

Behavioral interference and facilitation in the foraging cycle shape the functional response

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Individual forager behaviors should affect per capita intake rates and thereby population and consumer-resource properties. We consider and incorporate conspecific facilitation and interference during the separate foraging-cycle stages in a functional response model that links individual behavioral interactions with consumer-resource processes. Our analyses suggest that failing to properly consider and include all effects of behavioral interactions on foraging-cycle stage performances may either over- or underestimate effects of interactions on the shape of both functional responses and predator zero-growth isoclines. Incorporation of prey- and predator-dependent interactions among foragers in the model produces predator isoclines with potentials for highly complex consumer-resource dynamics. Facilitation and interference during the foraging cycle are therefore suggested as potent behavioral mechanisms to cause patterns of community dynamics. We emphasize that correct estimations of interaction-mediated foraging-cycle efficiencies should be considered in empirical and theoretical attempts to further our understanding of the mechanistic link between social behaviors and higher order processes. *Key words:* behavior, model, predation, social foraging. [*Behav Ecol* 18:354–357 (2007)]

Behavioral interactions among forager individuals may affect per capita food intake and thereby individual performance, population properties, and consumer-resource interactions (e.g., Fryxell and Lundberg 1998; Giraldeau and Caraco 2000; Krause and Ruxton 2002). To understand and correctly assess the important effects of individual behaviors on higher order processes, there is great need to incorporate the behavioral mechanisms in models that bridge the order scales from individuals to communities. The functional response maps resource availability to consumer population performance as it specifies the per capita intake rate of resources by the consumers in relation to resource abundance, and its exact nature can have far-reaching consequences for consumer-resource dynamics (Holling 1959; Fryxell and Lundberg 1998; Abrams and Ginzburg 2000). Several factors are responsible for the shape of this relationship, for example, the spatial distribution of resources, defensive or evasive behaviors of the prey, and forager social interactions. The latter issue has received quite some attention in the literature, and it has been shown that foraging in groups, where interference and/or facilitation may occur among conspecifics, could have substantial effects on individual foraging success. For example, intraspecific interference in foraging behavior has been documented in producer-scrounger and dominance-hierarchy systems (e.g., Barnard 1984; Goss-Custard 1996), and restricting effects on the functional response with stabilizing consumer-resource properties have been suggested (e.g., Hassell and Varley 1969; Beddington 1975; DeAngelis et al. 1975). Less is however known about the specific effects of intraspecific facilitation on per capita functional responses, even though the costs and benefits of foraging in groups have been thoroughly explored (Giraldeau and Caraco 2000).

To further our understanding of how interference and facilitation affect individuals, populations, and communities, we should pursue and consider the mechanistic origin of how

behavioral interactions among foragers affect per capita functional responses. To consume food, foragers have to successfully complete each stage of the foraging cycle (e.g., Holling 1965; Webb 1986), for instance: search for, encounter, attack, capture, and ingest prey. Intraspecific interactions, negative or positive, would act on these behavioral components. For instance, agonistic behaviors may decrease conspecifics' search intensity or efficiency, if interactions interrupt search or if avoidance of interactions requires passivity (e.g., Jenkins 1969; Nilsson et al. 2006). Cooperation may increase capture success among foragers (Giraldeau and Caraco 2000; Krause and Ruxton 2002), but group foragers could, however, also simply get in each other's way at large group sizes (Ruxton 1995) and thereby show, for example, positive interactions during prey search but negative during prey capture. Further, behavioral interactions that take place among group foragers may not directly affect consumption rates, as has been shown to occur among juvenile salmonids (Nilsson et al. 2004), whereas in other cases conspecific presence may decrease foraging even in the absence of observable behavioral interactions, as can be the case for blackbirds, northern pike, and redshank (Cresswell 1997; Stillman et al. 2000; Nilsson et al. 2006).

Behavioral observations of interacting foragers may lead to erroneous predictions of functional responses if, for instance, only one conspicuous behavioral interaction is quantified, but more subtle interaction behaviors remain unexplored. Quantifications of complete prey- and/or predator-dependent functional responses without study of behavioral interactions, on the other hand, would show the net effect of the separate foraging-cycle stage interactions, that is, the effect of prey and predator numbers on final prey consumption. However, to understand the mechanisms behind this net effect, we need to analyze interactions during the foraging-cycle stages. It is therefore crucial to correctly assess and include the effects of intraspecific behavioral interactions during the foraging cycle into functional response models to fully appreciate their influence on consumer-resource interactions. We present here an approach to link behavioral interactions with consumer-resource processes by presenting a framework for analysis of how interference and facilitation at different stages of the foraging cycle affect the functional response.

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Table 1
Description of 5 subjectively composed but reasonable scenarios illustrating the importance and effects of incorporating intraspecific interactions acting on foraging-cycle stages in functional responses

Foraging-cycle stage	Number	Scenario 1		Scenario 2		Scenario 3		Scenario 4		Scenario 5	
		Effect direction	<i>m</i>	Effect direction	<i>m</i>	Effect direction	<i>m</i>	Effect direction	<i>m</i>	Effect direction	<i>m</i>
Search	1	+	-0.15	0	0	-	0.15	0	0	0	0
Encounter	2	+	-0.35	-	0.3	0	0	0	0	0	0
Attack	3	+	-0.3	0	0	+	-0.7	0	0	-	0.25
Capture	4	-	0.2	+	-0.05	0	0	0	0	+	-1/ <i>P</i>
Ingestion	5	-	0.6	0	0	-	0.05	-	1/ <i>N</i>	0	0
Net effect		0	0	-	0.25	+	-0.5	-	<i>f(N)</i>	±	<i>f(P)</i>

The effects are expressed by the sign and value of the interaction parameter or function *m* in Equation 1 (see text). An important assumption for the use of this model is that *P* and *N* should be treated as numbers of individuals in the populations or densities should be scaled to never be less than one.

THE FUNCTIONAL RESPONSE

By studying how individual performance during the separate stages of the foraging-cycle is affected by the number of interacting conspecifics, it is possible to obtain the predator-dependent effects on functional responses. The complete foraging cycle is composed of separate stages (1, 2, 3 ... *k*; Table 1), and we consider the effects of interactions on each foraging-cycle stage separately and then incorporate them in a functional response model. Individual intake rates (*I*) should depend on individual ability to complete the foraging cycle when foraging alone (*A*), numbers of available prey (*N*) and interacting predators (*P*), the interaction effect (*m*) acting on each foraging-cycle stage, as well as a handling mediated restriction to food consumption (*h*),

$$I = \frac{AN \prod_{i=1}^k P^{-m_i}}{1 + AhN}, \quad i = 1, 2, 3 \dots k. \quad (1)$$

The literature holds a plethora of functional response models that consider predator interactions (e.g., Hassell and Varley 1969; Beddington 1975; Sutherland 1983; Skalski and Gilliam 2001; Jeschke et al. 2002). We here choose to use the above extension of the Hassell-Varley model as it can handle both constant and prey- or predator-dependent as well as both positive and negative values of interaction effects (*m*), as should be the case to enable description of as many types of interactions as possible, and as its basic form has proved useful for evaluating the relative importance and effects of forager interactions (Nilsson et al. 2004; Nilsson and Ruxton 2004). In the present study, the functional response model is developed to enable inclusion of mechanistic effects of interactions during the separate foraging-cycle stages. In Table 1, we summarize 5 unambiguous scenarios of different social interactions among foragers that illustrate the effects of positive, negative, or no interactions during different stages of the foraging cycle. As this work to our knowledge is the first to address the importance of incorporation of interaction-mediated foraging-cycle efficiencies in functional response models, detailed empirical studies of complete foraging cycles are largely lacking. The studies that contain information on intraspecific interactions for parts of the foraging cycle have inspired and qualitatively support our assumptions (e.g., Barnard 1984; Goss-Custard 1996; Giraldeau and Caraco 2000; Krause and Ruxton 2002; Nilsson et al. 2006, and references therein). Further, recalculation of the data from Nilsson et al. (2006) gives the stage-specific *m* values -0.88 and 1.94 for Eurasian perch capture efficiency and northern pike attack frequencies,

respectively, indicating that the parameter values used are within the range found in natural systems.

Incomplete knowledge of the effects of interactions on foraging-cycle success could over- or underestimate the functional response. With scenarios 1–3, we illustrate the importance of correctly including all foraging-cycle stages in analyses of the functional response. Scenario 1 includes both positive and negative interactions (Table 1, Figure 1a). The positive and negative effects on foraging-cycle efficiencies, however, compensate each other, resulting in no net effect on the functional response (Figure 1b,c). Failure to correctly include one or more interaction effects, hence, incurs erroneous predictions of the functional response (Figure 1b). Scenario 2, where foraging among conspecifics reduces prey encounters but increases capture efficiency, and scenario 3, where search and ingestion of prey are impaired but attack frequencies improve in the presence of conspecific foragers, also contain both positive and negative interactions. The net effect on the functional responses is negative in scenario 2 and positive in scenario 3 ($\sum m_i = 0.25$ and $\sum m_i = -0.5$, respectively, Table 1, Figure 1c). Therefore, incorrect estimations of effects on encounters and attacks for scenario 2 and 3, respectively, could produce predictions in the wrong directions. Comprehension of how social interactions affect individual foraging-cycle efficiency thus determines our mechanistic understanding of the shape of functional responses. Below, we continue with an evaluation of potential effects of foraging-cycle interactions on consumer-resource dynamics.

CONSUMER-RESOURCE DYNAMICS

The different types of interactions during the foraging cycle would affect per capita and thereby overall consumer functional responses, with consequences for consumer-resource dynamics. To illustrate the potential effects of foraging-cycle interactions on higher order processes, we use a classic Rosenzweig–MacArthur (1963) model of consumer-resource interactions

$$\begin{aligned} \frac{dN}{dt} &= rN \left(1 - \frac{N}{K} \right) - PI, \\ \frac{dP}{dt} &= P(cI - d), \end{aligned} \quad (2)$$

where *N* and *P* are numbers of individuals in the prey and predator populations, *r* is prey maximum per capita population growth rate, *K* is the equilibrium number of individuals in

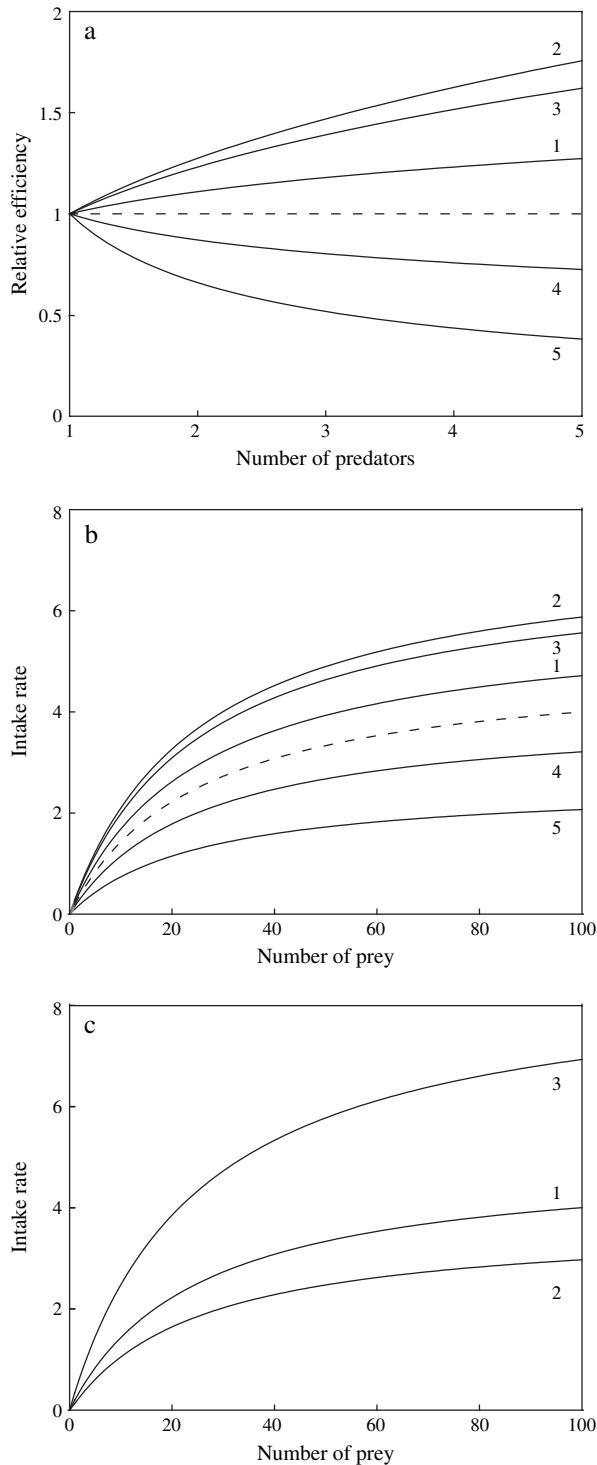


Figure 1 Effects of predator interactions, acting on foraging-cycle stages, on individual foraging efficiency, and resulting functional responses. (a) Individual efficiency at completing each stage of the foraging cycle (1–5; Table 1) relative to when foraging alone (dashed) may be predator dependent. (b) The separate efficiencies in (a) predict different functional responses, none of which correspond with the resulting, net functional response (dashed), which in this specific case shows no predator-dependent properties. (c) The functional responses of forager types with 1) no net effects of predator interactions, 2) an interference effect, and 3) a facilitating effect. The foraging-cycle stages in (a) and (b) correspond to scenario 1 and functional responses in (c) to their respective scenarios in Table 1. $A = h = 0.2$ and $P = 3$ in (b) and (c).

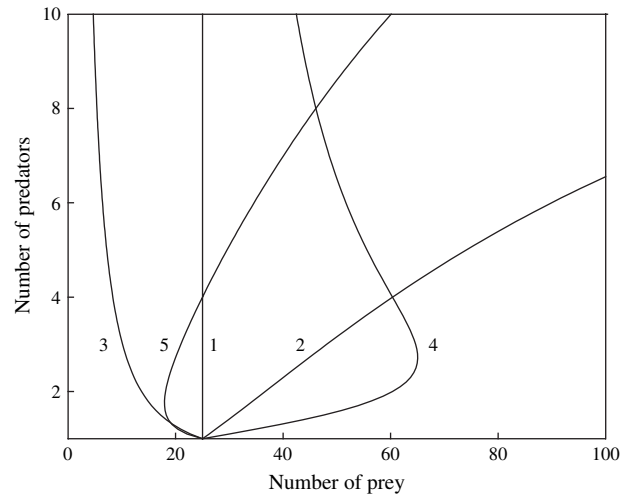


Figure 2 Predator zero-growth isoclines for noninteracting, interfering, or facilitating predators. The vertical and linear isocline (1) characterizes noninteracting predators. Isoclines to the right of (1) should stabilize and those to the left destabilize predator-prey dynamics. The isoclines 1–5 are derived from Equations 1, 2, and 3 (see text) with interaction properties according to their corresponding scenario number in Table 1 and $A = h = c = 0.2$, $d = 0.5$.

the prey population, c is predator conversion coefficient, d predator mortality rate, and I the per capita functional response in Equation 1. Solving for the equilibrium number of prey (N^*) as a function of number of individuals in the predator population gives the predator zero-growth isocline

$$N^* = \frac{d}{A(c \prod_{i=1}^k P^{-m_i} - dh)}, \quad i = 1, 2, 3 \dots k. \quad (3)$$

This general solution for N^* includes m_i that can depend on predator and prey numbers (Table 1). Figure 2 thus presents numerically derived illustrations of predator zero-growth isoclines. Scenario 1, that contains both negative and positive interactions, produces a vertical isocline, indicative of a system without net interference or facilitation (Figure 2). Scenario 2, that has a negative net effect on individual foraging-cycle completion, produces a predator isocline that increasingly diverges to the right of the vertical isocline. The facilitating net effect in scenario 3 results in an isocline that deceleratingly diverges to the left of the no-interaction, vertical isocline. Generally, predator isoclines with a positive slope would have a stabilizing effect, isoclines with a negative slope a destabilizing effect, and isoclines in between may create stable limit cycles. We suggest that this reflects the effects of scenarios 2, 3, and 1, respectively.

Scenarios 1 through 3 include only constant m_i 's. This is suitable for illustrating the above-mentioned examples and effects and should apply to situations where, for instance, foragers interact through intimidation interference, as can be the case for northern pike and juvenile salmonids (Griffiths and Armstrong 2002; Nilsson et al. 2006). It is however possible that the propensity for interaction itself depends on predator and/or prey numbers under natural conditions. For instance, interference propensity may decrease with increasing prey availability (Moody and Ruxton 1996). Such a situation is illustrated in scenario 4, where ingestion is affected by interactions, to demonstrate the potential effects of prey-dependent kleptoparasitism among foragers, as shown in

oystercatchers (Triplet et al. 1999). The resulting predator isocline first rapidly diverges to the right of the vertical, suggesting a stabilizing effect on consumer-resource dynamics, but then converges with the vertical isocline for higher prey equilibrium numbers of individuals, where the stabilizing effects would decrease. Further, scenario 5 illustrates the potential effects of social foragers that facilitate each others' capture success in groups but where foragers indirectly interfere by attacking the same prey when the number of predator individuals increases (e.g., Giraldeau and Caraco 2000). As the isocline from scenario 5 first diverges to the left and then to the right of the vertical, we assume both destabilizing and stabilizing effects of predator interactions, depending on the prey zero-growth isocline. We should, hence, presume quite complex and even unexpected effects on consumer-resource dynamics from predators interacting as in scenarios 4 and 5, and these effects could be greatly underestimated without thorough understanding of the impacts of interactions on the different foraging-cycle stages. We thus emphasize the importance of considering and evaluating all foraging-cycle stages in future pursuits of the understanding of effects of social forager interactions on functional responses.

IMPLICATIONS FOR HIGHER ORDER PROCESSES

We emphasize that social behaviors affect the functional response and that interfering or facilitating foragers can promote stability or instability, respectively, and thus that the social behavior of foragers may have strong effects on consumer-resource dynamics. The stability properties of the consumer-resource system may influence species coexistence and community composition (Rosenzweig 1971; Huisman and Weissing 1999) and therefore potentially also ecosystem function (McCann et al. 1998; Berlow 1999). Under some circumstances, consumer-resource interactions could, in combination with external perturbations, even incite systems to stay in either of or shift between alternative stable states (e.g., Scheffer and Carpenter 2003). We underline that small-scale behavioral interactions among foragers should be involved in such higher order processes and suggest that in order to fully understand and predict these ecological phenomena, the role of behavioral interactions during the different stages of the foraging cycle should be considered. This work introduces a framework for such an approach.

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