline with predator abundance, and additional prey are required to maintain a predator population of any given size.” In this case, the slanting line of predator zero-isocline stabilizes the system dynamics (**Figure 1B**). Nowadays, most researchers admit that for resolving the contradictions at a large spatiotemporal scale, the functional response should take into account the mutual interference of predator, being a function of both prey and predator densities (DeAngelis et al., 1975, 2021; Berdnikov et al., 1999; Cosner et al., 1999; Abrams and Ginzburg, 2000; Arditi and Ginzburg, 2012). Experiments with appropriate variation in predator densities also show evidence of predator dependence (Skalski and Gilliam, 2001; DeLong and Vasseur, 2011; Novak and Stouffer, 2021a). However, choosing a particular form of the predator-dependence remains a point of controversy (Abrams and Ginzburg, 2000).

Having suggested transferring the basis of the predation theory from the prey-dependent to the ratio-dependent edge of the spectrum (1), Arditi and Ginzburg (1989) proposed the simplest ratio-dependent modification of the H-II trophic function that assumes that predator interference diminishes the predator searching efficiency:  $a = a(P) = \alpha/P$ . The Arditi–Ginzburg trophic function (AGC, **Table 1**) coincides with the Contois (1959) model describing the *per capita* growth rate of bacteria. The joint article of Arditi and Ginzburg (1989) followed the studies of the two authors on the ratio-dependence (Ginzburg et al., 1971, 1974; Ginzburg, 1975, 1986; Arditi et al., 1978; Arditi, 1983) and the results of other authors on predator interference. **Table 1** represents examples and references from the review (Tyutyunov and Titova, 2020).

## Underlying Mechanisms and Minimal Model of Predator Interference

Some predator-dependent trophic functions in either particular or asymptotic case approach the ratio-dependence. Moreover, the identification of the Hassel–Varley–Holling (HVH) function



(Table 1) from the experimental data (Arditi and Akçakaya, 1990) has established that parameter  $m$  was often close to 1 (i.e., to ratio-dependence). Later, Novak and Stouffer (2021a) revealed that the estimates of interference strength in HVH model could be statistically biased upward by low sample sizes. In general, observations suggest that predator-dependence is widespread, more frequent than prey-dependence, and the most common values of  $m$  in HVH function are slightly less than 1 (DeLong and Vasseur, 2011, 2013). This agrees with the analytical results of Arditi et al. (2004) who provided evolutionary arguments in favor of a ratio-dependent pattern of consumption: both small and extremely large values of parameters characterizing mutual interference in the Hassel-Varley (HV), HVH, and Beddington-DeAngelis (BDA; Table 1) trophic functions destabilize the model, increasing the chances of predator extinction due to the accidental drop of population abundances. Some authors interpret the deviation of  $m$  from 1 as an argument against ratio-dependence, asserting that having a variety of predator-dependent trophic functions is more practical than a simple ratio-dependent model (Barraquand, 2014; Abrams, 2015). Replying to this criticism, Arditi and Ginzburg (2014) emphasized that their model is not an alternative to other existing models but rather a reasonable null model, i.e., a starting theoretical point for building a description of a predator-prey system. The AGC function is a minimal extension of the H-II dependence, which greatly widens the dynamical spectrum of model (2) and eliminates the shortcomings of the classical theory without adding extra parameters (Arditi and Berryman, 1991; Arditi et al., 1991; Ginzburg and Akçakaya, 1992; Akçakaya et al., 1995; Berezovskaya et al., 2001, 2007, 2021; Ginzburg and Colyvan, 2004; Arditi and Ginzburg, 2012). Zero-isocline  $IsoP$  for model (2) with the ratio-dependent AGC function is a straight line starting at the origin (line 2, Figure 1B). Thus, formally, similar to other predator-dependent trophic functions, the AGC relationship stabilizes the model due to the slant of  $IsoP$ . Problems with the behavior of ratio-dependent systems near the origin (Oksanen et al., 1992;

Freedman and Mathsen, 1993; Abrams, 1994, 2015; Barraquand, 2014) can be overcome by applying the blow-up technics in the analysis (Berezovskaya et al., 2001, 2007, 2021) or by adding the Allee effect to make the models more realistic by introducing the deterministic extinction of species at low density (Sen et al., 2012).

Plots of  $IsoP$  in the predator-dependent models can have different forms or layouts, e.g., line 1 in Figure 1 corresponds to the BDA model. However, the HV, HVH, BDA, Bazykin-Crowley-Martin (BCM), and Bazykin-Harrison (BH) functions have common shortcomings: there is a special parameter regulating the strength of predator interference ( $m$ ,  $w$ , or  $\beta$ , respectively). The gradual interference hypothesis (Arditi and Ginzburg, 2012) consists in the use of some universal trophic function  $g(N, P)$  exhibiting density-dependence for the high population abundances but weakening interference for the low population densities (zero-isocline 3, Figure 1). This conception allows synthesizing prey-dependent and predator-dependent models (Abrams and Ginzburg, 2000; Ginzburg and Jensen, 2008). Table 1 represents the examples of such hybrid trophic functions, allowing transition between prey- and ratio-dependence: non-saturating (Trân hybrid model of prey sharing and Trân hybrid model of prey depletion) and saturating [General RD model 1 (GRD-1) and General RD model 1 (GRD-2)] models of individual ration. Such universal functions can explain why Monod (1949) and Contois (1959), studying bacteria growth, came to different models coinciding with the dependences H-II and AGC, respectively. Monod was working with low concentrations of bacteria, while Contois experimented with high concentrations (Arditi and Ginzburg, 2012). Nevertheless, compared to AGC, HVH, and BDA trophic functions, universal GRD functions do not demonstrate far superior performance and flexibility in fitting the observed data (Tyutyunov et al., 2010; Prokopenko et al., 2017; Novak and Stouffer, 2021b). Accordingly, simpler models provide just as good approximations to reality.

Finally, the functional response depends on the spatiotemporal scale. DeAngelis et al. (2021) stressed that the ratio-dependent functional response focuses on accurately capturing dynamics emerging at the coarse landscape scale and is not derivable in following the assumptions of the Holling-type responses. DeAngelis et al. (2021) suggested a conceptual approach of hierarchical patch-centered functional response models functioning as a bridge to scale up from local to landscape scale. This conception agrees with the idea that while prey-dependent trophic functions  $g(N)$  are suitable to model small microcosms with low consumer density, choosing an appropriate tool for studying large-scale heterogeneous ecosystems, one should select some predator-dependent function. Within the frameworks of non-spatial (point) predator-prey systems, taking the AGC function as a null model of mutual interference can be a good decision (Ginzburg and Colyvan, 2004). This function provides a modeler with the simplest possibility to implicitly include the various effects of the environmental heterogeneity and the spatial behavior of consumers into a non-spatial model. Recent studies emphasize the importance of spatial effects in predator-prey systems, in particular, the mechanisms of pattern formation and dynamic properties emerging at a large spatiotemporal scale (Tyutyunov et al., 2020; Frank et al., 2021; Sun et al., 2021; Xue et al., 2021; Wang et al., 2022). Modeling gives a mechanistic explanation for the emergence of mutual interference. With a model that considers prey refuges, Poggiale et al. (1998) explained the emergence of donor control, i.e., a special case of ratio-dependence. Spatially explicit continuous (Arditi et al., 2001; Tyutyunov et al., 2002) and individual-based (Tyutyunov et al., 2008, 2013) models revealed that the motility of predator and its ability to move directionally in response to the heterogeneity of prey distribution (*prey-taxis*) is a key factor causing the emergence of the predator- and ratio-dependence at the population level. These results agree with feeding patterns observed in the laboratory cascade of reservoirs, demonstrating the emergence of consumer interference caused by the spatial clustering of cladocerans (Arditi and Saïah, 1992). They confirm also the theoretical conjectures by Cosner et al. (1999) and Arditi and Ginzburg (1989, 2012) about different behaviors corresponding to different functional responses: passive consumption leads to prey-dependence, and active predation leads to predator- and ratio-dependence (see also Ginzburg and Jensen, 2008). Unfortunately, opponents of the ratio-dependent theory did not acknowledge justification for ratio-dependence obtained with the prey-taxis models. Arguing against the spatial heterogeneity justification, they refer to a simple two-patch model (Abrams, 1994) and to spatial models (Barraquand, 2014; Abrams, 2015) that ignore directed movements of predators, and thus cannot demonstrate the emergence of predator- or ratio-dependence at the population level. Predator-prey models with prey-taxis show that the active movements of predators generate spatially heterogeneous dynamics, stabilizing trophic systems at both local and landscape scales (Sapoukhina et al., 2003; Tyutyunov et al., 2019). Emerging population clustering induces predator interference at the population level. Besides, the movements of the predator density patches create temporal refuges for the prey, providing an advantage for both predator

(increasing consumption) and prey (increasing abundance) (Arditi et al., 2001; Sapoukhina et al., 2003; Tyutyunov et al., 2017, 2020).

## CONCLUSION

Interestingly, the first trophic function taking into account the mutual interference of predators was ratio-dependent. Ivlev (1947, 1961) suggested this function (IRD, **Table 1**) to describe the phenomenon of “*complicated competition*” of fed individuals, which he discovered empirically in experiments with fish. Later, Park (1954) termed this phenomenon as “*mutual interference*.” Designing his experiments, Ivlev devoted much attention to the spatial distribution of food and jointly foraging consumers, reproducing natural conditions in detail. Since then, models assuming the dependence of predator ration on ratio  $N/P$  were based on the natural and laboratory observations, which provided evidence for ratio-dependence (Arditi and Saïah, 1992; Vucetich et al., 2002; Jost et al., 2005; Tyutyunov et al., 2010; DeLong and Vasseur, 2011; Arditi and Ginzburg, 2012; Spataro et al., 2012; Hebblewhite, 2013; Médoc et al., 2013, 2015; Hossie and Murray, 2016; Prokopenko et al., 2017; De Troyer et al., 2021). While predator interference can be overestimated due to systematic bias arising at a low sample size (Novak and Stouffer, 2021a), the parsimonious ratio-dependent model could satisfactorily describe the predation process, providing a reasonable trade-off between complexity and performance, particularly in such cases of scarce data (Ginzburg and Colyvan, 2004; Weijs and Ruddell, 2020).

The “alternative” approach to the mathematical description of the trophic relationship between species, proposed by Arditi and Ginzburg, gradually supersedes the traditional Lotka-Volterra model, taking deserved place in monographs and textbooks. Since its 7th edition, the popular textbook on ecology (Molles, 2016) presents both LV and AGC models as the fundamental predator-prey systems. The theory of ratio-dependent predation had already given an impetus to the development of the modern trophic theory. However, many challenging multidisciplinary problems remain unsolved. As such, future studies will benefit from collaboration between empiricists, field biologists, and theoreticians (Arditi and Ginzburg, 2014; Hossie and Murray, 2016).

## AUTHOR CONTRIBUTIONS

YuT designed the scope of the manuscript. YuT and LT reviewed the literature and prepared the manuscript. Both authors have equally contributed to this study.

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