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Optimal Feeding via Constrained Processes

SHANDELLE M. HENSON† AND THOMAS G. HALLAM‡

†*Department of Mathematics, University of Arizona, Tucson, AZ* 85721 *and*
‡*Department of Mathematics and Graduate Program in Ecology, University of Tennessee, Knoxville, TN* 37996-1300, *U.S.A.*

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An organism's optimal feeding rate is governed by constraints imposed by processes associated with consumption. In this paper a generic representation of feeding rates is derived based upon process constraints, and mechanistic representations of the module processes are illustrated for a filter feeder, *Daphnia magna*, and a pursuit feeder, rainbow trout (*Oncorhynchus mykiss*). The generic feeding rate models are presented in a spectrum of forms as dictated by process constraints and are convenient for application to a wide range of macroheterotrophic organisms.

Introduction

Numerous functional responses have been developed and explored for resource–consumer and predator–prey interactions (e.g. Holling, 1959, 1965, 1966; Sabelis, 1986; Kooijman, 1993). A mechanistic approach to unify physiological, environmental, and behavioral determinants of feeding is useful for both the representation of organismal growth and the integration of individual information into population ecology. We develop a deterministic methodology for representing individual feeding rates based upon the premise that all organisms feed optimally subject to environmental and biological constraints. A principle goal of this paper is to indicate how generic representation of feeding by macroheterotrophs can be developed as a function of mechanistically represented tasks associated with feeding.

A model of individual organism growth, written in continuous form, is

$$\frac{\mathrm{d}m}{\mathrm{d}t} = G(t) - L(t), \qquad (1)$$

where $m = m(t)$ is the mass of the consumer organism at time t, $G(t)$ is the biomass created by consumption per unit time and $L(t)$ is the mass lost per unit time. The term $L(t)$ represents loss rates of mass due to sinks such as maintenance, activity and reproduction. The resource conversion term $G(t)$ in the individual model (1), measured in units of mass per time, is determined by the feeding rate and assimilation efficiencies of the organism. If A is the assimilation efficiency for the resource, F is the feeding rate in units of number of prey items per time and M_p is the mass of each prey item, then the resource conversion to biomass can be modelled continuously as $G = AFM_p$. Processes such as search, pursuit, capture, handling, digestion and gut clearance of prey constrain feeding and allow a modular partitioning of F into tasks required for feeding. An objective of this paper is the delineation of how this feeding rate is constrained by processes associated with feeding.

Feeding Rate Models

As demonstrated below, theoretically there are a multitude of feasible feeding representations; the appropriate model is determined by the constraints on the consumption processes applicable to the specific individual organism. As illustrations, we first describe two types of models, designated here as sequential process feeding and parallel process feeding, that are circumscribing formulations for feeding rate represen-

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tations. We assume the resource exists in discrete particles of mass M_p which are ingested one at a time by the consumer. Sequential process feeding describes a resource particle flow where a set of tasks associated with feeding such as encounter, pursuit, attack, capture, handling and gut clearance, must be completed sequentially for a given resource particle before an additional resource item may begin to be processed. Parallel process feeding represents a bulk resource flow in that all feeding tasks may be executed simultaneously; for example, a predator might search for a new prey item while continuing to digest the last. We show that numerous other feeding models can be constructed utilizing combinations of these types of feeding where some, but not all, of the feeding tasks may be completed simultaneously.

Assume the consumption process is governed by resource flow through a feeding system structured as n delineated tasks associated with feeding. Let a resource be processed through a sequence of tasks $\{i\}$ at a maximal rate of R_i items per unit time, $i = 1, 2, \ldots, n$. R_i can be a function of the age and mass of the feeding organism, time, and parameters and variables associated with physiology, resource, and the environment. The feeding rate is governed by a host of factors, including the number of processes necessary for feeding, the constraints associated with the processes such as the maximal flux rates R_i, and parallel process activity.

Sequential Process Feeding

Sequential process feeding requires that items of resource are only allowed to pass through the feeding system one at a time; that is, a given resource particle must be processed by the final feeding task before the next resource item can begin initial processing through the feeding system. From a consumer's perspective, this model, designated here as Ilk 1, corresponds to a consumer executing all feeding tasks sequentially before turning attention to another resource particle.

In the Ilk 1 model, the time budget for the feeding process (Holling, 1959) gives the time required for a resource particle to pass through the system:

$$\sum_{i=1}^{n} T_i,$$

where T_i is the time required for task i to be completed for the resource item. The optimal rate at which a resource particle is completely processed is

$$F = \frac{1}{\sum_{i=1}^{n} T_i} = \frac{1}{\sum_{i=1}^{n} R_i^{-1}} \tag{2}$$

resource items per unit time. F is optimal in the sense that the T_i are calculated from the maximal task rates R_i.

If processes are not implemented sequentially, formulation (2) cannot be used; however, the process rates may still be used to determine F. Before proceeding to this more general setting, we describe an alternate derivation of (2).

ALTERNATE DERIVATION OF THE ILK 1 MODEL

The Ilk 1 feeding model can be derived from the assumption that an organism feeds in proportion to its hunger, an assumption utilized in related projects by Rashevsky (1959) and Lassiter (1986).

The execution of a task is called *effective* if it ultimately leads to completion of the feeding process; for example, effective encounters are those that lead to successful completion of all tasks which must be performed for feeding. Let E_i be the "optimal" rate of effective executions of task i; this is also the number of items of prey that can be consumed per unit time given the constraints imposed by the maximal rates R_j for the tasks $j = i, i+1, \ldots, n$. Note that $E_i \leqslant R_i$ for all i, $E_1 \leqslant E_2 \leqslant \cdots \leqslant E_n$, and

$$E_n = R_n. \tag{3}$$

To find an expression for $F = E_1$, the feeding rate of the organism as constrained by all tasks, we first find an expression for E_{n-1}, the feeding rate if feeding were constrained only by the last two tasks n and $n-1$, given that we already know E_n. Let P_{n-1} denote the conditional probability that the feeding organism will choose to complete task n given an additional completion of task $n-1$. We assume P_{n-1} has the form: $P_{n-1} = c(E_n - E_{n-1})$. $E_n - E_{n-1}$ measures the attainable consumption per day constrained only by task n less the "actual" daily consumption which is constrained by both tasks n and $n-1$. This measure of "relative hunger" indicates the daily equivalent of that portion of the gut which could be used under the constraint of task n, but isn't. If $E_n = E_{n-1}$, then an additional completion of task $n-1$ will not yield additional feeding because the organism is already feeding at capacity with respect to task n. Thus, $P_{n-1} = 0$. If $E_{n-1} = 0$, then a completion of task $n-1$ will lead to completion of task n since the organism is not feeding at capacity with respect to task n, and hence $P_{n-1} = 1$. Thus, $c = 1/E_n$, and so we assume

$$P_{n-1} = \frac{E_n - E_{n-1}}{E_n}. \tag{4}$$

We now assume the condition $E_{n-1} = R_{n-1}P_{n-1}$; and this, together with (3) and (4), gives

$$E_{n-1} = \frac{1}{R_{n-1}^{-1} + R_n^{-1}}. \tag{5}$$

Similarly, if P_{n-i-1} is the probability of an *effective* completion of task $n - i$ given an additional completion of task $n - i - 1$, then we assume

$$P_{n-i-1} = \frac{E_{n-i} - E_{n-i-1}}{E_{n-i}}. \tag{6}$$

In this case, $E_{n-i} - E_{n-i-1}$ is the effective feeding associated with task $n - i$ less the "actual" effective feeding associated with task $n - i - 1$. When $E_{n-i} = E_{n-i-1}$, an additional completion of task $n - i - 1$ will not yield additional feeding, so $P_{n-i-1} = 0$. When $E_{n-i-1} = 0$, $P_{n-i-1} = 1$.

Applying the relationship $E_{n-i-1} = R_{n-i-1}P_{n-i-1}$ for $i = 1$ yields

$$E_{n-2} = \frac{1}{R_{n-2}^{-1} + R_{n-1}^{-1} + R_n^{-1}}. \tag{7}$$

Proceeding inductively, we find that the Ilk 1 feeding rate is

$$F = E_1 = \frac{1}{R_1^{-1} + R_2^{-1} + \cdots + R_n^{-1}}. \tag{8}$$

Parallel Process Feeding

At the other end of the feeding process spectrum, the resource might be allowed to pass in parallel through the n feeding task compartments; that is, all feeding tasks are performed simultaneously. We refer to this type of model as Ilk n. For an example of this Ilk, consider an organism that executes two tasks, encounter and gut clearance, simultaneously. When a given food item enters the gut, the forager is free to forage for another food item, even though the first item has not yet cleared the gut.

In the Ilk n model, the rate at which resource passes through the feeding system will be constrained by the minimum compartment rate. Thus, the maximal rate at which feeding occurs is

$$F = \min\{R_1, R_2, \ldots, R_n\} \tag{9}$$

resource items per unit time.

General Constrained Feeding Models

Feeding probably involves many combinations of the constraints illustrated by these two basic models. Suppose, for example, that a given food item must be encountered, then pursued; but when the food item enters the gut, the forager can encounter and pursue another prey while digesting the first. In this case, the feeding rate could be modeled as

$$F = \min\left\{\frac{1}{R_e^{-1} + R_p^{-1}}, R_g\right\}, \tag{10}$$

where R_e, R_p, and R_g are the maximal encounter, pursuit, and gut clearance rates in resource items per unit time. More generally, if j groups of tasks $i = 1, \ldots, m_1$, $i = m_1 + 1, \ldots, m_2$, $i = m_2 + 1, \ldots, m_3$, through tasks $i = m_{j-1} + 1, \ldots, m_j$ may be performed simultaneously with the remainder of the tasks $i = m_j + 1, \ldots, n$, but the tasks within each group must be performed sequentially, then, the feeding representation takes the form

$$F = \min\left\{\frac{1}{R_1^{-1} + R_2^{-1} + \cdots + R_{m_1}^{-1}}, \ldots, \frac{1}{R_{m_{j-1}+1}^{-1} + R_{m_{j-1}+2}^{-1} + \cdots + R_{m_j}^{-1}}, R_{m_j+1}, \ldots, R_n\right\}. \tag{11}$$

Other representations for feeding rates are necessary when additional feeding constraints are associated with parallel processes within groups already constrained. For example, if process 3 occurs in parallel with process 1 but not with process 2 then the feeding rate is

$$F = \min\left\{\min\{R_1, R_3\}, \frac{1}{R_2^{-1} + R_3^{-1}}\right\}.$$

Because functional representation of feeding is species dependent and each constraint places a restriction on the representation, the procedures for combining constraints to formulate feeding rates indicate that numerous types of representations could exist.

Process Module Representations

The formulations of optimal feeding rates in the previous section are prescribed in terms of maximal rates for generic feeding processes. Modular forms of feeding allow representation of appropriate models of the task rates R_i according to species or ecotype. We illustrate that rates associated with the feeding processes can vary as functions of endogenous and exogenous factors with two simple examples.

FILTER FEEDERS

Filter feeders such as *Daphnia* do not, in general, pursue prey; they feed as they encounter. Assuming the daphnids feed in an Ilk 1 sequence, feeding will have the form

$$F = \frac{1}{R_e^{-1} + R_g^{-1}}, \qquad (12)$$

where R_e and R_g are the maximal encounter and gut clearance rates respectively. Under conditions of continuous steady-state feeding, $R_g = I_m$, the maximum ingestion rate (numbers day^{-1}) and $R_e = F_m x$, where F_m is the maximal filtering rate (mm^3 day^{-1}) and x is the resource density (numbers mm^{-3}). Thus,

$$F = \frac{x}{F_m^{-1} + xI_m^{-1}} \qquad (13)$$

numbers day^{-1}, which is a Holling Type-II hyperbolic response when F_m and I_m are constants. At high resource levels, F approaches I_m, but at other resource levels, F_m is also important. That is, when food is sufficiently abundant, feeding is constrained only by maximum gut clearance; and when food is scarce, filtering becomes an important constraining task.

Hallam *et al.* (1990) used eqn (13) to model *Daphnia* with F_m proportional to the daphnid surface area, and I_m proportional to daphnid volume. Another version of this model accounts for a more appropriate representation of gut clearance rate that results in a formulation for I_m which is proportional to surface area (see also Kooijman 1986, 1993).

PURSUIT FEEDERS

Hallam has modeled the resource uptake of an individual rainbow trout (*Oncorhynchus mykiss*) by

$$F = \frac{1}{R_e^{-1} + R_p^{-1} + R_g^{-1}}. \qquad (14)$$

The encounter rate is expressed as $R_e = a_d N_p$ (numbers day^{-1}), where N_p is the density of the prey (numbers volume^{-1}) and the encounter rate coefficient a_d (volume day^{-1}) is a function of the reaction distance of the fish and the velocities of the fish and prey and represents the volume swept per unit time by the foraging fish. The pursuit rate is $R_p = \delta_v / s_d$ (numbers day^{-1}), where s_d is an expression for the reaction distance of the fish and δ_v is the relative pursuit velocity. The gut clearance rate is $R_g = kM_g/M_p$ (numbers day^{-1}), where k, the gut clearance rate coefficient, is proportional to (fish mass)$^{-0.7)}$, M_g is the mass capacity of the fish's gut, and M_p is the mass of the prey (grams). Thus,

$$FM_p = \frac{N_p}{[a_d M_p]^{-1} + \left[\frac{s_d}{M_p \delta_v} + [kM_g]^{-1}\right] N_p} \qquad (15)$$

To further illustrate the flexibility of the modular approach of (11), consider the different collections of empirical data on the gut clearance of a rainbow trout meal. Some data sets (Jobling, 1981) can be fitted to the exponential gut clearance model

$$m_g = m_{g0}\,\mathrm{e}^{-kt}, \qquad (16)$$

where m_g and m_{g0} are the masses of the gut contents at time t and time 0, respectively, and k is a constant on small time intervals but is dependent on other quantities such as fish mass and temperature. The derivative $\mathrm{d}m_g/\mathrm{d}t = -km_g$ of (16) is not the gut clearance rate we seek; (16) is a model of continuous gut emptying whereas $R_g = 1/T_g$ is the number of prey items which can be cleared per unit time and T_g is the characteristic time for clearance of one prey item of mass M_p. In model (16), the gut is never completely emptied, so we specify a percentage P of the original meal and declare the gut empty when only the fraction P of the meal remains. The evacuation time is thus $\ln P^{-1}/k$, and we take $R_g = k/\ln P^{-1}$.

Other gut clearance data are better described by the square root model $\sqrt{m_g} - \sqrt{m_{g0}} = -bt$ (Jobling, 1981). In this case, the evacuation time is $T_g = \sqrt{M_p}/b$, and so we take $R_g = b/\sqrt{M_p}$. The coefficient b, like k, will in general depend on fish mass and temperature.

Discussion

As a step toward unifying individual-based approaches to population ecology, we have focused on generic representation of consumption of macroheterotrophs based on process constraints. Optimal feeding rates were found to have many forms; these forms are governed by species or ecotype dependent processes. Once the feeding rate model is determined according to the organism's consumptive constrained processes, it is necessary to express the constraints in mechanistic form.

We have presented two examples, one for a filter feeder and one for a pursuit feeder, to demonstrate how to develop modules employed in the generic feeding representations. It is necessary to find formulations for feeding tasks which produce a feeding rate model that varies as a function of environmental (such as temperature and resource density) and organismal characteristics (such as weight and locomotion). This is, in general, a non-trivial task requiring a significant amount of data, but one that should be completed to obtain a faithful representation of feeding rates.

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