

A DIRECT, EXPERIMENTAL TEST OF RESOURCE VS. CONSUMER DEPENDENCE: COMMENT

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Consumer–resource system dynamics hinge upon the rate at which consumers capture, consume, and convert resources into biomass. In classical functional and numerical response theory, this rate is assumed to depend on resource density but not on consumer density (reviewed in Jeschke et al. [2002]). In assuming that both densities determine this rate, consumer-dependent functional responses (e.g., Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989) challenge the resource-dependent tradition. This challenge has produced a long-standing debate (reviewed in Abrams and Ginzburg 2000). The traditional approach of fitting functional response models to time series data has yielded equivocal results (e.g., Jost and Arditi 2001) and may not be capable of resolving the debate (Lundberg and Fryxell 1995). In a recent issue of *Ecology*, Fussmann et al. (2005) tried to enrich the debate with empirical data. They described functional response experiments in the rotifer–algae system *Brachionus calyciflorus*–*Monoraphidium minutum* that detected consumer dependence only at unnaturally high *Brachionus* densities and concluded that consumer dependence plays only a minor role for planktonic rotifers in natural environments. Here, we outline why this conclusion is an over-interpretation of their results. Their experimental approach only considers direct physical interference between *Brachionus* and excludes all other and more important forms of consumer-dependent effects (e.g., chemically mediated interfer-

ence, induced responses in the algal resource, resource depletion). Fussmann et al.'s results cannot therefore be considered as evidence against consumer dependence.

In contrast with the traditional resource-dependent form, the inclusion of a consumer-dependent functional response changes both the equilibria (Ginzburg and Akçakaya 1992, Akçakaya et al. 1995) and stability (Berezovskaya et al. 2001) of a trophic system. We agree that consumer density determines how important interference will be in a consumer–resource system (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000). At very low consumer density, the functional response will be resource-dependent. At very high consumer density, the functional response will be consumer dependent. In seeking to determine the threshold consumer abundance at which a trophic system switches from resource to consumer dependence, Fussmann et al. have correctly framed one unanswered question of consumer–resource dynamics.

However, the only form of consumer dependence detectable by their approach is direct physical interference between consumers. All other forms of interference (e.g., chemically mediated interference, induced responses in the algal resource, resource depletion) were excluded. The results of Fussmann et al. show that physical interference is not significantly influencing *Brachionus* consumption rate at naturally occurring *Brachionus* densities, but they provide no evidence for or against other more important consumer-dependent effects. Therefore, the results cannot be considered as evidence against consumer-dependent consumption.

The philosophy underlying Fussmann et al.'s experiment provides an illustrative example of a theoretical error we call instantism (Ginzburg and Colyvan 2004, Jensen and Ginzburg 2005). Whenever theorists use differential equations they make assumptions about what comprises an “instant,” as the dt in such equations represents this “instant.” Our main concern is that the “instant” be consistent with the time scale of consumer reproduction, which drives the dynamics of any consumer–resource system. In contrast, instantism assumes that because in theory differential equations describe instantaneous rates, we should consider the dt in ecological models to literally represent infinitely small intervals. This modeling perspective has strong advocates (e.g., Murdoch et al. 2003) but has been questioned for decades (e.g., Arditi and Ginzburg 1989, Jensen and Ginzburg 2005). Fussmann et al. clearly advocate the instantist view when they criticize previous studies for taking a “non-instantaneous approach to the problem”; we prefer these so-called non-instantaneous approaches, as they address the more biologically relevant time scale of consumer reproduction.

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A key issue addressed by Fussmann et al. is the phenomenon of resource depletion: when consumption intervals increase, resource abundance decreases over the period during which consumption is measured. Fussmann et al. treat resource depletion as a source of error in measuring the functional response; to minimize this error the experimenters have monitored consumption over an extremely short time interval. The scale of this interval is clearly designed to observe behavioral phenomena, ignoring the fact that the reproductive time scale (i.e., the dt in the consumer equation) involves a much longer interval (Arditi and Ginzburg 1989). Given that the generation time of *B. calyciflorus* is approximately five days (Fontaine and Gonzalez 2005), the four-minute consumption interval Fussmann et al. used is three orders of magnitude smaller than the focal consumer's reproductive interval. This massive discrepancy between the measured (behavioral) time scale and a biologically and dynamically relevant (reproductive) time scale leads us to question whether these results provide any evidence for using the resource-dependent functional response in dynamic models of this or any other system.

Consumer–resource models should accurately capture the consequences of consumption: whether or not the systems are stable, and the densities at which stable systems equilibrate. These consequences result from both the functional response and the numerical response. Even organisms like *Escherichia coli*, which seemingly reproduce continually, do not respond numerically to changes in resource abundance instantaneously (i.e., on the time scale of cell division). A delay always exists between changes in consumption and the resulting effects on reproduction, and this delay introduces the potential for resource-depletion effects. Consumer-dependent functional responses may account for these delays and bridge the gap between the time scales of consumption (i.e., functional response) and reproduction (i.e., numerical response).

Resource depletion should not be treated as an error but as a biologically important phenomenon. The experiments of Salt (1974) provide an illustrative example. Salt measured the consumption rate of *Didinium* on *Paramecium* at hourly intervals. While this time scale is still about one order of magnitude smaller than the reproductive time scale of *Didinium* (Veilleux 1979), it allowed Salt to observe clear consumer dependence in his functional responses. Even when every consumptive and reproductive act can be monitored, as is the case with wolf and moose on Isle Royale (e.g., Vucetich et al. 2002), the time interval over which consumption is integrated influences the degree of consumer dependence observed (Ginzburg and Colyvan 2004, Jost et al. 2005). Because the functional response can vary in response to the chosen consumption interval, the debate over which functional response form to use

really centers on identifying the appropriate consumption interval. This unanswered question is not a question for Fussmann et al.: they assume that the smallest consumption interval is the only biologically relevant interval. All we can learn from the experiment of Fussmann et al. is that physical interference is not important at natural densities in this system: their experiment does not address the dynamic consequences of functional response, so we cannot conclude that the consumptive interval employed is correct for even this system.

Accordingly, we reject the contentions of Fussmann et al. that their experiment represents “treatment of the most general case” and warn ecologists against their suggestion that “[resource] dependence...should be the norm in dynamical mathematical models.” If we want to use the results of short-term experiments like that of Fussmann et al. to parameterize our model, we need to make the model consistent with the varying time scales of consumption and reproduction. Such an “instantaneously realistic” model would have to take into account the discrete nature of reproduction (we suggest an integro-differential equation), spatial heterogeneity, and a host of other potential mechanisms that, over biologically reasonable time periods, appear to produce a degree of consumer dependence. Such a model would be overly complex, heavily over-fitted, and impossible to parameterize with any confidence (Ginzburg and Jensen 2004). Instead of taking the instantist stance and using the resource-dependent functional response as the building block of a complex, analytically intractable model, we suggest that ecologists consider using the appropriate consumer-dependent functional response (e.g., Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989). In doing so, we are suggesting that ecological modeling should broaden its understanding of mechanism beyond the behavioral time scale.

Fussmann et al. assert that “it is obviously true that consumption will be exclusively resource dependent if consumer density is extremely low because interference cannot occur.” We suggest that it is almost equally obvious that consumption will be resource dependent if the measured consumptive interval is very small (only direct physical interference, which is usually relatively unimportant, produces detectable consumer dependence). Over appropriate time intervals—those closer to the consumer's generation time—natural densities of consumers will produce consumer-dependent effects. We already have strong experimental evidence (as reviewed in Fussmann et al. 2005) that over longer consumptive intervals, consumer dependence emerges. An important unanswered question remains: “What is the appropriate time interval over which to measure the functional response?” If we want to use functional responses to better understand or even predict population dynamics,

we should also measure functional responses on the time scale of population dynamics. Most of the 814 responses recently reviewed by Jeschke et al. (2004) were not measured on this time scale, and those that were did not discriminate between resource and consumer dependence. A few experiments have contrasted the predictions of resource and consumer-dependent functional responses in terms of predicted equilibria (Bohannon and Lenski 1997, Kaunzinger and Morin 1998) and stability (Fussmann et al. 2000), but these experiments did not measure the functional response, even over a single time interval. In order to provide better advice to ecologists who want to build models of trophic interaction, we need experiments that simultaneously compare the functional response measured at a variety of time intervals with the equilibrium and stability properties of a dynamic system. For instance, the experimental system of Fussmann et al. could be used to explore the effect of system enrichment on equilibrium resource abundance (Oksanen et al. 1981, Ginzburg and Akçakaya 1992); contrasting this result with direct measures of functional response over varying consumptive intervals would provide a more valuable insight into what form functional response should take. Results of this kind are more likely to suggest a biologically relevant functional response.

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