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An allometric vision and motion model to predict prey encounter rates

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ABSTRACT

Question: Can we develop simple allometric relationships based on predator and prey body size to more easily parameterize optimal foraging models and thereby make them more useful to community ecologists interested in studying species interactions?

Model: The rate at which a predator encounters its prey is often the most difficult parameter to estimate in any foraging model. We develop a simple geometric model to predict prey encounter rates as a function of predator mass, prey mass, and prey density using allometric relationships between predator search velocity and vision as a function of body size.

Empirical test: We suggest that the model has both strategic and tactical uses. Tests geared towards both uses are performed and these tests validate the model within the limits of existing data.

Conclusions: It appears possible to parameterize optimal foraging models through easily measured variables such as body size. This provides hope that Lotka-Voltera style community matrix models could be replaced with more mechanistic models based on optimal foraging that are easy to parameterize for an entire community. If so, this research agenda holds promise for developing the link between foraging models and species interactions that the original inventors of optimal foraging theory envisioned.

Keywords: allometry, encounter rates, optimal foraging.

INTRODUCTION

The rate at which a predator encounters its prey is crucial to determining the predator's diet, its rate of energy intake, and its impact on the prey community. Encounter rates are normally denoted by λ and measured in units of encounters/time. Despite the fundamental importance of this parameter to almost every predator–prey model, the ability to easily estimate prey encounter rates remains a significant stumbling block to applying foraging models to study population- and community-level processes. The original inventors of optimal foraging theory, for example, perceived the theory as a tool that could be used to

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predict consumer resource use and thus lead to a better understanding of species interactions and community structure (MacArthur and Pianka, 1966). However, with a few exceptions (Werner, 1977; Mittelbach, 1981; Rosenzweig, 1987; Brown, 1990; Mittelbach and Osenberg, 1994; Wanink and Zwarts, 2001), optimal foraging theory has not delivered on its promise to provide insights into species interactions. Instead, most studies of foraging theory have focused on examining predator behaviours and tests have been laboratory based. As Fryxell and Lundberg (1998) note, attempts to extend predictions of foraging theory to the field often suffer from the inability to measure crucial parameters. Phenomenological relationships for specific predator–prey systems are known for both handling time and encounter rates (Mittelbach, 1981; Persson and Greenberg, 1990). Inspired by this, we outline the development of a mechanistic theory that allows one to estimate prey encounter rates simply by using the body size of organisms and a few allometric constants.

THE ENCOUNTER RATE MODEL

The goal is to derive a prediction for encounter rates:

$$\lambda = f(M_{\text{prey}}, M_{\text{predator}}, N_{\text{prey}}, A) \tag{1}$$

where M is mass in kilograms, N is the number of individuals, and A is the area of the community (and hence N/A is the density of a species). We make the assumption that the function f, or encounter rate, can be derived from a simple geometric model (Fig. 1B) and allometric relationships between speed of movement versus body size and visual acuity versus body size. Clearly, the use of vision as a limiting factor on encounters restricts the applicability of our model to species that search visually. As we show below, our model works somewhat less well for predators that search in structurally and visually complex habitats (such as heavy vegetation) and would not apply at all to predators using non-vision-based search methods such as touch (Piersma *et al.*, 1998).

The study of the allometry of speed (velocity) as a function of body mass has a long history (Peters, 1983; Calder, 1984). The general finding is that this allometry has good predictive ability ($r^2 = 0.6$–0.95) with an exponent (slope in log–log space) typically between 0.1 and 0.35 (see Appendix VIb in Peters, 1983). This allometry of motion is accurate for many different organisms, although the slope and intercept vary between types of organism. Studies of the allometry of vision are much less common, but Kiltie (2000) examined the allometric scaling of visual acuity in birds and mammals. He tested the hypothesis that acuity is proportional (scales with an exponent of 1) with body length. This hypothesis derives from the fact that focal length is proportional to eye diameter which is proportional to body length, assuming cone density in the retina is constant (Breck and Gitter, 1983; see also Tamura and Wisby, 1963). The hypothesis can be written allometrically as:

$$\text{acuity} = c_{\text{acuity}}\, L^{b_{\text{acuity}}} \tag{2}$$

In this paper, we write all allometries as a function of mass (in kilograms), so we need the allometry $M = c_{\text{lm}} L^{b_{\text{lm}}}$ or $L = (1/c_{\text{lm}})^{1/b_{\text{lm}}} M^{1/b_{\text{lm}}}$, where $b_{\text{lm}} \approx 3$ and c_{lm} depends on the shape and density of the organism (Mittelbach, 1981; Peters, 1983; Calder, 1984; Kooijman, 2000), giving:

$$\text{acuity} = [c_{\text{acuity}} * (1/c_{\text{lm}})^{1/b_{\text{lm}}}]\, M^{(1/b_{\text{lm}}) * b_{\text{acuity}}} = [c_{\text{acuity}} * (1/c_{\text{lm}})^{1/b_{\text{lm}}}]\, M^{b_{\text{acuity}}/b_{\text{lm}}} \tag{3}$$

where $b_{\text{acuity}} \approx 1$. Kiltie (2000) found this to be true; visual acuity scaled as $cM^{1/3}$. More precisely, Kiltie found that acuity scaled with $M^{0.93/3}$ for diurnal species and $M^{1.10/3}$ for nocturnal species, but that the slopes of 1.1 and 0.93 in the regressions versus $M^{1/3}$ were not significantly different from 1. The constant, c_{acuity}, varies with taxonomic group and environment (diurnal bird and mammal species have three times the acuity of nocturnal mammal species), but the allometric constant (exponent) remains the same.

Our model proceeds by estimating the maximum distance, d_{max}, at which prey of a given size, L_{prey}, can be observed using the geometric model in Fig. 1A. We start with an allometry for acuity of the form $\text{acuity} = c_{\text{acuity}} M^{b_{\text{acuity}}}$ (we assume the constants c_{lm} and b_{lm} for the predator mass–length allometry are absorbed into the constants c_{acuity} and b_{acuity} as given by equation 3). By definition, angular resolution, θ (in radians) $= 1/\text{acuity} = (1/c_{\text{acuity}})M^{-b_{\text{acuity}}}$. By a simple geometric model (Fig. 1A), the maximum distance, d_{max}, at which prey of size L_{prey} is visible is given by:

$$\tan(\theta/2) = L_{\text{prey}}/2/d_{\text{max}} \tag{4}$$

which, solving for d_{max} gives:

$$\begin{aligned} d_{\text{max}} &= L_{\text{prey}}/[2 * \tan(\theta/2)] \approx L_{\text{prey}}/[2 * \theta/2] = L_{\text{prey}}/\theta = L_{\text{prey}} * \text{acuity} \\ &= (1/c_{\text{lm}})^{1/b_{\text{lm}}} M_{\text{prey}}^{\;1/b_{\text{lm}}} c_{\text{acuity}} M_{\text{prey}}^{\;b_{\text{acuity}}} \end{aligned} \tag{5}$$

where the approximation comes from the fact that $\tan(\theta) = \theta + \theta^3/3 + \ldots$ and the fact that theta is relatively small.

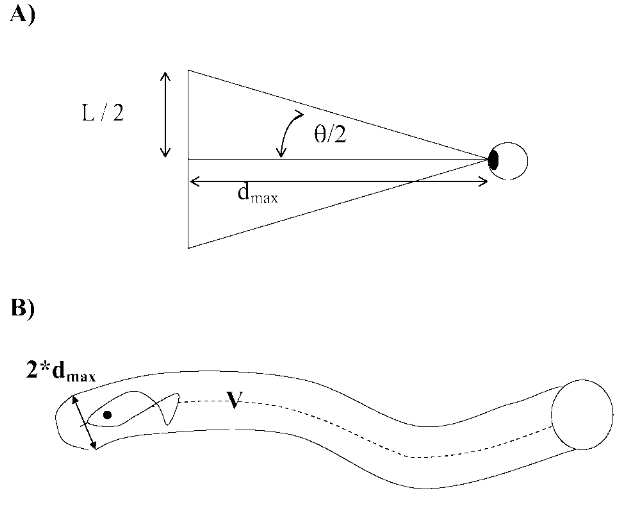

Fig. 1. Geometric models used. (A) Model relating visual acuity (θ) and prey length (L) to maximum distance at which prey is observable (d_{max}). It follow directly from the definition of $\tan(\theta)$. (B) Model relating maximum distance at which prey can be observed with velocity. As an organism moves, searching in two dimensions, looking left and right, it will constantly sweep out a half-circle of radius d_{max}. As it moves along the dotted line at a velocity, V, for a length of time, T, it will move along a line $V * T$ long, and it will sweep out an area of $2 * d_{\text{max}} * V * T$ (plus the half-circle endcaps shown on the left side, which will be a vanishingly small portion of the area as T increases). If, instead, the animal searches in three dimensions, then the volume searched will be a tube (as represented by the right side with endcaps being half spheres), with the volume given by $V * T * \pi d_{\text{max}}^{\;2}$. Note that this model assumes that the area of re-crossing (where an animal crosses its own path) is a small portion of the total area.

Now assume that prey are Poisson-distributed in space (no clumping or over-dispersion), so that mean number of encounters per unit time is given by density * search area = $N/A_{\text{community}} * A_{\text{search area}}$. Also assume that the search area in a given time is approximated by visual search width * search velocity = $2d_{\text{max}}v_{\text{search}}$ (Fig. 1B). Search velocity can be estimated by the allometric relation $v_{\text{search}} = c_{\text{veloc}}M^{b_{\text{veloc}}}$ ($\text{m} \cdot \text{s}^{-1}$). Then the encounter rate is given by:

$$\begin{aligned}\lambda &= \text{prey density * visual search width * velocity} = N_{\text{prey}}/A_{\text{community}}\, 2d_{\text{max}}v_{\text{search}} \\ &= N_{\text{prey}}/A_{\text{community}} * 2 * (1/c_{\text{lm}})^{1/b_{\text{lm}}} M_{\text{prey}}{}^{1/b_{\text{lm}}}\, c_{\text{acuity}} M_{\text{prey}}{}^{b_{\text{acuity}}} * c_{\text{veloc}} M_{\text{pred}}{}^{b_{\text{veloc}}} \\ &= [2 * 1/c_{\text{lm}}{}^{-1/b_{\text{lm}}} * c_{\text{acuity}} * c_{\text{veloc}}] * M_{\text{prey}}{}^{1/b_{\text{lm}}} M_{\text{pred}}{}^{b_{\text{veloc}} + b_{\text{acuity}}}\, N_{\text{prey}}/A_{\text{community}} \end{aligned} \tag{6}$$

If we wish to modify to species searching in three dimensions, then we have

$$\begin{aligned}\lambda_{3\text{D}} &= \pi d_{\text{max}}{}^2\, v_{\text{search}}\, N_{\text{prey}}/V_{\text{community}} \\ &= \pi[(1/c_{\text{lm}})^{1/b_{\text{lm}}} M_{\text{prey}}{}^{1/b_{\text{lm}}}\, c_{\text{acuity}} M_{\text{pred}}{}^{b_{\text{acuity}}}]^2\, c_{\text{veloc}} M^{b_{\text{veloc}}} N_{\text{prey}}/V_{\text{community}} \\ &= [\pi c_{\text{lm}}{}^{-2/b_{\text{lm}}}\, c_{\text{acuity}}{}^2 c_{\text{veloc}}]\, M_{\text{prey}}{}^{2/b_{\text{lm}}} M^{2b_{\text{acuity}} + b_{\text{veloc}}} N_{\text{prey}}/V_{\text{community}} \end{aligned} \tag{7}$$

AVAILABLE EMPIRICAL DATA

We are aware of three studies that have measured rates of prey encounter as a function of the variables of interest (i.e. equation 1) (Mittelbach, 1981; Perrson and Greenberg, 1990; Aljetlawi *et al.*, 2004). All of these have been conducted on fish. Two of these studies (Mittelbach, 1981; Persson and Greenberg, 1990) perform a regression of a multivariate power function or Cobb-Douglas (Jehle and Reny, 2001) function (i.e. $f(x,y) = cx^{\alpha}y^{\beta}$), while Aljetlawi *et al.* (2004) derive a slightly more complex but still largely phenomenological model. All three papers find broadly similar results: encounter rate (λ) is an increasing, decelerating function of predator size and prey size and density. Each paper then goes on to predict optimal diets based on these functional relationships for the predator under varying conditions (prey size and density, predator size) and shows that the model accurately predicts predator diet in simple habitats; predictions in more complex habitats are less accurate.

For testing our model we have access to the calculated regression coefficients from Mittelbach (1981) and Persson and Greenberg (1990) to describe the empirical data obtained for two fish species (bluegill, *Lepomis macrochirus*, and European perch, *Perca fluviatilis*) as well as the raw data for the Mittelbach bluegill, open-environment scenario. The reported regression coefficients were standardized to common units (mass in kilograms) using the following length–mass allometries:

- prey (*Daphnia*): $M(\text{mg}) = 0.012L(\text{mm})^{2.63}$ (Mittelbach, 1981)
- predator (bluegill): $M(\text{g}) = 0.000026L(\text{mm})^{3.043}$ (Mittelbach, 1981)
- predator (perch): $M(\text{g}) = 0.0092L(\text{cm})^{3.24}$ (Froese and Pauly, 2005) (many allometries listed, used median allometry)

The resulting standardized empirically observed regression coefficients are given in Table 1.

To develop the predicted allometries, it was also necessary to identify appropriate vision and velocity allometries. For birds, these are:

Table 1. Empirically observed coefficients for fish in various environments

	c	b_{dens}	b_{mprey}	b_{mpred}
Bluegill in open	25 116.00000	0.667	0.3502	0.6592
Reanalysis bluegill in open	24 119.00000	0.721	0.3946	0.507
Bluegill in vegetation	0.69319	0.779	0.4838	0.2281
Bluegill on sediment	0.04440	0.719	0.4132	0.0861
Perch on sediment	0.000025	0.741	0.1987	0.3293
Perch in vegetation	4.07220	1.088	1.0134	0.3225

Note: Comparison of coefficients (as in Table 2; $\lambda = cD^{b_{\mathrm{dens}}} M_{\mathrm{prey}}{}^{b_{\mathrm{mprey}}} M_{\mathrm{pred}}{}^{b_{\mathrm{mpred}}}$) estimated from empirical observation of fish encounter rates, λ. The bluegill data are from Mittelbach (1981), while the perch data are from Persson and Greenberg (1990). All coefficients are normalized to use units of mass (kg) for prey and predator size and so the coefficients may appear to differ from the values reported in the original papers. The units for density, D, vary with habitat type, causing some of the variation in the constant coefficient, c, which varies dramatically among habitat types. Two results are reported for bluegill in open water: original and reanalysis. When we reanalysed the data from Mittelbach (1981) using Matlab 6.5 (second row in table), we obtained slightly different coefficients from those reported in the original study (first row in table). The cause of this discrepancy is unknown, but it appears small; similarly, the goodness of fit is very similar between the two analyses ($r^2 = 0.77$ vs. 0.78).

- prey (insect) length–mass: $M(\mathrm{kg}) = 8.8L(\mathrm{m})^{2.62}$ (Appendix IIa in Peters, 1983)
- velocity: $V(\mathrm{m \cdot s^{-1}}) = 13.3M(\mathrm{kg})^{0.21}$ (Peters, 1983, p. 89)
- acuity: $A(1/\mathrm{rad}) = 41.67M(\mathrm{kg})^{0.93}$ (Kiltie, 2000)

and for mammals:

- prey (mammal) length–mass: $M(\mathrm{kg}) = 14L(\mathrm{m})^{3.23}$ (Appendix IIa in Peters, 1983)
- velocity: $V(\mathrm{m \cdot s^{-1}}) = 0.33M(\mathrm{kg})^{0.21}$ (Appendix VIb in Peters, 1983)
- acuity: $A(1/\mathrm{rad}) = 41.67M(\mathrm{kg})^{0.93}$ (Kiltie, 2000)

Note that acuity is given by the same allometry for diurnal birds and mammals.

To make vision and velocity predictions for fish was more challenging. There were several allometries for velocity. We chose:

- fish velocity: $V(\mathrm{m \cdot s^{-1}}) = 4.4M(\mathrm{kg})^{0.35}$ (Peters, 1983)

This one is for a sprinting fish, which might normally be considered too fast for search velocity, but the fish used in Mittelbach's (1981) experiment were hungry and moved about five times faster than predicted by this allometry, so a sprinting allometry appears appropriate for these data. For vision allometries, two studies present data showing that there is an allometric relationship between visual acuity and fish size specifically for the bluegill (Breck and Gitter, 1983; Li *et al.*, 1985). However, they do not report the raw data or the fitted regression equations. Therefore, we calculated a general allometric equation for fish using minimum resolvable angles summarized for 16 species of fish in Douglas and Hawryshyn (1990). These authors did not report the body mass of the fish species studied. Therefore, we approximated mass by using the L_∞ and length–mass allometries reported in FishBase (Froese and Pauly, 2005) for 10 of these species. Although this certainly overestimated the size of the fish measured in the laboratory, it was at least consistent across species and hopefully the effects of overestimation will be small in the log–log space of allometric analyses. The data are available in an Excel spreadsheet from the corresponding author. The resulting allometric equation had an $r^2 = 0.29$ and the form:

- fish vision acuity: $A(1/\mathrm{rad}) = 13.846M(\mathrm{kg})^{\mathbf{0.107}}$

The exponent (0.107) is similar to our estimate of the exponent of an allometric equation estimated for the bluegill data contained in Li and colleagues' (1985) plot (estimated exponent 0.116). This allometry with its low coefficient (0.107 vs. 0.333 expected) implies that mass has much less effect on visual acuity in fish than in birds and mammals.

It has been suggested that fish, like birds, live in a three-dimensional world. Thus it was unclear whether a two- or three-dimensional model would be more appropriate for fish. However, past studies of another model (Eggers, 1977) suggested that the two-dimensional model provides a much better fit to field diet data (Werner *et al.*, 1983), so we have an *a priori* expectation that the two-dimensional model should work better. This raises the question of appropriate units for prey density (normally expressed in individuals per litre or individuals per m^3 but now needed in individuals per m^2). We made the somewhat arbitrary (but *a priori*) decision using dimensional analysis that since a litre is 10 cm per side and therefore converting from individuals per litre to individuals per m^3 one multiplies by 10^3, we would multiply individuals per litre by 10^2 to give individuals per m^2. This dimensional argument also equates to the idea that the fish explore a 10 cm thick slice of their three-dimensional world, which seems reasonable.

In addition to allometries, we had the raw data from a set of laboratory studies of bluegill feeding on *Daphnia* in open water (Mittelbach, 1981). These data consisted of the length of bluegill predators varying from 33 to 109 mm, length of *Daphnia* prey varying from 1.14 to 2.20 mm, prey densities varying from 0.5 to 15 individuals per litre, and encounter rates ranging from 0.21 to 299.0 encounters per second for 69 experimental runs. The lengths were converted to mass (kg) using the above length–weight allometries. Coefficients for the empirical model:

$$\lambda = cD^{b_{\mathrm{dens}}} M_{\mathrm{prey}}{}^{b_{\mathrm{mprey}}} M_{\mathrm{pred}}{}^{b_{\mathrm{mpred}}}$$

(roughly comparable to equation 6) were calculated by $\log_{10}$ transforming the data and then using simple linear regression (and then back-transforming the coefficient c by 10^c). Analysis of the residuals shows that the data are normally distributed, but there are several outliers. We chose not to eliminate the outliers because they do not present a problem to our analysis, which is based on a simple comparison of r^2 statistics.

TEST OF THE MODEL

Is this model successful? We suggest that developing an appropriate test of the model in light of the scarce amount of empirical data against which to test it requires consideration of the intended use of the model. May (1974, pp. 10–12) describes a continuum of models in ecology from strategic to tactical. Strategic models 'do not correspond in detail to any single real community, [but] aim to provide a conceptual framework' often containing hypothesized mechanisms. Tactical models 'strive for a detailed and pragmatic description of a quite specific system' often providing precise numerical predictions for applied problems. We suggest that our model of encounter rates could prove useful in three contexts:

1. An intraspecific strategic model to explain and demonstrate mechanism (vision and motion allometries) for an empirically observed pattern (Mittelbach, 1981; Persson and Greenberg, 1990).
2. An intraspecific tactical model to predict encounter rates for a species based on masses and prey density for use in conservation and management.
3. An interspecific tactical-strategic model to provide approximate estimates of encounter rates for many different species where it would be prohibitive to empirically measure actual encounter rates.

To test the model, one must first specify the intended use. Below, in three sub-sections we test the model in an appropriate fashion for the targeted use and discuss implications for using the model in this fashion.

Intraspecific strategic explanation of empirical phenomenon

The model predicts that the functional form of the encounter rate–body size relation is a power or Cobb-Douglas function (Jehle and Reny, 2001). This is the same function Mittelbach (1981) and Persson and Greenberg (1990) use to describe their data. Aljetlawi *et al.* (2004) use a different functional form to describe λ as a function of the variables used here and it is difficult to make a direct comparison of our and their results. Thus, on this simplest of levels – predicting the correct functional form – the model is successful. Often tests of strategic models do not proceed further, although we would argue this is a relatively weak test (McGill, 2003).

A stronger test (McGill, 2003) would be given by predicting perturbations. A simple test of this fashion can be achieved by noting that in a more complex habitat (vegetation or sediment vs. open water column), the importance of both predator speed and acuity would go down (exponent for M_{pred} gets smaller) since the fish is no longer able to search at top speed or to see at the farthest distances of which its vision is capable. Similarly, due to the partial obstruction expected in complex habitats, one might expect the importance of prey size to go up (exponent for M_{prey} to get larger). Both of these predictions happen with bluegill (Table 2). A much stronger confirmation could be obtained by experiments in which the effects of velocity and vision were more directly manipulated and manipulated independently of each other; for example, by increased turbidity of water and by fin clipping. In summary, the evidence available suggests that the vision and motion model is a good strategic model capturing important mechanisms for encounter rates for visual predators, but more experiments are needed.

Intraspecific tactical model for precise estimates of encounter rates

Resource managers would often like to predict the diet of a species given its environmental context. Foraging theory provides a potential route to such predictions based on energetics, handling times, and encounter rates. Furthermore, Osenberg and Mittelbach (1989) and Mittelbach and Osenberg (1994) show that a knowledge of encounter rates alone can sometimes explain a significant fraction of the variance in predator diets in nature. How well

Table 2. Predicted coefficients for encounter rate model for various organisms

	c	b_{dens}	b_{mprey}	b_{mpred}
Fish on invertebrate (2D)	12 518	1	0.38	0.46
Fish on invertebrate (3D)	2.80×10^6	1	0.76	0.56
Land mammal on land mammal (2D)	12.154	1	0.31	0.52
Flying bird on insect (3D)	13 804	1	0.83	0.76
Standardized 2D	N.A.	1	1/3 = 0.33	¼ + 1/3 = 7/12 = 0.5833
Standardized 3D	N.A.	1	2/3 = 0.67	¼ + 2/3 = 11/12 = 0.9166

Note: This table predicts the coefficients of the model $\lambda = cD^{b_{\mathrm{dens}}} M_{\mathrm{prey}}{}^{b_{\mathrm{mprey}}} M_{\mathrm{pred}}{}^{b_{\mathrm{mpred}}}$ found in equations (6) and (7) using the allometries described in the 'Available empirical data' section. The standardized entries follow the allometric practice of assuming rational (ratio of integer) values for exponents (Peters, 1983; Calder, 1984) and uses the expected value for these exponents rather than observed exponents. N.A. = not available.

does our model perform in predicting actual encounter rates? Using the data and allometries described in the 'Available empirical data' section, we were able to produce estimates of all coefficients for five empirical scenarios (Table 1) and for six scenarios under our hypothesized model (Table 2). The only overlapping scenario is the bluegill open water scenario (Table 1) versus either the fish two- or three-dimensional model (Table 2). One can see that the predicted two-dimensional fish coefficients are approximately equal to the empirical fish coefficients (Table 1). In particular, the range of coefficients in Table 1 spans the predicted values of the two-dimensional fish model. More importantly, the bluegill open water scenario coefficients are close to the predicted two-dimensional fish model. This is the relevant comparison because our model assumptions match the open water environment. To explore the effects of the small difference in these coefficients, we can examine the r^2-values (proportion of variance explained of the different models). A purely phenomenological (all four parameters in equation 8 allowed to vary to maximize fit) gives an $r^2 = 0.78$, while the predicted model (all four parameters predicted *a priori* by the model and fish-specific allometries leaving no free-fitting parameters) gives $r^2 = 0.69$ for the two-dimensional model with fish allometries and $r^2 = -0.47$ (worse than a constant model) for the three-dimensional model. Thus our *a priori* expectation of the two-dimensional model working better is confirmed. It appears that as long as the correct (two- vs. three-dimensional) model is chosen and good allometries are available, the vision and motion model can successfully make numerical predictions of encounter rates (r^2 improves by only 0.08 with the addition of four parameters), at least for the one test case possible with published data.

We caution, however, that the success of numerical prediction depends heavily on the constant, c. Changes by a factor of 2 or 3 can reduce the r^2-value drastically. A factor of 2 or 3 may sound large, but in the log–log world of allometry it is not difficult to find allometries that vary by this much. This suggests another approach to using the vision and motion model for numerical predictions. The standard predictions given in Table 2 use rational exponents (⅓, ¼) and should represent typical exponents for all organisms (Calder, 1984; a common practice in allometry: Peters, 1983). The intercept constant, c, is what varies greatly between organisms. If one manages to obtain, say, five empirical estimates of encounter rates for a particular organism under a variety of prey and predator sizes and densities, this combined with the standard allometry should be enough to obtain a reasonable value of c. When we chose 5 of our 69 points at random from the bluegill data set and used this method, we typically predicted encounter rates with $r^2 > 0.60$ for all 69 data points. Thus a handful of measurements of real-world encounter rates can suffice for making tactical predictions of encounter rates without any organism-specific allometries. In other words, using a few measured encounter rates to estimate the single intercept parameter c combined with universal allometric exponents that apply to all taxonomic groups works well to give quantitative predictions of encounter rates for a specific system.

Interspecific strategic-tactical model for approximate estimates

There are no measurements of encounter rates across species to our knowledge. This makes direct testing of this use of the model impossible. However, the success of the previous two tests suggests that this approach has a good chance of success. Moreover, it is well known that the allometries become more predictive (higher r^2) the greater the variation in the independent variables (mass, density) (Peters, 1983; Calder, 1984). Thus, as the number of species and scope of independent variables increases, the r^2 should improve beyond what we have already seen.

DISCUSSION

We have developed a mechanistic model to predict prey encounter rates as a function of mass and density. The model uses allometries for vision and motion and some simple geometric identities. We plug in the allometries for specific sets of organisms to predict the functional relationship between encounter rate and masses and densities in a variety of situations (Table 2), but tests can only be conducted for the case of fish where empirical data exist. We suggest that there are several different uses for this model and correspondingly different tests. Testing the model as a strategic model used to elucidate the mechanism behind an empirical phenomenon appears to succeed within the limits of existing data, but more experiments, especially manipulative experiments, are needed. At the opposite extreme, using this model to make numerical predictions of encounter rates in a specific system also appears to succeed in the one case where we had access to data to test. We caution, however, that this depends primarily on having the constant (c) estimated accurately, which depends on using good organism-specific allometries. Alternatively, this model can be used together with organism-independent allometries to successfully extend a handful of measurements of encounter rates to the entire parameter space.

We were unable to test the third model usage, predictions across species. However, we believe in the long run this may be an important use of this model. Our long-term goal is to produce a realistic, rapidly parameterizable model of community dynamics using optimal foraging theory. The community matrix is often used to characterize the interactions between species within a food web (May, 1971, 1974; MacArthur, 1972; Taylor, 1988; Pimm, 1991; Law and Morton, 1996; Wilson *et al.*, 2003). The community matrix captures not only which species interact with each other (by non-zero entries in the matrix) but also the strength of their interactions (the magnitude of the matrix entries), and it leads directly to a model of species dynamics. However, determining the interaction coefficients for any species assemblage is problematic. Currently, there are two ways to estimate the values of the community matrix. One is by measuring them directly (Moore, 1996), but this is difficult in systems with many species. The alternative is to generate the elements of the matrix randomly and assume that this represents a realistic community (May, 1971, 1974; Pimm, 1991), but there are serious doubts about the validity of this approach (Lawlor, 1978; Berlow *et al.*, 2004). This has led Berlow *et al.* (2004a) in a recent review to suggest that 'the ecological community urgently needs to explore new ways to estimate biologically reasonable model coefficients from empirical data, such as foraging rates, body size, metabolic rate, biomass distribution, and other species traits'.

We suggest that optimal foraging theory provides a useful tool to estimate the matrix of interaction coefficients in those cases where searching is visual and the consumption of prey is limited by encounter rates rather than digestion or other factors (Jeschke *et al.*, 2002; van Gils *et al.*, 2005). Of the three parameters in the standard optimal diet model, one parameter, e_i or energetic content, is fairly trivial to calculate. Herein we have demonstrated a mechanistic model that makes the second parameter, encounter rate or λ_i, easy to calculate from a few easily measured variables (mass and prey abundance). The next step in this research programme would be to develop an easily calculated, mechanistic model of h_i or handling time. With this in place, it will be possible to explore the original promise of optimal foraging theory as a tool to study species interactions and community dynamics (MacArthur and Pianka, 1966).

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