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

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In a recent study (Fussmann et al. 2005), we used an experimental rotifer–algal system to show that the functional response of the consumer depends on the resource but not on the consumer concentration. We concluded that resource dependence should be the norm in dynamical mathematical models. Jensen et al. (2007) published a Comment on our paper in which they criticized us for overinterpreting our experimental results. We reject this point of view. This controversy must be viewed in the historical context of a long-standing debate between supporters of consumer- and supporters of resource-dependence. In the 1990s, *Ecology* was a forum for this debate (e.g., Abrams 1994, Akcakaya et al. 1995), which appeared to have come to its conclusion with a synthesis paper in *TREE* (Abrams and Ginzburg 2000). Here we reply to the Comment by addressing the most important points of criticism.

"Instantism" and the appropriate time scale of observation

We are content to be labeled as "instantists." It stands for how we think processes should be measured if they are used in a differential equation framework. We do not believe that our conclusions are flawed because we attempted to measure the functional response at short time intervals. In our four-minute trials, each consumer ate on average 175 algal resource cells. Thus, the time interval we chose was sufficiently long to catch the process of taking up resources. Longer trial times could have impaired the quality of the data due to resource depletion, consumer reproduction, and excretion of algae. Jensen et al. (2007) argue that the time interval should be consistent with the time scale of consumer reproduction and, therefore, explicitly allow for resource depletion. We counter that experimental trials in which the resource is depleted and not replaced have only one possible, unsurprising, and artificial result: they must corroborate consumer dependence by design. This is intuitively clear because more consumers will faster reduce the resource concentration in the experimental unit; therefore, the consumers' per capita integral of intake over the experimental duration has to decrease with increasing consumer concentration (Fig. 1). It is true, however, that in consumer–resource systems functional and numerical response do not necessarily operate on the same time scales. We share P. Abrams's view (Abrams and Ginzburg 2000) that this situation "calls for the use of methods that represent the functional response on a continuous basis and reproduction on a discrete basis." The proponents of consumer dependence believe that the functional response term in a differential model should integrate over the longer time scales that are relevant for the consumer's reproduction. The theoretical and logic inconsistencies of this approach, which attempts to incorporate the time scale of the numerical response into the functional response term, have already been explained by Abrams (1994).

Physical interference vs. other mechanisms

Our study focused on direct, physical interference as a potential mechanism generating consumer dependence. In classical consumer–resource models, consumers and resources encounter each other randomly and, with increasing consumer density, the probability that consumers encounter other consumers instead of resource particles increases. This is the most basic potential mechanism how consumer dependence might arise. We found no evidence of physical interference being important in our study with more or less randomly moving plankton organisms. Hence, we have no reason to propose consumer-dependence as the norm in dynamical models. This is not to say that physical interference or other mechanisms are never important in natural systems. In the case of wolves preying on moose (Vucetich et al. 2002), for instance, one moose may be sufficient for several wolves to feed on but the predators are forced to meet where the prey is, and, thus, will interact with each other. The induction of prey defenses by consumers is another obvious example of a type of interaction that generates consumer dependence. Jensen et al.'s (2007) assertion, however, that such non-physical interferences are a priori "more important," is unsupported and, in our opinion, these and other examples do not suggest that consumer density should be generally a part of the functional response. If there is reason to believe that consumer dependence will occur, we find it preferable to reformulate the functional response in a way that allows for the specificity of the mechanism (e.g., Vos et al. 2004).

How to resolve the controversy?

At its core, the controversy is about dynamics of consumer–resource communities, in which the function-

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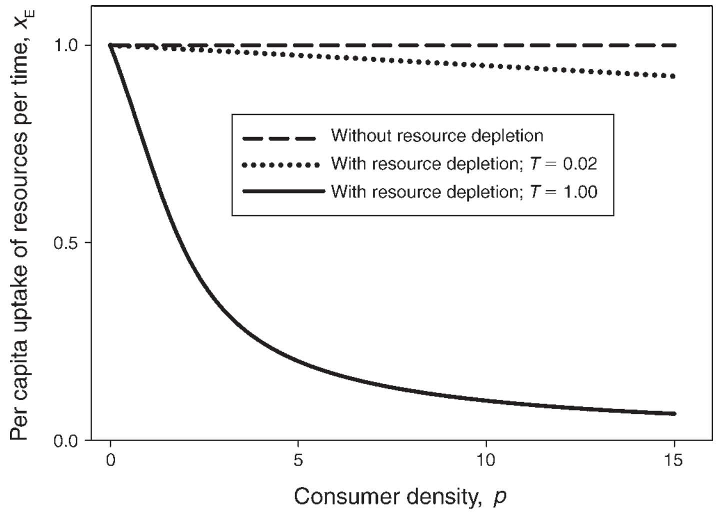

FIG. 1. Resource uptake (x_E, number of resources eaten) per consumer individual and per time as a function of consumer density in a hypothetical experiment. We modeled consumption based on the Holling type 2 functional response, allowing for the fact that resource concentration changes during the experiment if resources are not replaced. Without resource depletion (i.e., with replacement of resource items), uptake is constant and independent of p and T [$x_E = ax_0/(1 + bx_0)$] where x_0 is the constant resource concentration and a and b are parameters of the Holling type 2 response). If resource depletion is allowed to occur during the experiment, uptake decreases with consumer density (p) although consumption is not consumer dependent. Shorter experimental duration ($T = 0.02$) can reduce this effect, which potentially confounds the results of experiments aimed at detecting consumer dependence. For the case of resource depletion the Holling type 2 response needed to be integrated over time. For our computations, we used the explicit solution (obtained with MATLAB version R2006a; The Mathworks, Natick, Massachusetts, USA): $x_E = (bx_0 - W[bx_0 \exp(bx_0 - apT)])/(bpT)$, where x_0 is the initial resource concentration, T is the duration of the experiment, and W is the Lambert W function (Corless et al. 1996). Parameterization: $x_0 = b = 1$; $a = 2$; units are arbitrary.

al and numerical responses tend to be tightly linked, although they operate on different time scales. Which time scale in the system should take priority when describing the system as a mathematical model? The slower, reproductive time scale or the faster time scale, governed by resource uptake? And, after settling for either scale, what is the most realistic compromise to describe the process that operates off-scale? We believe that neither we nor Jensen and colleagues have the definitive answer to this question. Therefore, we agree with our critics that future experiments should be designed to test in a community context for the strongly different dynamical properties that resource- and consumer-dependent models predict.

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