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A Bioenergetic Biomagnification Model for the Animal Kingdom

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Species vary greatly in the degree to which they accumulate dietary contaminants. Bioenergetic processes play a key role in chemical uptake and elimination, and interspecific variation in bioaccumulation can be attributed in large part to variation in how species feed, digest, and allocate energy. We present a quantitative treatment of this relationship for the entire animal kingdom. We derive a model to predict the biomagnification factor for nonmetabolizable, slowly eliminated chemicals, BMF_{max}. We test the model with observed biomagnification factors and independently derived bioenergetic parameters for a diverse suite of species, including herbivores and carnivores, heterotherms and homeotherms, vertebrates and invertebrates, adults and juveniles, domestic/laboratory animals and wild individuals from freshwater, marine, and terrestrial environments. The model successfully predicts species-specific BMF_{max} values across this range of taxa, with values ranging from less than 1 in caterpillars to nearly 100 in some carnivores. In addition, we make novel predictions of BMF_{max} for several taxa for which no measured bioaccumulation data are available. Our analysis provides new insights into the role of ecology in chemical dynamics across the animal kingdom, providing a general framework for understanding how characteristics of an organism and its ecological context influence the degree to which that organism accumulates chemicals present in its diet.

Introduction

The 2004 United Nations Environment Programme (UNEP) persistent organic pollutants (POPs) protocol established criteria that are being adopted by many countries to identify bioaccumulative substances used in commerce. These criteria are largely based on bioaccumulation observed in fish and, hence, are applicable only to fish. Unfortunately, the toxicological effects of many POPs are borne by a much wider variety of organisms (e.g., raptors, pinnipeds, humans), and it is important to expand the criteria to include these and other organisms. The need for a broader taxonomic assessment is further demonstrated by observations that certain substances (e.g., perfluorinated sulfonic acids, β-hexachlorocyclohexane, endosulfan) can biomagnify in species such as wolves, seals, and whales to a much greater extent than in fish. Fish are therefore not always an appropriate indicator species for bioaccumulation or risk assessment. In addition, the development and application of exposure and risk assessment methodologies for fish and aquatic invertebrates have outpaced those for many other classes of organisms. Given the enormous taxonomic diversity on this planet, there is a need to develop models that can assess the bioaccumulative nature of commercial substances in a variety of species.

The purpose of this article is to provide a general framework for integrating bioenergetic reasoning into the analysis and prediction of chemical dynamics in a wide variety of organisms. Chemical concentrations in consumers arise from a complex interplay of processes that promote (e.g., gastrointestinal magnification) and counteract (e.g., growth dilution, respiratory elimination, metabolic transformation) bioaccumulation. The relevant vital rates, feeding rate, egestion rate, respiration rate, and growth rate, are highly variable entities—any or all can vary greatly with characteristics of the consumer (e.g., size, feeding mode, physiology), the diet (e.g., biochemical composition, abundance), or the environment (e.g., temperature, physical structure). Any attempt to analyze or predict bioaccumulation in real systems must take into consideration the ecological and physiological variables that have an important influence on the process (*1*). Explicitly linking chemical accumulation models to the bioenergetic processes underlying bioaccumulation is a powerful way to do this (*2*−*6*). The field of bioenergetics is rich with theory, key parameters have been well studied, and the central role of energy provides a common currency with which to link bioaccumulation models to other aspects of ecology or physiology. Furthermore, a bioenergetic approach allows the exploitation of the interrelationships among vital rates, such as consumption and growth (*3*−*6*), and precludes implausible parameter combinations (*4*).

This bioenergetically based model is intended to predict the major patterns of biomagnification as manifestations of fundamental and universal bioenergetic processes. If this can be done, then it should be easier to interpret and investigate the remaining variation due to respiration, metabolic transformation, and other processes. It is our hope that universal treatments such as the model we present here will stimulate a more thorough integration of ecological theory into the analysis of chemical dynamics in organisms.

Theory

Biomagnification. Biomagnification is the process by which a chemical in a consumer organism achieves a thermodynamic activity (often measured by the lipid normalized concentration or fugacity) in excess of that in its diet (*7*, *8*). This is distinct from bioconcentration, whereby an organism accumulates a chemical from its ambient environment (water or air) via respiratory surfaces. Bioconcentration is often controlled by passive, reversible diffusion and raises an organism's internal chemical activity up to, but not above, that of the ambient medium (*9*). Biomagnification is distinct in that it can produce internal concentrations and thermodynamic activities of chemicals well above those in either the diet or the external environment (*7*, *8*, *10*). This process can occur at each step in a food chain, potentially producing very high and toxic concentrations in upper-trophic-level species.

Following the body/gut two-compartment model described elsewhere (*8*, *10*), we can derive a general expression for the steady-state biomagnification factor (BMF) as the ratio of chemical fugacities in the consumer's body (f_B) and diet (f_D) (see Supporting Information for complete derivation)

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$$\mathrm{BMF} = \frac{f_B}{f_D} = \frac{D_R\left(\frac{f_R}{f_D}\right) + D_D E_D}{(D_G + D_M + D_R) + \left(\frac{D_{BG}}{D_{GB}}\right) D_F E_D} \quad (1)$$

where f_R is the fugacity in the respired medium (air or water); D represents the fugacity-based transport parameters (mol day^{-1} Pa^{1-}) for dietary uptake (D_D), metabolic transformation (D_M), respiratory exchange (D_R), fecal egestion (D_F), and growth dilution (D_G), as well as the rates of gut-to-body (D_{GB}) and body-to-gut (D_{BG}) chemical transport; and E_D is the gross chemical absorption efficiency from the gut, i.e., the rate of absorption of chemical from the gut relative to the total rate of elimination of chemical from the gut [$E_D = D_{GB}/(D_{GB} + D_F)$].

The ratio D_{BG}/D_{GB} in eq 1 has been assumed to be unity in fish (*8*, *10*) on the basis of the premise that a molecule diffusing from a consumer's gut into its body is assumed to encounter the same serial resistances as a molecule diffusing in the opposite direction. However, it has also been suggested that this ratio is on the order of 0.50−0.33 (a D_{GB}/D_{BG} ratio of 2−3), reflecting a greater resistance for organism-to-gut transport than for gut-to-organism transfer (*11*).

To focus on the model's ability to assess variation in the extent of biomagnification among a wide array of consumer organisms, we consider in our analysis a simplified form of eq 1, restricted to situations in which metabolic transformation is negligible and respiratory uptake and elimination are insignificant. This applies to many POPs that are non- or poorly metabolizable by many organisms and that, because of low solubility in the respiratory medium, are not accumulated or eliminated to an appreciable extent via respiratory exchange. This permits us to focus on differences in maximum possible BMF among animal taxa and simplifies the model such that the role of energetic efficiencies can be elucidated. Under these simplifying assumptions, the maximum steady-state BMF of a consumer becomes

$$\mathrm{BMF}_{max} = \frac{D_D}{\left(\frac{1}{E_D}\right) D_G + \left(\frac{D_{BG}}{D_{GB}}\right) D_F}$$

or

$$\mathrm{BMF}_{max} = \frac{G_D Z_D}{\left(\frac{1}{E_D}\right) g Z_B + \left(\frac{D_{BG}}{D_{GB}}\right) G_F Z_F} \quad (2)$$

where D_D has been replaced by the product of the feeding rate (G_D, m^3/day) and the sorptive capacity of the diet (Z_D, mol m^{-3} Pa^{-1}), D_F has been replaced by the product of the egestion rate (G_F) and the sorptive capacity of feces (Z_F), and D_G has been replaced by the product of the growth rate (g) and the consumer's sorptive capacity (Z_B). Because vital rates (feeding, growth, egestion) occur in all three terms of eq 2, they can have any units as long as they are uniform. Because sorptive capacities occur in all three terms, absolute Z values are unnecessary, and one need only be concerned with the relative sorptive capacities of diet, feces, and consumer.

In this formulation, biomagnification is promoted by the process of digestion and macronutrient absorption (*8*, *10*). The fecal egestion rate, G_F, is less than the feeding rate, G_D, because much of the ingested diet is absorbed and assimilated by the consumer. Similarly, the sorptive capacity of feces (Z_F) is typically less than that of fresh dietary material (Z_D) because lipids, with a relatively high sorptive capacity for hydrophobic chemicals, are efficiently and preferentially absorbed by most consumers. The ratio $G_D Z_D D_{GB}/G_F Z_F D_{BG}$ combines these two processes to express the maximum BMF of an organism under conditions of no growth. This ratio will always exceed unity for real consumers and will be greatest when the diet is highly digestible (e.g., lipid-rich animal prey) and/or the consumer has a highly efficient digestive system. Any asymmetry that might exist in gut-to-body vs body-to-gut transport (i.e., $D_{GB} > D_{BG}$) will further promote the biomagnification process. Biomagnification is opposed in eq 2 by limitations on the kinetics of chemical absorption ($1/E_D$) and by growth dilution (gZ_B). Organisms with high egestion rates (inefficient digestion, short gut residence time) and/or low chemical diffusion rates (low gut temperature, low gut surface area, high resistance to diffusion) will have low E_D values, and consequently, the effect of growth dilution will be maximized.

Prediction of BMF_{max} can be greatly simplified by considering the relationships among these parameters. The consumer's growth rate, g, and egestion rate, G_F, are related to the feeding rate, G_D, and the digestion and absorption of ingested materials. Similarly, the sorptive capacity of fecal matter, Z_F, is a function of the sorptive capacity of the diet, Z_D, and the degree to which dietary constituents are absorbed by the consumer. A general energy budget can be used to define these relationships as

$$I - L = R + P \quad (3)$$

where I is energy ingestion, L is the sum of fecal and urinary losses, P is production, and R is respiration. Note that respiration in this context means energy expenditure, not gas exchange. The terms in eq 3 are expressed in units of energy flux (kJ day^{-1}). These can be converted to mass fluxes (g day^{-1}) by an energy−biomass interconversion ratio.

Digestive Efficiency. The left-hand side of eq 3 represents the net assimilation of energy and is sometimes expressed as $I\alpha_E$, where α_E is the net efficiency with which ingested food energy is digested and assimilated. Digestive efficiency is commonly expressed in terms of energy (α_E) or dry-matter digestibility (α_D). α_E and α_D are functions of the composition of the diet and the ability of the consumer to digest and absorb the various constituent fractions. We can also express the reduction in the sorptive capacity of the consumed diet for the chemical substance that occurs during food digestion in terms of an efficiency α_Z, which expresses the volume-weighted sorptive capacity of the digesta relative to that of the ingested diet [i.e., $G_F Z_F = (1 - \alpha_Z) G_D Z_D$].

Production or Growth Efficiency. The right-hand side of eq 3 represents the possible fates of assimilated energy. A fraction is expended on various forms of respiration: basal metabolism, thermoregulation, specific dynamic action (the energy expended in digestion, absorption, and assimilation), and activity. The remainder is then allocated to production of somatic and reproductive tissue and secretions such as silk, mucus, or milk. The ratio of production to assimilated energy ($P/I\alpha_E$) is referred to as net production efficiency, which we shall denote as e (*12*−*16*). The fraction of assimilated energy allocated to production of somatic tissue alone (excluding production of offspring and secretions) is the net growth efficiency. If the animal is nonreproductive and has no important secretions, the net production and net growth efficiencies are equal. Sources of variation in e include thermoregulatory strategy (homeothermy vs heterothermy) and elements of the activity budget such as food-acquisition strategy (e.g., livestock and laboratory animals have unusually high e values because of low food-acquisition costs; *12*, *17*). e also declines with age in most species (*12*, *18*) because juveniles expend relatively little energy on reproductive development, activity, and thermoregulation. In animals with determinate growth, net production efficiency decreases as the animal asymptotically approaches its maximum size and

can even reach zero in long-lived species. Growth rates in adult birds and mammals are often small, but even very low growth rates can have an influence on contaminant concentrations (*19*, *20*).

The total production rate, expressing the combined production associated with somatic growth, development of offspring, and secretions, can be derived from the feeding rate, energetic efficiencies, and relative energy density of consumer and diet as:

$$g = \frac{I\alpha_E e}{\delta_B} = \frac{G_D \delta_D \alpha_E e}{\delta_B} \quad (4)$$

where δ_D and δ_B are the energy densities of the diet and the consumer, respectively. Expressing g as a function of both digestive efficiency and net production efficiency permits one to distinguish between the effect of consumer physiology and diet composition (α_E) and the effect of consumer life history and the resulting allocation of assimilated energy (e). Expressing g as a rate of total production (rather than production of somatic tissue alone) ensures that contaminant elimination resulting from reproduction and secretion are included in the bioaccumulation model. In this way, reproductive elimination is expressed as a form of growth dilution; this approach recognizes that, although parturition is associated with an immediate loss of contaminant mass, the chemical fugacity in the organism undergoes no change (assuming that mother and offspring are at equifugacity).

We can now reformulate our expression for BMF_{max} in terms of the bioenergetic efficiencies derived above. Substituting eq 4 into eq 2 and dividing through by $G_D Z_D$ gives

$$BMF_{max} = \frac{1}{\left(\frac{1}{E_D}\right)\alpha_E e\left(\frac{\delta_D}{\delta_B}\right)\left(\frac{Z_B}{Z_D}\right) + \left(\frac{D_{BG}}{D_{GB}}\right)(1-\alpha_Z)} = \frac{1}{\gamma + \beta} \quad (5)$$

The second term in the denominator of eq 5, $(D_{BG}/D_{GB})(1 - \alpha_Z)$, or β, contains the driving forces for biomagnification. The first term, $(1/E_D)\alpha_E e(\delta_D/\delta_B)(Z_B/Z_D)$, or γ, represents processes that counteract the biomagnification process.

Model Parametrization. With the exception of E_D, D_{BG}/D_{GB}, and e, all of the terms in eq 5 can be expressed as simple functions of biochemical composition and characteristic values of α, δ, and Z for the major constituents (i.e., lipid, protein, carbohydrate and water) of consumer and diet. The energy densities of the diet (D) and the consumer (B) can be derived as

$$\delta_D = \sum_i \delta_i \phi_{i,D} \quad (6)$$

and

$$\delta_B = \sum_i \delta_i \phi_{i,B} \quad (7)$$

where δ_i represents the energy density (kJ cm^{-3}) of the major biochemical constituents of the diet or consumer and ϕ_i represents the volume fraction (cm^3 cm^{-3}) of the diet or consumer composed of lipid, protein, carbohydrate, or water. As energy densities of lipid, protein, and carbohydrate vary little among organisms, we can use standard values for δ_i of 35.6 kJ cm^{-3} for lipid, 26.8 kJ cm^{-3} for protein, 26.2 kJ cm^{-3} for carbohydrate, and 0 kJ cm^{-3} for water [corresponding to characteristic values of 39.5 kJ g^{-1} for lipid, 19.7 kJ g^{-1} for protein, 17.2 kJ g^{-1} for carbohydrate, and 0 kJ g^{-1} for water and using densities of 0.9, 1.4, 1.5, and 1.0 g cm^{-3}, respectively (*21*)]. The sorptive capacities of the diet (D) and the consumer (B) can be derived as

$$Z_D = \sum_i Z_i \phi_{i,D} \quad (8)$$

and

$$Z_B = \sum_i Z_i \phi_{i,B} \quad (9)$$

where Z_i represents the fugacity capacity of the major biochemical constituents. Z_i can be expressed as a fraction of the fugacity capacity of lipids, i.e., Z_i/Z_{lipid} is approximately 0.05, 0.1, and 1.0 for simple hydrophobic organic chemicals in proteins, carbohydrates, and lipids, respectively (*10*, *22*). The absolute value for Z_{lipid} is not required for the model calculations. In many organisms or tissues, the sorptive capacity for hydrophobic organic chemicals is dominated by lipids. However, in organisms or tissues with low lipid content (e.g., algae, mussels, feces), the contribution of nonlipid constituents can also be important (*10*, *19*, *23*). Differences in sorptive capacities among different types of lipids, proteins, and carbohydrates have been observed, but the differences are relatively small in most cases (*24*–*26*).

Digestive efficiencies on a dry-matter basis, α_D, and an energy basis, α_E, are

$$\alpha_D = \sum_i \alpha_i \phi_{i,D} \quad (10)$$

and

$$\alpha_E = \frac{\sum_i \alpha_i \phi_{i,D} \delta_i}{\sum_i \phi_{i,D} \delta_i} \quad (11)$$

where α_i represents the dry-matter digestibility of each of the major biochemical constituents of the diet by the consumer. The digestive efficiency scaled to the sorptive capacity of the diet for a chemical substance is measured by α_Z, calculated as

$$\alpha_Z = \frac{\sum_i \alpha_i \phi_{i,D} Z_i}{\sum_i \phi_{i,D} Z_i} \quad (12)$$

The dietary absorption efficiency of a chemical, E_D, is, in many cases, available from empirical observations. E_D is related to α_D and α_E. The same processes that produce a large α (e.g., long gut residence time, high surface area for absorption, high body temperature) will contribute to a high E_D. Thus, broad taxa (fish, birds, mammals) tend to have characteristic values of E_D for simple nonionic hydrophobic organic chemicals up to log K_{OW} values of approximately 7.5 that are not metabolized in the gastrointestinal tract (*27*–*30*). The ratio D_{BG}/D_{GB}, which reflects asymmetry in a chemical's gut-to-body exchange, appears to be approximately 1 in fish and possibly aquatic invertebrates. There is evidence that D_{BG}/D_{GB} can be somewhat less than 1 in birds (*28*). As part of this study, we will explore possible values for D_{BG}/D_{GB} in different taxa. Characteristic values of e and net growth efficiency for major taxa have been reviewed (*13*–*16*), and species-specific values are available in the literature for many taxa.

Methodology

General. To test the performance of the model to make estimates of the BMF values of poorly metabolizable sub-

stances in a range of taxa, we calculated BMF_{max} using published bioenergetic and chemical transport parameters. We then compared the model-calculated BMF_{max} to BMF values observed under field and laboratory conditions. Only poorly metabolizable substances were considered, to ensure that D_M can be assumed to be 0.

Biomagnification Factors. We compiled studies that reported chemical concentrations in both consumer and diet, measured under field or laboratory conditions. For invertebrates and fish, we included group I and II (i.e., poorly metabolizable) PCBs (*31*), mirex, and ∑DDT. For birds and mammals, we included group I PCBs, mirex, ∑DDT, and hexabromodiphenyl ethers. For two bird species, we included pentachlorodibenzodioxin, although it is metabolized to some degree. When congener-specific PCB values were not reported, we included homologue group sums for hexachloro- and higher chlorinated PCBs. When concentrations were reported on a dry-weight or wet-weight basis, we normalized to lipid content reported in the study (animals) or to a lipid equivalence value calculated from the biochemical composition of the diet (plants). Laboratory observations were included only if the authors reported that the chemical concentrations in the consumer were near steady state with those in the diet. If data were reported separately for males and females, we considered males only so that we could use net growth efficiency as a surrogate for net production efficiency. We used the geometric mean of reported or calculated BMFs for non- or poorly metabolizable substances as our estimate of the observed BMF_{max} for each species. A total of 169 BMFs from 35 published studies met the above criteria. These study results produced estimates of BMF_{max} for 35 species−age combinations, including 7 species of invertebrates (both aquatic and terrestrial), 6 species of fish, 9 species of birds, and 10 species of mammals (Table S1). For three species (great tit, ringed seal, wolf), we were able to estimate observed BMF_{max} values for both juveniles and adults.

Bioenergetics Parameters. We next compiled data to parametrize eq 5 for (i) all species−age combinations for which estimates of observed BMF_{max} were obtained and (ii) five additional taxa for which no measured bioaccumulation data appear to exist (wolf spider, python, oilbird, vampire bat, and insectivorous bat), to illustrate how our model can be used to make predictions of the BMF in unstudied taxa (Table S1). The only values required to parametrize eq 5 are the net production efficiency (e), the digestive efficiency (α), and the proximate composition of the species and its diet. We included fish in the model's performance analysis only if the study from which BMFs were obtained also reported enough information to estimate net growth efficiency. Fish growth is plastic within and among species (*32*), largely because of variation in the energetics of food acquisition (*33*). Growth efficiency varies between 30−35% for fish raised in captivity (*34*) and 10−20% in wild fish (*13*, *14*), but can approach 0 in lakes without appropriately sized prey (*35*). Only six of 32 studies reported the necessary data and are included in Figure 2 below. Data from the remaining studies are plotted in Figure S1 to illustrate the importance of access to accurate net growth efficiency data to correctly calculate BMF_{max} values in fish.

Chemical Transport Parameters. We used gross chemical absorption efficiencies (E_D) of 0.50 in fish (*25*) and invertebrates (*36*), 0.95 in birds (*28*), and 0.90 in mammals (*29*, *30*). To explore the role of asymmetry in gut/body chemical diffusion rates, we used values for D_{GB}/D_{BG} of 1 (*8*, *10*) and 3 (*11*).

Uncertainty Analysis. To assess the effect of error and uncertainty in the model input parameters on the calculated BMF_{max} values, we used Monte Carlo simulation ($n = 10\,000$). When multiple values were available for a model input parameter, we calculated a geometric mean (shown in Table S1) and coefficient of variation (CV) assuming a log-normal distribution. When only a single value was available, we assumed a CV equal to the mean CV of that parameter for all species with multiple values. In this way, distributions were generated for every parameter except E_D for each species used in the simulations.

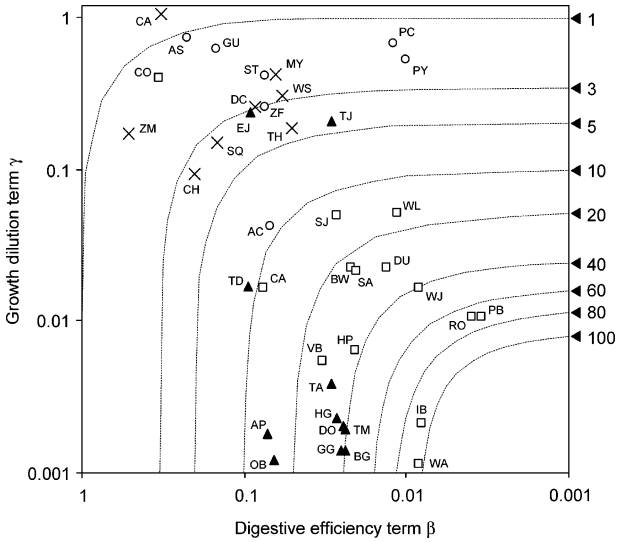

FIGURE 1. Predicted maximum biomagnification factors (BMF_{max}, dashed isopleths) for all realistic combinations of digestion efficiency (β) and growth dilution (γ) terms in eq 5 (see text for details). Symbols indicate where species in our validation set fall within this parameter space (×, invertebrates; ○, fish and reptiles; ▲, birds; □, mammals). Labels are AC, arctic cisco; AP, Adelie penguin; AS, Atlantic salmon; BG, black guillemot; BW, bowhead whale; CA, caribou; CA, caterpillars; CH, chaetognath; Co, cow; DC, dungeness crab; Do, dovekie; Du, dugong; EJ, common eider juvenile; GG, glaucous gull; Gu, guppy; HG, herring gull; HP, harbor porpoise; IB, insectivorous bat; MY, freshwater mysid; OB, oilbird; PB, polar bear; PC, polar cod; PY, python; RO, river otter; SA, ringed seal adult; SJ, ringed seal juvenile; SQ, squid; ST, three-spined stickleback; TA, great tit adult; TD, tufted duck; TH, marine mysid; TJ, great tit juvenile; TM, thick-billed murre; VB, vampire bat; WA, wolf adult; WJ, wolf juvenile; WL, walrus; WS, wolf spider; ZF, zebrafish; ZM, zebra mussel.

Results and Discussion

Model-Calculated BMF Values. Figure 1 shows isopleths of the BMF_{max} values predicted by eq 5 as a function of β and γ. In this general survey of parameter space, BMF_{max} is predicted to range from approximately 1 for species with inefficient digestion and highly efficient growth to greater than 100 for species with highly efficient digestion and negligible growth. Invertebrates, juvenile birds, and cows are predicted to have $BMF_{max} < 10$, whereas adult birds and wild mammals are predicted to have $BMF_{max} > 10$ and in some cases (e.g., adult wolves) approaching 100. Estimates of observed BMF_{max} values varied over a range similar to that of predicted values: from less than 1 in caterpillars to nearly 100 in adult wolves (Table S1). In general, invertebrates exhibited lower observed BMF_{max} values than birds and mammals. The exceptions were cows, juvenile birds, and clam-eating tufted ducks because of their low-fat diets and high growth efficiencies. Juvenile great tits, common eiders, and wolves showed lower observed BMF_{max} values than their adult counterparts because of greater growth efficiency at the juvenile stage.

Model Performance. Figure 2 compares model-predicted BMF_{max} values to observed BMF_{max} values for a range of taxa and animal life stages. Thirty of the 35 observed BMF_{max} values

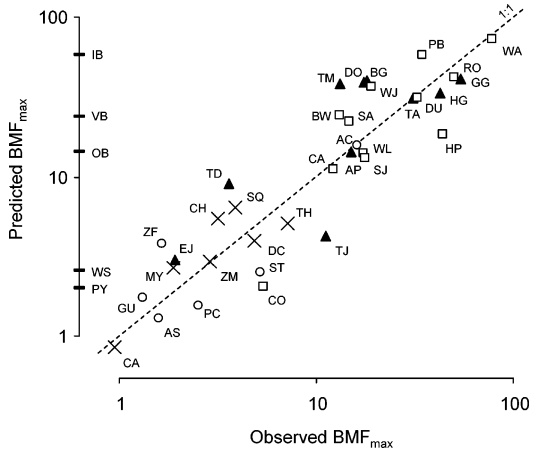

FIGURE 2. Predicted vs observed maximum biomagnification factors (BMF_{max}) for 40 species−age combinations. Symbols are as in Figure 1. Symbols on the *y* axis are species for which no observed BMF_{max} is available. Labels are defined in Table S1.

were within a factor of 2 of the model-calculated BMF_{max} values. All of the observed BMF_{max} values were within a factor of 3 of the model-predicted BMF_{max} values. The good fit between predicted and observed BMF_{max} values for nearly all species in the model performance evaluation supports our contention that bioenergetic efficiencies play a key role in the biomagnification process and are useful parameters for assessing the biomagnification potential of chemicals among taxa. Differences between calculated and observed BMF_{max} values might be due to errors in the model and uncertainty in model input parameters but might also originate from errors or uncertainty in observed BMFs. For example, inaccurate diet concentration, lack of steady state between consumer and diet, occurrence of metabolic transformation (e.g., pentachlorodibenzodioxin), and analytical error are model-unrelated factors that might cause discrepancies between observed and model-predicted BMF_{max} values in Figure 2.

We were unable to make predictions of BMF_{max} for most of the observed BMF values reported for fish because of insufficient data to estimate net growth efficiency. However, model calculations using net growth efficiencies ranging between 0 and 0.5 (Figure S1) produced calculated BMF_{max} values that encompass the range of values observed. Farmed and laboratory-reared fish showed low observed BMF_{max} values because of the high growth efficiency of animals with restricted activity and readily available food (*34*). Marine fish also exhibited low BMF_{max} values because of access to a wide prey base of energetically favorable items and, hence, efficient growth. Freshwater fish showed a large range of observed BMF_{max} values (between 1.2 and 45), possibly because prey assemblages vary greatly among freshwater systems, and this has important implications for the net growth efficiency of fish (*32*, *35*).

Asymmetry in Gut-Body Transport. Figure 3 illustrates model-predicted BMF_{max} values in relation to observed BMF_{max} values for $D_{GB}/D_{BG} = 1$ and 3, representing symmetry and asymmetry, respectively, in gut/body exchange rates. Assuming $D_{GB}/D_{BG} = 1$, eq 5 underpredicted observed values for some taxa, although the relationship between predicted and observed BMF_{max} values was highly significant (Table S2). Assuming $D_{GB}/D_{BG} = 3$ for all taxa or for birds and mammals only, model-calculated BMF_{max} values followed a highly significant 1:1 relationship with observed values across all species (Table S2, Figure 3). A model scenario using D_{GB}/D_{BG} values of 1 for fish and aquatic invertebrates and 3 for birds and mammals produced the best agreement (i.e., slope nearest unity, intercept near 0, high r^2) between observed

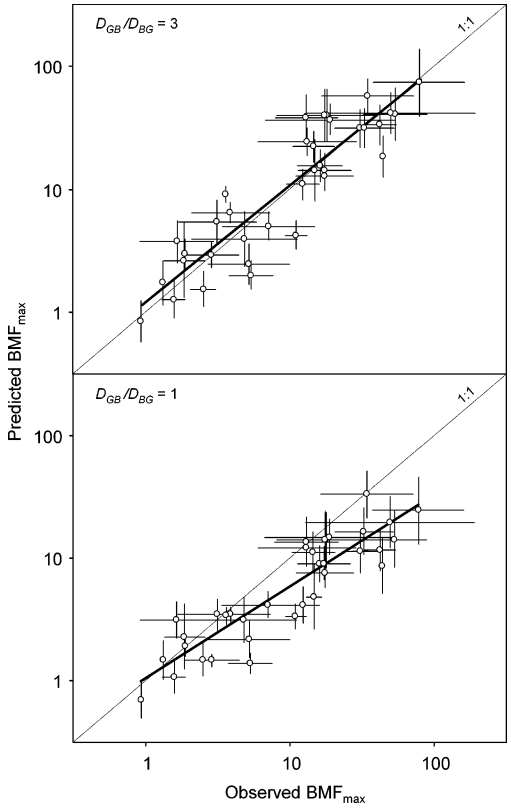

FIGURE 3. Predicted vs observed maximum biomagnification factors (BMF_{max}) for 40 species−age combinations, shown for two possible values of gut/body chemical transport asymmetry. Error bars are standard error of the mean. Equations and statistics for regression lines are shown in Table S2.

and predicted BMF_{max} values. These findings are consistent with the hypothesis that gut-to-body transport is faster than body-to-gut transport when expressed in terms of fugacity-based transport parameters and indicates that this asymmetry can be best expressed by a D_{GB}/D_{BG} value of 3 in birds and mammals. As the magnitude of the growth dilution term γ increases, the importance of gut/body asymmetry decreases.

Novel Predictions. Figure 2 also shows predicted BMF_{max} values for five taxa for which no measured bioaccumulation data are available. The species for which we make novel predictions of BMF_{max} illustrate several interesting parameter combinations. Wolf spiders and pythons are known to have very efficient digestion and might therefore be expected to have high BMF_{max} values. Spiders have extra-oral digestion; ingest only the most soluble, digestible components of their prey; and have very large midgut caecae to maximize nutrient absorption. Pythons have extremely long gut residence times and use basking to raise gut temperature and enhance digestion (Table S1), giving these snakes a digestion ratio, D_D/D_F, of approximately 100. However, spiders and pythons also have high net growth efficiency, and their predicted BMF_{max} values are consequently on the order of 2−3. Bats, on the other hand, have a very low net growth efficiency. Many bats are "energy-maximizers" (*37*) with extremely high consumption rates, but their high activity level allows them to maintain a favorable body mass for flight. Growth dilution is therefore less important for bats, whose BMF_{max} value is determined primarily by digestive efficiency. Vampire bats, adapted to a protein-rich diet, have low lipid digestive efficiency (Table S1) and, consequently, low (negative) α_Z. Insectivorous bats digest lipids very efficiently (Table S1), giving them a very high α_Z and thus a higher predicted BMF_{max}. Oilbirds (*Steatornis caripensis*) are ecologically similar to fruit bats, with high feeding rates and low growth

efficiency. However, oilbirds have a relatively low digestive efficiency for their lipid-rich fruit diet (Table S1). Fecal egestion is therefore an efficient elimination route, and the predicted BMF_{max} is relatively low for adult birds.

Bioenergetic Efficiencies vs Vital Rates. The model developed here is expressed in terms of bioenergetic efficiencies, and this allows for an examination of the effects on bioaccumulation of ecological traits such as growth strategy, thermoregulatory strategy, and prey availability. For example, it is clear from eq 5 that absolute growth rate has no bearing on BMF_{max}; it is the rate of growth *relative to other rates* that determines the magnitude of growth dilution. Our analysis highlights the strong influence of growth dilution on biomagnification in animals with high growth efficiency such as heterotherms, juvenile homeotherms, and domestic animals. Animals in captivity (e.g., in laboratory bioaccumulation tests or farms) are likely to have unnaturally high net growth efficiencies, giving these individuals a lower BMF_{max} value than wild individuals.

Equation 5 also sheds light on the role of feeding rate in bioaccumulation. Extrinsic factors such as prey abundance can influence feeding rate and, consequently, the rate of dietary intake of contaminants, but if this extrinsic factor has no effect on the bioenergetic efficiencies e and α, then egestion and growth vary in proportion to feeding, and the steady-state BMF_{max} value remains the same. A similar argument explains the generally higher BMFs observed in homeotherms than in heterotherms (e.g., *38*). Homeotherms have lower growth efficiencies and consequently higher BMFs because a substantial portion of their energy budget is devoted to homeothermy and activities required to ensure a minimum daily energy intake. Domestic mammals eat vastly more than wild snakes, but have similarly low BMFs, in part because their growth efficiency is inflated by low activity costs. High feeding rates in homeotherms might permit them to more rapidly approach a new steady-state BMF after a diet shift or change in energetic allocation (e.g., at maturation), but the level of that steady state is determined by digestive and growth efficiencies, not feeding rate.

Production Dilution: Offspring, Milk, and Slime. In parametrizing eq 5, we used net growth efficiencies to approximate net production efficiencies, and thus our predictions apply to males, juveniles, and nonreproductive females that have no important secretions (e.g., slime, milk, or silk). It is conceptually simple to extend the analysis to include all animals. The key is to consider the additional production (offspring or secretion) as analogous to growth. The additional production term(s) then produce "production dilution".

Production efficiencies for offspring and milk are much higher than growth efficiencies in wild adult mammals (e.g., *12*, *39*, but cf *17* for domestic mammals), which has the approximate effect of making a gestating or lactating female's steady-state BMF value closer to that of a juvenile. Females that accumulate fat reserves before breeding also have an elevated production efficiency during this period, although total production efficiency can be negative with respect to ingested energy while these stores are being depleted. When the female's "normal", pre-reproductive parameters are restored, her steady-state BMF returns to its previous, relatively high level. She might approach this level slowly, however, and a steady-state BMF model might not produce accurate predictions. Species with high feeding rates (e.g., bats, otters, kingfishers) and species that experience relatively small changes in growth or production efficiency during reproduction (e.g., invertebrates, fish, reptiles) will be most likely to return to steady state quickly.

The sorptive capacity of produced material will determine the magnitude of the effect of production dilution on the animal's BMF. Offspring and milk might have higher lipid contents than the female, and so, the effect of this efficient production on the steady-state BMF might be disproportionately large (*17*). Slime and silk probably have very low sorptive capacities, at least for hydrophobic chemicals, and so, secretion of these materials might represent a negligible elimination route.

The efficiency of chemical redistribution into the produced tissue must also be considered. Animal growth is usually slow enough that chemical redistribution can keep pace and newly produced tissue will be at equilibrium with the rest of the animal (e.g., *5*). However, if production of offspring or secretion is very fast relative to rates of chemical redistribution within the consumer's body, the produced material might not be at thermodynamic equilibrium with the consumer when it leaves the body (*40*, *41*).

Biomagnification of Other Chemicals. Notably absent from eq 5 is an expression for the chemical's properties, such as the octanol−water or octanol−air partition coefficients, K_{OW} or K_{OA}. This is the consequence of the simplifying conditions chosen to evaluate the model. The model calculates the maximum possible biomagnification in the absence of significant rates of elimination via respiratory exchange to water (controlled by K_{OW}) or air (controlled by K_{OA}) or metabolic transformation. The role of bioenergetics in the biomagnification process is the same for all chemicals. However, the extent to which the maximum biomagnification factor is attained is a function of the chemical's elimination and metabolic transformation rates, which are chemical-specific. The only exception is for E_D, which, at very high K_{OW} values, tends to drop with increasing K_{OW} (*27*). For the chemicals used in the current model evaluation, this drop is negligible.

Steady State. Equation 5 predicts the steady-state BMF_{max} of an animal and is therefore appropriate only for animals that are at or near steady state with their diets. Animals in laboratory experiments are often exposed to contaminants for short durations and might (if depuration rates are slow) not reach steady state during the exposure period. Wild animals, however, begin life with contaminant concentrations that already reflect the mother's diet. Early development can, in some cases, magnify the contaminant concentration as the juvenile absorbs yolk or lipid stores (*42*, *43*) or receives an additional contaminant load via milk (*5*). Upon commencing exogenous feeding, an animal begins to egest and grow and can rapidly attain its relatively low, juvenile steady state (*2*, *5*). As the animal approaches maturity, specific rates of feeding, egestion, and growth decline, and the steady-state BMF_{max} increases. If the change in these vital rates is large and rapid, the animal might spend a period of time below steady state with its diet. This is most likely to be an issue for birds (*1*, *2*) and possibly mammals (*5*). Juvenile invertebrates, fish, and other heterotherms undergo a slow, gradual change in specific vital rates and are more likely to maintain steady state with their diet (*1*). Other issues that could prevent an animal from reaching steady state include ontogenetic and seasonal diet shifts; seasonal lipid cycles; and other large, rapid changes in bioenergetic parameters. The issue of whether an animal is at steady state is key to assessing the utility of eq 5 and will be a fruitful avenue for future research.

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Supporting Information Available

Derivation of eq 1, biomagnification and bioenergetics parameters for taxa included in this study, effect of gut/body

transport asymmetry (D_{GB}/D_{BG}) on the relationship between predicted and observed log BMF_{max} values, and calculated maximum biomagnification factors as a function of net growth efficiency. This material is available free of charge via the Internet at http://pubs.acs.org.

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