

From controversy to consensus: the indirect interference functional response

Lev R. Ginzburg and Christopher X.J. Jensen

Introduction

Theoretical debate between advocates of the prey-dependent and ratio-dependent functional responses has given way to an understanding that most functional responses exhibit some form of predator dependence (ABRAMS & GINZBURG 2000). The intermediate models of BEDDINGTON-DEANGELIS (BD; DEANGELIS et al. 1975) and HASSELL-VARLEY (HvH; HASSELL-VARLEY 1969) capture some of the properties of ratio dependence without the extreme assumption of total prey sharing. When and how to use these intermediates remains a mystery; this uncertainty prevents prediction of: (1) the equilibrium response of trophic systems to enrichment; (2) the length of trophic chains; and (3) the stability of trophic systems.

Whether the goal of an applied project is to keep population densities low (e.g., when managing a pest or counteracting an algal bloom) or to maintain sufficient population densities (e.g., when conservation is the goal), functional response assumptions directly impact the decision-making process. With the eventual goal of using predator-prey equations to aid in management and conservation efforts, some guidance in choosing an appropriate functional response needs to be provided. We delineated the strengths and weaknesses of the prey- and ratio-dependent forms and suggest a novel predator-dependent form that preserves the viable attributes of both extremes.

Key words: predation, predator dependence, predator interference, prey dependence, ratio dependence

Experimental evidence for ecological domains

Aquatic microbial experiments that consider equilibrium predator-prey densities over a continuum of system enrichment (BOHANNAN & LENSKI 1997, KAUNZINGER & MORIN 1998) show that the densities of both predators and prey respond to enrichment, with the prey responding to a lesser degree. This result is inconsistent with both prey- and ratio-dependent predictions but can be explained equally well by the BD and HvH models if we assume particular intermediate levels of interference.

Because the Kaunzinger and Morin experiment looked at a 3-level chain, it could detect a key prediction of the prey-dependent and BD models: the top predator was excluded from the system at lower levels of enrichment. Considering both equilibrium predictions and predator exclusion patterns simultaneously, only the BD model with significant interference can account completely for the results of this important experiment. Microbial experiments have also shed light on the role of enrichment on predator-prey interaction stability. While none of these experiments provides an ideal test of the paradox of enrichment, the work of LUCKINBILL (1973), VEILLEUX (1979), and FUSSMANN et al. (2000) all suggest that system enrichment can destabilize the interaction.

A crucial question remains unanswered: do aquatic microbial predator-prey systems behave analogously to their more macroscopic cousins? Unfortunately, macroscopic trophic systems are usually enriched for a short period of time ("pulse"), a manipulation that is neither analogous to the continually enriched ("press") microbial experiments nor capable of distinguishing between competing functional responses. We know of only 2 examples of systems in which the consequences of prolonged enrichment have been analyzed; both are aquatic. The equilibrium response to enrichment of an estuarine trophic chain with 4 levels was shown to match the predictions of the ratio-dependent model (BISCHOP et al. 2006). Similarly, greater standing producer biomass was correlated with higher consumer biomass in an oceanic trophic system (WARE & THOMSON 2005).

Stepping back from data described above, a consistent pattern emerges: for some criteria, prey-dependent predictions hold up, while for others the predictions of ratio dependence makes more sense. We can also see where each model fails: prey-dependence seems to get the equilibrium response to enrichment wrong, while ratio-dependence makes inaccurate predictions about the lengths of food chains at low levels of enrichment. These contradictory results suggest that neither model is wrong and that the major theoretical shortcoming has been the failure to identify where each model functions best. We became further intrigued by the idea that each functional response might be assigned to a particular "ecological domain" when we saw the results of 2 recent studies. When a Bayesian approach is used to fit to the time series data of VEILLEUX (1979)

and the functional response is allowed to vary uniquely across the phase space of predator and prey densities, a critical pattern emerges: the behavior of the system is best described by prey dependence at low predator densities and by ratio dependence at higher predator densities (PATIL & MUNCH 2007 pers. comm.). Similarly, individual-based predator-prey modeling produces an isocline that is vertical at low predator densities and slanted at high predator densities (TYUTYUNOV et al. 2008).

Experimental evidence unequivocally supporting a particular functional response would end the theoretical debate. Support for so many different functional response forms suggests that multiple models work, each under particular and separate conditions (DIEHL et al. 1993, ABRAMS & GINZBURG). We call these conditions “ecological domains.”

Capturing both domains in one model

A critical question frames the functional response debate: how important is predator interference? Such interference can take 2 forms: direct and indirect. Direct interference occurs when per capita consumption rates are depressed at high predator densities because predators waste time “handling” each other, and it provides the mechanism behind the BD model. Indirect interference occurs when per capita consumption rates are depressed at high predator densities solely by the presence of other predators and not direct interaction. The simplest form of indirect interference is prey depletion. At higher predator densities, prey are captured and consumed at higher rates, causing a rapid decrease in prey density. Prey depletion has been well-documented, but whether you think depletion is critical to understanding predator-prey dynamics depends on whether you believe that consumption should be measured instantaneously (FUSSMANN et al. 2005) or over a discrete time interval (JENSEN et al. 2007).

An objection to the ratio-dependent functional response is that the implied prey sharing cannot emerge in a purely instantaneous framework (MURDOCH et al. 2003). We agree that prey sharing can only emerge in non-instantaneous consumption intervals, but suggest that the appropriate time scale of population dynamics depicted by differential equations is determined by the scale of important system processes (JENSEN & GINZBURG 2005, JENSEN et al. 2007). The essence of the debate can be seen by comparing the 2 equations used to model a simple obligate predator-prey system:

$$dN/dt = g(N) - f(N,P)P \quad (1a)$$

$$dP/dt = ef(N,P)P - \mu P \quad (1b)$$

where N is the density of prey; P is the density of predators; $g(N)$ is the growth function of the prey; $f(N,P)$ is the functional response; e is the conversion efficiency; and μ is the death rate of the predator.

Equation (1a) represents the growth and consumption of the prey population. The appropriate time scale of population dynamics for this equation depends on the relative time scales of these processes. Equation (1b) describes the reproduction of predators in response to consumption, which has its own time scale. Because these equations are simultaneous, a single time scale must be selected for every predator-prey system, determined by the process (i.e., prey reproduction, consumption of prey by predators, or predator reproduction) that occurs on the longest time scale. If we want to know whether predators interfere with each other, we need to know how the time scales of predator consumption of prey, prey reproduction, and predator reproduction compare. Simply assuming that all processes can be adequately represented by an instantaneous dt is erroneous.

One way of understanding how differing time scales determine the functional response form is to consider a simple spatial depiction of predator consumption. For the purpose of simplicity we assume that: (1) prey are uniform in density over a 2-dimensional habitat; (2) predators behaviorally minimize overlap between their search areas and the search areas of other predators; (3) predators with overlap in their home ranges show a reduction in consumption rate due to “sharing” available prey with their neighbors (indirect rather than direct interference). We assume that for longer periods of time predators search larger areas (“home ranges”) and orient themselves to minimize sharing of potential prey within these areas (Fig. 1). When the appropriate time scale of population dynamics is nearly instantaneous, predator home ranges are near zero. Predators cannot interfere with each other, regardless of whether predator densities are low (Fig. 1A), medium (Fig. 1B), or high (Fig. 1C). The predator isocline that best represents the system is vertical for all reasonable predator densities (Fig. 2A) and the equilibrium response to enrichment follows the predictions of OKSANEN et al. (1981). At high carrying capacities the system is unstable (the intersection of the 2 isoclines occurs to the left of the hump-shaped prey isocline), displaying the paradox of enrichment described by ROSENZWEIG (1971).

When the appropriate time scale of population dynamics is discrete but relatively short, predator home ranges are small. Predators do not interfere with each other at low (Fig. 1D) and medium (Fig. 1E) densities: even with a moderate home range size, there is no overlap between home ranges. Interference emerges only at higher predator densities as home ranges begin to overlap (Fig. 1F). The predator isocline that best represents the system is vertical at low predator densities but slanted at higher predator densities (Fig. 2B). Such a system can display a

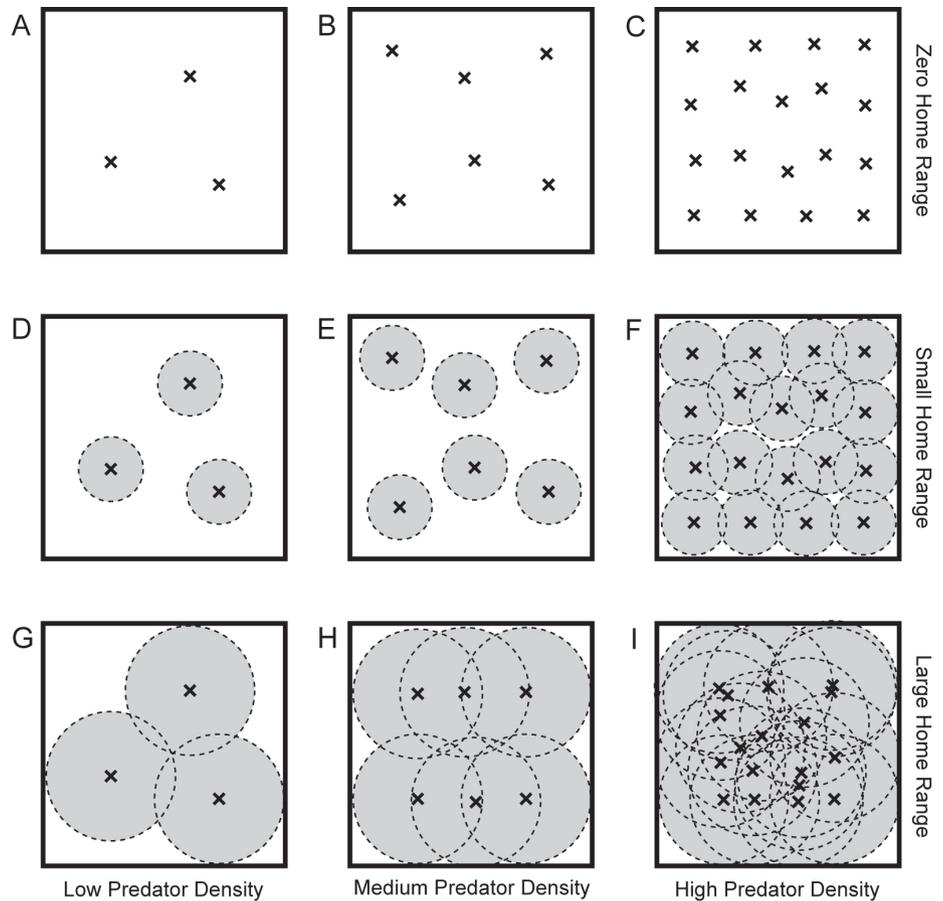


Fig. 1. Overlap of predator home ranges. When predators are considered to have infinitely small home ranges, they cannot share prey regardless of whether they are at low (A), medium (B), or high (C) density. When home ranges are relatively small, prey sharing only emerges at high predator densities (F), but is absent at lower densities (D and E). When home ranges are large, some prey sharing occurs at low densities (G), and can become complete at medium (H) and high densities (I).

mix of prey- and ratio-dependent properties: at low carrying capacities the equilibrational density of prey remains unchanged by enrichment, but at higher carrying capacities the equilibrational density responds proportionally to enrichment. The emergence of predator dependence stabilizes the system and we see no paradox of enrichment (the intersection of the 2 isoclines never occurs on the left side of the hump-shaped prey isocline; Fig. 2B).

When the appropriate time scale of population dynamics is discrete and relatively long, predator home ranges are large. Interference emerges at almost all predator densities (Fig. 1G-I), and the predator isocline that best represents the system is slanted at all but the lowest predator densities (Fig. 2C). This system displays ratio-dependent properties at all but the lowest predator densities: prey equilibrational density responds proportionally to enrichment and there is no paradox of enrichment destabilization.

The isoclines depicted by Fig. 2 are produced by a novel functional response. We call this the “indirect interference” functional response after its underlying mechanism. Regardless of whether predator dependence emerges at high (Fig. 2A) or low (Fig. 2C) predator densities, the predator isocline depicted above never intersects

with zero (in contrast to pure ratio-dependence). This means that in all systems, predators require a minimum density of prey to persist. This property corrects 2 disputable predictions of the ratio-dependent and HVH predator-dependent models, because under indirect interference: (1) when predators are too far from each other to interact, prey sharing via mutual interference cannot occur, and (2) when prey density is very low, predators starve and die before encountering another prey individual (the rate of consumption falls below the metabolic rate), and predators cannot persist. This kind of minimum prey density for predator survival was first incorporated into a ratio-dependent system by AKÇAKAYA (1992), who has offered the most parsimonious explanation of lynx-hare cycles to date (GINZBURG & JENSEN 2004). The abrupt shift from a prey- to ratio-dependent isocline (Fig. 2) relies on the assumption that predators can minimize overlap in their home ranges; if this assumption is relaxed, the abrupt shift is replaced by a gradual curve connecting prey- and ratio-dependent regions of the isocline (TRÂN 2007).

We argue that few if any predator-prey systems are truly instantaneous: for most systems, consumption occurs on a time scale that is shorter than reproduction,

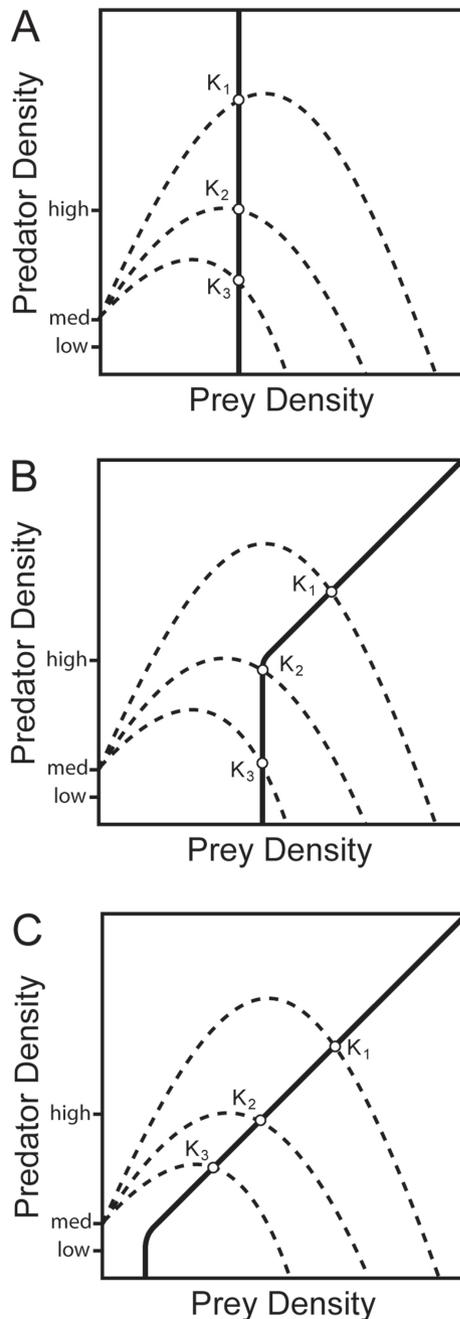


Fig. 2. Predator isoclines vary with home range size. (A) When predator home ranges are infinitely small, the predator isocline is purely vertical. With this vertical isocline, equilibrational prey densities are invariant to increases in carrying capacity (prey density at $K_3 = K_2 = K_1$). (B) When predator home ranges are small, the predator isocline slants at the population density where prey sharing emerges. Prey density is initially invariant to increases in carrying capacity ($K_3 = K_2$), but increases proportionally past the critical predator density at which prey sharing emerges ($K_2 < K_1$). (C) When predator home ranges are large, prey sharing emerges at very low predator densities, leading to an isocline which is mostly slanted. Prey density is proportional to carrying capacity for all but the smallest carrying capacities (prey density at $K_3 < K_2 < K_1$).

leading to some potential for interference. As a result the question should not be whether predator dependence emerges, but instead at what predator density it emerges. Even when the time scales of reproduction and consumption are relatively close, predators will search for prey over a discrete area during a discrete time period. What we need to know is how densely packed predators must be to share prey. The longer the appropriate time scale of population dynamics, the larger the home range searched by predators, the lower the density at which predator dependence emerges. For every predator-prey system, we need to assess the appropriate consumptive interval and determine how this time scale relates to predator home range.

To parameterize the indirect interference functional response empirically, the following biological data are needed: (1) the time scale of predator reproduction; (2) the area searched by predators in this time interval; and (3) the probability of capturing and consuming prey within this area. Such data is observable for many important predator-prey systems. Adopting the indirect interference functional response would defuse much of the controversy associated with choosing between the prey and ratio-dependent functional responses. By encompassing the reasonable characteristics of each model and eliminating those properties that produce biologically-unrealistic predictions, such an idealized model has the potential to reconcile longstanding debates. Our mechanistic understanding of prey sharing (shown in Fig. 1) is now being developed into an analytical expression (TRÂN 2007).

Acknowledgements

Christopher X Jon Jensen was supported by a National Science Foundation Graduate Research Fellowship. Initial theoretical work by J. Khải Trần allowed us to better understand the potential mechanism behind the indirect interference model. Insightful comments on earlier drafts were contributed by Gregor Fussmann, Peter Abrams, Marcel Holyoak, Jeffrey Yule, Roberta Harnett, and Saad Arif. We would especially like to thank Roger Arditi, who provided valuable feedback and agrees with major conclusions of this article.

References

- ABRAMS, P.A. & L.R. GINZBURG. 2000. The nature of predation: Prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* **15**: 337–341.
- AĞÇAKAYA, H.R. 1992. Population-cycles of mammals – evidence for a ratio-dependent predation hypothesis. *Ecol. Monogr.* **62**: 119–142.

- BISHOP, M. J., B. P. KELAHER, M. P. L. SMITH, P. H. YORK & D. J. BOOTH. 2006. Ratio-dependent response of a temperate Australian estuarine system to sustained nitrogen loading. *Oecologia* **149**: 701–708.
- BOHANNAN, B. J. M. & R. E. LENSKI. 1997. Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. *Ecology* **78**: 2303–2315.
- DEANGELIS, D. L., R. A. GOLDSTEIN & R. V. O'NEILL. 1975. Model for trophic interaction. *Ecology* **56**: 881–892.
- DIEHL, S., P. A. LUNDBERG, H. GARDFJELL, L. OKSANEN & L. PERSSON. 1993. Daphnia-phytoplankton interactions in lakes: Is there a need for pragmatic consumer-resource models? *Am. Nat.* **142**: 1052–1061.
- FUSSMANN, G. F., S. P. ELLNER, K. W. SHERTZER & N. G. HAIRSTON. 2000. Crossing the Hopf bifurcation in a live predator-prey system. *Science* **290**: 1358–1360.
- FUSSMANN, G. F., G. WEITHOFF & T. YOSHIDA. 2005. A direct, experimental test of resource versus consumer dependence. *Ecology* **86**: 2924–2930.
- GINZBURG, L. R. & C. X. J. JENSEN. 2004. Rules of thumb for judging ecological theories. *Trends Ecol. Evol.* **19**: 121–126.
- HASSELL, M. P. & G. C. VARLEY. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* **223**: 1133–1137.
- JENSEN, C. X. J. & L. R. GINZBURG. 2005. Paradoxes or theoretical failures? The jury is still out. *Ecol. Model.* **188**: 3–14.
- JENSEN, C. X. J., J. M. JESCHKE & L. R. GINZBURG. 2007. A direct, experimental test of resource vs. consumer dependence: Comment. *Ecol.* **88**: 1600–1602.
- KAUNZINGER, C. M. K. & P. J. MORIN. 1998. Productivity controls food-chain properties in microbial communities. *Nature* **395**: 495–497.
- LUCKINBILL, L. S. 1973. Coexistence in laboratory populations of paramecium aurelia and its predator *didinium nasutum*. *Ecology* **54**: 1320–1327.
- MURDOCH, W. W., C. J. BRIGGS & R. M. NISBET. 2003. Consumer-resource dynamics. Princeton University Press, Princeton, N.J.
- OKSANEN, L., S. D. FRETWELL, J. ARRUDA & P. NIEMELA. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* **118**: 240–261.
- ROSENZWEIG, M. L. 1971. Paradox of enrichment – destabilization of exploitation ecosystems in ecological time. *Science* **171**: 385–387.
- TRẦN, J. K. 2008. A predator-prey functional response incorporating indirect interference. *Verh. Internat. Verein. Limnol.* **30**: (in press)
- TYUTYUNOV, Y., L. TITOVA & R. ARDITI. 2008. Predator interference emerging from trophotaxis in predator-prey systems: And individual-based approach. *Ecolog. Complexity* **5**: 48–58.
- VEILLEUX, B. G. 1979. An analysis of the predatory interaction between *paramecium* and *didinium*. *J. Anim. Ecol.* **48**: 787–803.
- WARE, D. M. & R. E. THOMSON. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science* **308**: 1280–1284.

Author's addresses: L. R. Ginzburg, Department of Ecology and Evolution, Stony Brook University, Life Sciences 650, Stony Brook, NY 11794-5245. E-mail: lev@ramas.com

Christopher X. J. Jensen, Department of Ecology and Evolution, Stony Brook University, Life Sciences 650, Stony Brook, NY 11794-5245 and Department of Math and Science, Pratt Institute, ARC Building G-49, 200 Willoughby Avenue, Brooklyn, NY 11205