

A Geometry of Regulatory Scaling

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ABSTRACT: Over recent years, data have accumulated for an ecologically and taxonomically diverse range of animals showing that the mechanisms of feeding regulation prioritize a balanced gain of multiple nutrients. This emerging generality calls for an approach, equivalent to multidimensional morphometrics in the field of evolutionary morphology, in which regulatory systems are represented in more than one dimension. We use geometry to provide a quantitative metric of such regulatory phenotypes, which enables us to empirically address the evolutionarily interesting question of how the parameters of regulatory systems reflect performance outcomes. First, we develop a parameter-efficient geometry characterizing regulatory scaling strategies in two nutrient dimensions. We then take empirical data from several species (insects, birds, and mammals, including humans) in which individuals were limited to one of a small number of diets varying in the balance of macronutrients, and we explore which metrics and scaling techniques best unite within a common descriptive framework their patterns of regulation. We next show how a similar approach might be applied in the context of equilibrium models of operant conditioning and briefly discuss the potential for integrating such an approach into evolutionary and ecological studies.

Keywords: nutrition, Euclidean metric, regulation, cost, Geometric Framework, operant conditioning.

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Understanding organismal integration requires approaches that quantify and integrate across multiple metrics of phenotypes (Wake and Roth 1989; Pigliucci and Preston 2004). In this regard, an important contributor to the successes of evolutionary morphology (Budd and Olsson 2007) has been the deployment of increasingly sophisticated morphometric techniques for quantifying and comparing across dimensions of physical form (e.g., Evans et al. 2007). In contrast, multivariable techniques for quantifying and integrating across components of behavioral and physiological phenotypes are severely lacking. Our general aim in this article is develop such a technique, in the context of data for feeding regulation, and to briefly explore its extension more broadly to cognition.

Behavior and physiology share as an important function the maintenance of internal state variables within defined bounds that correspond to positive fitness outcomes. A major advance in modeling homeostatic systems came with the implementation of control theory from engineering (Toates 1980; Huntingford 1984; Houston and Sumida 1985). However, such models do not deal comfortably with the fact that behavior and physiology must integrate multiple exogenous and endogenous stimuli, weight these appropriately, and deal with conflicts that arise between different state variables as they compete for access to the motor pathways controlling behavior. To deal with these aspects in the study of behavior, McFarland and collaborators developed a class of state-space models of animal motivation (McFarland and Sibly 1972; McFarland and Houston 1981). Although conceptually elegant, these models were operationally intractable because of the practical and conceptual difficulties with the family of concepts whose members include “motivation,” “drives,” and “behavioral tendencies” (Kennedy 1992).

More recently, a new generation of state-space models, known as the Geometric Framework (GF), has been developed specifically to deal with feeding behavior and nutritional regulation (Raubenheimer and Simpson 1993, 1997; Simpson and Raubenheimer 1993; Simpson et al. 2004). In the GF, an animal’s current nutritional state is represented as a point within an n -dimensional nutrient space, as are target states for intake, growth, and metabolism. Foods are represented as vectors determined by the

balance of nutrients each food contains (“nutritional rails”). As it feeds, the animal changes its nutritional state along the vector coincident with the chosen food. By selecting a nutritionally balanced food, a consumer can reduce to zero any discrepancy between current state and optimal state. A nutritionally imbalanced food, by contrast, does not enable the animal to satisfy its optimal intake requirements for all nutrients simultaneously but forces it into a compromise between overingesting some nutrients and underingesting others and bearing the associated costs. The animal can nonetheless achieve its intake target when eating a nutritionally imbalanced food if it mixes its intake from this with a food containing a complementary imbalance of nutrients (i.e., one whose rail falls on the opposite side of the intake target in nutrient space). When neither nutritionally balanced nor complementary foods are available, the animal cannot reach its nutrient intake target. The challenge in this case is to arrive at a compromise between over- and underingestion that minimizes the costs of this predicament. Numerous experimental studies using the GF have shown that animals as diverse as insects, spiders, fish, rodents, and birds have the capacity to regulate intake of protein and nonprotein energy (fat and/or carbohydrate) to an intake target when challenged with different pairings of complementary foods or dilution of the diet with indigestible bulk or after a period of confinement to an imbalanced diet (e.g., Raubenheimer and Simpson 1997; Simpson and Raubenheimer 2000; Mayntz et al. 2005; Raubenheimer and Jones 2006). The position of the intake target depends on prevailing and past environmental conditions, and the animal’s phylogeny, ecology, and developmental stage. Animals also differ both within and between species in their propensity to eat too much of some nutrients and too little of others, relative to the intake target, when confined to imbalanced diets (Simpson et al. 2002; Raubenheimer and Simpson 2003; Simpson and Raubenheimer 2005; Lee et al. 2006).

Among the key issues arising from state-space models of behavior is the question of how the multiple causal axes scale relative to one another in terms of fitness. In the simplest case, a scaling of 1 : 1 in a protein-carbohydrate nutrient space would mean that 1 unit of protein intake was weighted by natural selection similarly to 1 unit of carbohydrate intake, whereas the scaling would be 2 : 1 if one nutrient were twice as important as the other. Simpson et al. (2004) derived an empirical solution to this problem by confining caterpillars to one of a range of points in outcome space (points of nutrient intake), measuring the performance consequences associated with being at each point, and then using these values to model a fitness landscape from which actual costs could be derived and related to points of intake. This approach was implemented to

quantify the relationship between nutrition, longevity, and reproduction in a recent study on *Drosophila* (Lee et al. 2008).

In addition to fitness scaling, a second important question that arises in state-space models of behavior is how the animal itself scales the multiple causal axes relative to each other in terms of its regulatory priorities. In the simple case where the animal has access to foods that enable it to orthogonally regulate its position on the various axes, the scaling is given by the proportion of the nutrients that it elects to eat. However, in reality, animals are frequently confronted with the more challenging situation where available foods are to some extent imbalanced relative to requirements and do not enable the intake target to be reached. In this case, the regulatory systems must achieve an appropriate balance, not between the intake of the nutrients per se but between the discrepancies (excesses and deficits) of these nutrients relative to the regulatory target.

Our aim here is to develop a geometric approach for deriving the regulatory scaling factor for this more complex scenario, where animals are constrained to balance discrepancies between conflicting nutrient requirements. We take as a baseline the geometric configuration of intake points that would minimize the deviation from the intake target if the nutrients were treated as equals by the regulatory system and derive the scaling factor as the transformation between this and the observed array of intake points. Such a scaling factor provides a quantitative metric of regulatory phenotypes, which is of considerable interest in its own right. It also enables us to empirically address the evolutionarily interesting question of how the parameters of regulatory systems reflect performance outcomes and underlying fitness cost structures (Simpson et al. 2004).

Finally, a quantitative metric of behavioral regulation is needed to answer the call for biologically realistic organism-level parameters that can transfer the extraordinary predictive power of homeostatic systems to ecological models of community-level processes (Raubenheimer and Simpson 2004; Kearney and Porter 2006). The utility of this approach has been proven in the field of ecological stoichiometry, where the simple characterization of homeostasis as constant elemental body composition has facilitated the integration of organism- and ecosystem-level processes (Elser and Hamilton 2007). It has yet, however, to be extended to the more complex and more ecologically salient (Real 1992) case of behavioral regulation.

We begin by developing a parameter-efficient geometry that can be used to characterize regulatory scaling strategies. We then take nutrient intake arrays from several species in which individuals were limited to one of a relatively small number of diet compositions and explore which metrics and scaling techniques best unite these ar-

rays from different species within a common descriptive framework. Finally, we show how a similar approach might be applied in the context of equilibrium models of operant conditioning.

Geometry

We derive measures of distances based on linear and quadratic cost structures for ingested excesses and deficits of two nutrient dimensions as outlined by Simpson et al. (2004) and then use the metrics to fit chosen sets of data. For measures of the distance of a consumption pattern from the intake target point, we used two metrics. As we explain more fully in “Discussion,” the city-block metric corresponds to linear costs, while the familiar Euclidean metric corresponds to quadratic costs. The city-block metric computes distances by adding discrepancies separately for each dimension. The Euclidean metric uses the familiar formula for calculating the straight-line distance between two points on the plane, squaring the deviations in each dimension, and then taking the square root. Each case that we modeled contains two nutritional dimensions. For scaling purposes, a weighting parameter, called *W*, is required; it is a multiplier applied to discrepancies along the *X*-axis. It basically compares the cost of a unit of discrepancy along the *X*-axis relative to a unit of discrepancy along the *Y*-axis. Our equations for computing the distance between points (x_1, y_1) and (x_2, y_2) then, are

$$\text{city-block metric } D = W|x_1 - x_2| + |y_1 - y_2|,$$

$$\text{Euclidean metric } D = [W(x_1 - x_2)^2 + (y_1 - y_2)^2]^{1/2}.$$

Details are in appendix A, and proofs and derivations are in appendix B; both appendixes are available in the online edition of the *American Naturalist*.

Figure 1 shows signature patterns of rail data demonstrating the use of city-block and Euclidean metrics in minimizing the distance to the target, for selected target points and weighting factors (*W*). Geometrically, a rail is represented by a straight line of a given slope from (0, 0) into the top right quadrant. The animal is forced to “travel” on a rail when the proportion of nutrient *x* to nutrient *y* is fixed. A signature pattern for the city-block metric is that the animal defends mostly either one or the other target level. This is represented by a vertical line at the target level for *x*, or a horizontal line at the target level for *y*. With increasing slope of rails, an abrupt switch takes place from defending one nutrient to defending the other. With a Euclidean metric, the locus of points minimizing the distance to the target forms an ellipse.

In some cases, adding an extra process, in the form of an interaction term linking the two nutrient dimensions

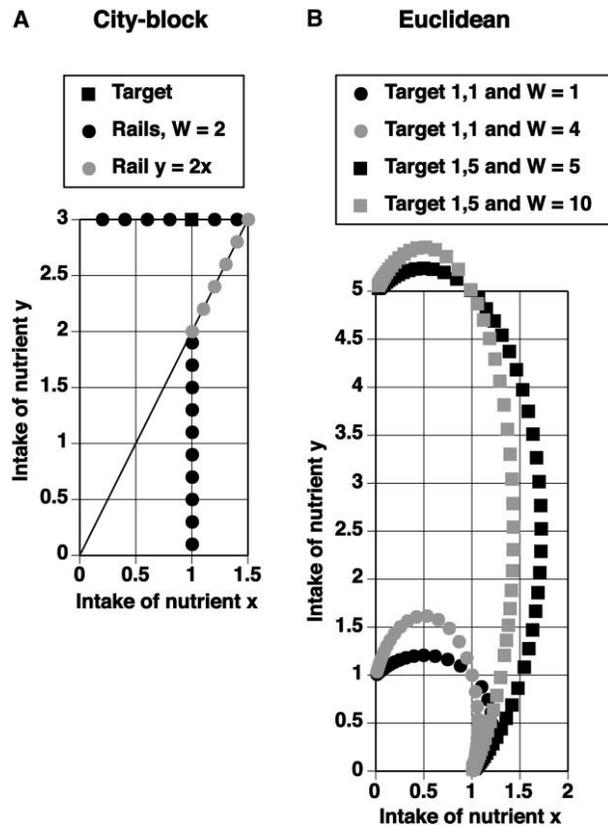


Figure 1: Predicted patterns of nutrient intake (*X*-axis is intake of one nutrient; *Y*-axis is intake of another) on nutritional rails according to rules of minimizing the city-block (*A*) or Euclidean (*B*) distance to the target. The *W* represents the weight given to the *x* dimension relative to the *y* dimension. Each point represents a nutritional rail along which the ratio *x* : *y* is fixed. In eating a diet of this composition, the animal travels along this rail from (0, 0) into the top right quadrant. Graphically, a rail is a line through (0, 0) with a fixed slope. For the city-block metric, if the rail slope is 2, which is also the value of *W* in the example, all the points (gray) between (1, 2) and (1.5, 3) are equally minimal in distance from the target. For the Euclidean metric, if the target point is much higher in the *y* dimension than in the *x* dimension (the target [1, 5] in the figure), then *W* needs to be very large to keep *x* from deviating too much from its target in proportional terms. This is especially so for deficits in *x*.

(Simpson et al. 2004; their figs. 2*d*, 3), fits the data better, sometimes much better. An interaction term indicates that the costs of ingested deficits of either nutrient are ameliorated by a surplus of the other. The explanation given by Simpson et al. (2004) was that nutrients *x* and *y*, protein and carbohydrates in both cases, are to some degree (but not totally) substitutable for one another. What this means is that excess protein can partially make up for deficits in carbohydrates and excess carbohydrates can partially make up for deficits in protein. The former can occur through deamination of protein and use of the remaining carbon

skeleton, whereas the latter is possible only through surplus carbohydrate sparing any use of limiting protein for energy metabolism, since carbohydrate, unlike protein, is not a source of dietary nitrogen. For the Euclidean metric, the effect of partial substitutability is to “unbend” an ellipse outward toward the straight line through the target point with a slope of -1 , which represents the limiting case of complete substitutability (app. A). Another geometric technique can be used for the “unbending,” and that is to rotate the axes by 45° and fit the data with an ellipse through the rotated target. We prefer to use our parameter of substitutability, b , because the biological interpretation of substitutability is much clearer than that of rotated axes of nutrient consumption. For the city-block metric, with $b = 0$ and $W = 1$, the locus of points minimizing the distance to the target parallel the axes and meet at the target. As b increases, the angle at which the two line segments meet increases until, with $b = 1$, they too form a straight line of slope -1 through the target (app. A).

Data Sets

Six published data sets were fitted: three on locusts and one each on chickens, mink, and humans. Each data set examined the balance of intake between two kinds of nutrients: protein versus carbohydrates (three cases), a near-balanced complement of protein and carbohydrates versus salt (one case), and protein versus carbohydrates and fats combined (two cases). We chose these data sets for a number of reasons. First and foremost, together they illustrate all the principles discussed in “Geometry.” Second, for each set, we could estimate a target intake. As discussed above, this means the amount and, importantly, proportions of relevant nutrients consumed by the animals given free choice over a range of foods. For nonhuman data sets, the free-choice condition was included in the studies. For humans and their consumption of protein versus carbohydrates and fats combined, we used a target proportion of 15% protein, based on existing literature (see Simpson and Raubenheimer 2005). Third, except for humans, each data set comes from a single study, which means that the target intake was obtained under conditions similar to those for the data on nutritional rails, making the entire data set comparable. For humans, we needed to pool data across studies to obtain sufficient numbers of nutritional rails. Fourth, the data sets represent a range of species, living conditions, and nutritional ecologies.

Curve-Fitting Procedure

We aimed to minimize the number of free parameters used in any stage of curve fitting. This makes the procedure both easier and less arbitrary. The target position was es-

timated first, by adjusting its position along the rail on which it sits. For the human data, we chose the data point closest to 15% protein (by kJ) as the target.

For a city-block fit, the data points had to parallel the X and Y axes. We did not have to choose any free parameters for curve fitting. For a Euclidean fit, the weighting factor W had to be chosen; we estimated it to three decimal places. In two cases from locusts, including the parameter of intersubstitutability b led to better fits; in one case, the fit was much better. In the human case, a single ellipse resulted in systematic errors. We then fitted the data with two ellipses, one for protein deficits and one for protein excesses, relative to the chosen target. Each had its own estimated W . Details are in appendix A.

Fits of Data

Chickens, Protein vs. Carbohydrates: Single Ellipse

The first data set came from layer hens (Shariatmadari and Forbes 1993), as replotted in Raubenheimer and Simpson (1997). Four data points on nutritional rails of fixed protein to carbohydrates ratio and a target intake were obtained in the study (fig. 2). The rail data were fitted with

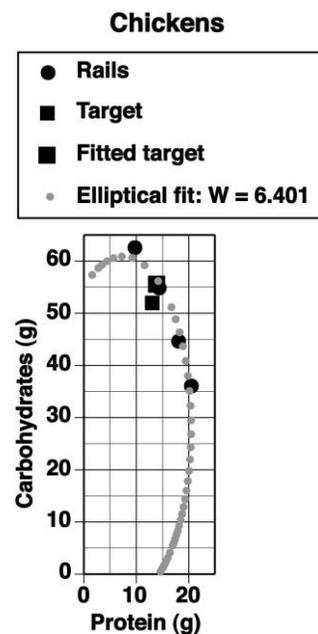


Figure 2: Euclidean fit of data from chickens. The data set contained a regulated target point and four points on nutritional rails. The rail data were fitted with a quadratic function (not shown) to determine a fitted target. The data were fitted by a single ellipse, with W representing the weight given to protein relative to carbohydrates. Hence, chickens weight deviations in protein intake from the target highly relative to carbohydrate deviations.

Table 1: Parameters and residuals (square root of mean squared error) for the data sets fitted using a Euclidean metric

Data set	Unit	Target	W, b	Residual	Proportion residual
Chicken	Gram	57.3	6.401	1.282	.022
Mink	Kilojoule	4,982.7	1.874	69.084	.014
<i>Locusta</i> (salt vs. P and C)	Milligram	104.5	1,000	4.743	.045
<i>Locusta</i> (P vs. C):					
Ellipse	Milligram	165.0	.792	7.303	.044
Partial substitutability	Milligram	165.0	1, .069	4.867	.029
<i>Schistocerca</i>	Milligram	149.0	1, .760	6.647	.045
Human:					
Protein deficit	Kilojoule	8,492.6	53.489	.937	.000
Protein excess	Kilojoule	8,492.6	11.427	1,364.144	.161
Combined	Kilojoule	8,492.6		393.795	.046

Note: The proportion residual is obtained by dividing the residual by the target length. The target length (|Target|) is the Euclidean distance from the fitted target point to (0, 0). P = protein; C = carbohydrate. W indicates the weighting factor for the nutrient indicated on the X-axis relative to that on the Y-axis; b is the parameter of substitutability between nutrients on X and Y axes.

a quadratic curve (not shown), which provided an excellent fit. For this data set, the city-block metric does not fit well. The data points do not go through a vertical or horizontal line through the target point. For the Euclidean metric, however, the data were fitted well, without systematic errors, with a single ellipse with $W = 6.401$ (fig. 2; table 1). This means that errors in protein measured in grams (or energy units, since protein and carbohydrate are of similar energy density) are weighted more than errors in carbohydrates.

Mink, Protein vs. Fats and Carbohydrates: Single Ellipse

The next data set came from mink, a carnivorous mammal (Mayntz et al., forthcoming). Because fats have a substantially different energy density (kJ g^{-1}) from proteins and carbohydrates, nutritional units were measured in energy (kJ) rather than mass. Five data points on nutritional rails of fixed protein : fat and carbohydrate were obtained, along with a target intake based on four different pairs of nutritionally complementary foods (fig. 3). The rail data again could be fitted excellently with a quadratic curve (not shown).

For this data set as well, the city-block metric does not provide a good fit, while the Euclidean metric does. Once again, the data points do not go through either a vertical line or a horizontal line through the target point. In contrast, the data were fitted well with a Euclidean metric, without systematic errors, with a single ellipse with $W = 1.874$ providing the best fit (fig. 3; table 1). While protein, in energy terms, is weighted more than fats and carbohydrates, the weighting is quite a bit lower than that found for chickens.

Locusta migratoria, Protein and Carbohydrates vs. Salt

The third data set came from the African migratory locust *Locusta migratoria* and pitted the intake of macronutrients (protein and carbohydrates combined) against the intake of salt (Trumper and Simpson 1993). Data along four nutritional rails were obtained along with a strongly regulated target intake (fig. 4). The rail data were fitted with a straight line by standard regression technique (not

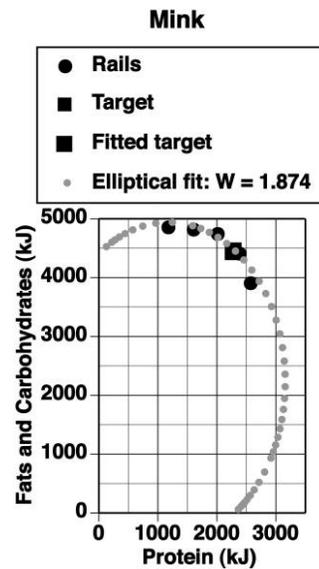


Figure 3: Euclidean fit of data from mink, fitted with the same procedure used for figure 2. The data set contained a regulated target point and four points on nutritional rails. The weighting factor W indicates that mink weight deviations in protein intake from the target higher relative to carbohydrate deviations.

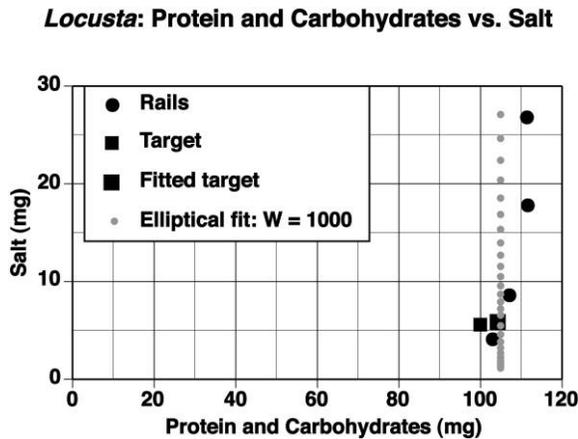


Figure 4: Euclidean fit of data from *Locusta*. The data set contained a target point and four points on nutritional rails. The rail data were fitted with a straight line by standard regression techniques to determine a fitted target (not shown). The data were fitted by a single ellipse, with W representing the weight given to protein and carbohydrates combined, relative to salt. The fit approximates a straight line defending the macronutrients. Given the data set, the best-fitting W would be infinite, but $W = 1,000$ provides a close approximation.

shown). The slope through the data is slightly positive, but a vertical straight line through the target point would provide a reasonable fit. This data set can be fitted by either metric. A vertical line through the target is a possible pattern for the city-block metric. For the Euclidean metric, the best fit of the transformed data would have W at infinity. A fit using $W = 1,000$ is illustrated in figure 4 and table 1, and it can be seen that both the data and the fit approximate a vertical straight line. This shows that with a very large (or very small) W , the Euclidean fit approximates a straight line. With either metric, it also means that *Locusta* basically defends macronutrient intake against fluctuations in the content of the micronutrient salt when confined to a single food. It is important to emphasize that this does not mean that salt intake is unregulated. When the locust can choose between complementary foods, the intake level of salt is clearly regulated, along with macronutrient intake. The target point shows this. It is the case, however, that precedence is given to minimizing deviations in macronutrient intake.

Locusta migratoria, Protein vs. Carbohydrates:
Single Ellipse

The fourth data set was from the same species (Raubenheimer and Simpson 1993; Chambers et al. 1995). Five different nutritional rails of fixed protein : carbohydrate ratio and a tightly regulated target intake were obtained (fig. 5). We excluded one rail at 0% carbohydrates because

no animal survived on this diet, thus marking it as pathological. In fitting the data from rails, a spline, drawn in DeltaGraph, was used (not shown). The intersection of the target rail and the spline was measured using a graphics package. As in the case of the mink, the city-block metric does not fit the data well because the data points deviate from the vertical and horizontal lines through the target point. A Euclidean metric, however, fits the data well, with a single ellipse with the scaling factor $W = 0.792$ providing the best fit (fig. 5; table 1). A weighting factor of less than 1 indicates that the locusts weighted deviations in carbohydrates a little more than deviations in protein by weight.

The deviations from the fit are larger than those in figures 2 and 3. And it is possible that the errors are systematic, in that a fitting procedure that “unbends” the ellipse a little might fit better. We identified this process as arising from partial substitutability between the nutrients. That is, to a small extent, the locusts can balance a

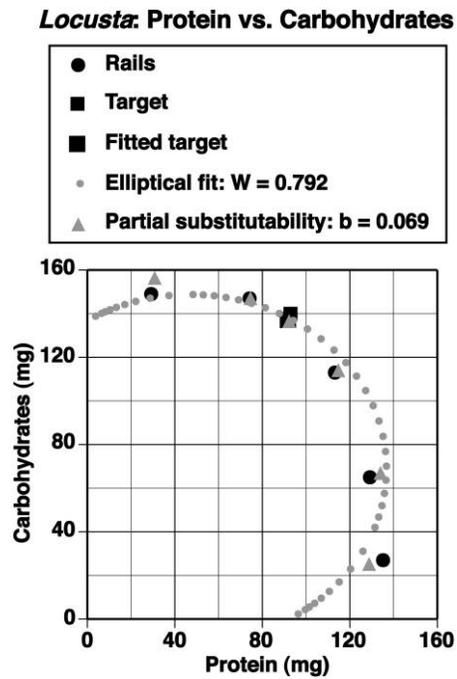


Figure 5: Euclidean fit of data from *Locusta*. The data set contained a target point and five points on nutritional rails. The rail data were fitted with a spline (not shown) to determine a fitted target. The data were fitted in two ways: (1) by a single ellipse, with W representing the weight given to protein relative to carbohydrates, and (2) with W fixed at 1 and an assumption added that proteins and carbohydrates are partially substitutable for one another, with b representing the degree (proportion) of substitutability in both the protein-carbohydrate and the carbohydrate-protein directions. As shown in table 1, the partial-substitutability model provides a better fit.

deficit in one dimension (e.g., carbohydrates) with an equivalent amount of excess in the other dimension (e.g., protein). Geometrically, we needed a parameter of inter-substitutability, b ($0 \leq b \leq 1$), which represents the extent to which the two nutrients are functionally interchangeable (app. A). We fixed $W = 1$, and the best fit shown in figure 5 does an excellent job of fitting the data, somewhat better than the ellipse (table 1). The parameter b was small, indicating that *Locusta migratoria* has little ability to ameliorate a shortage of one nutrient with an excess of the other (see below).

Schistocerca gregaria, Protein vs. Carbohydrates

Schistocerca is a generalist that feeds on many kinds of plant foods. Data were obtained on five nutritional rails of fixed protein : carbohydrate ratios, along with the target intake (Raubenheimer and Simpson 2003; fig. 6A). The rail data were fitted with a straight line that minimized the sums of squares of errors (in effect, Euclidean distances) measured along rails, yielding a best-fitting slope of -0.909 . Other fitting methods, standard regression (which measures errors along the Y-axis) and the use of a principal axis (which measures errors as perpendicular distances from data points to the line of fit), delivered similar estimates of slopes.

The data clearly cannot be fitted well with a city-block

metric. The points deviate a good deal from vertical and horizontal lines going through the target point. Using the Euclidean metric, we tried fitting the data with a single ellipse (not shown). The fit was not good, with systematic errors in the rails with protein deficit (points with $x < x_c$). A double ellipse still did not fit well (fig. 6A).

The data points approximated a straight line through the target with a slope of -1 . This is a clear sign of inter-substitutability. If two nutrients are totally substitutable for one another, then it is only the total amount of the two nutrients and not their relative proportions that matters. The geometric representation of a fixed total is a straight line with a slope of -1 . A pattern close to a line of slope -1 thus suggests a good deal of substitutability. But note that in this case, we can rule out total inter-substitutability. If that were the case, the locusts should be indifferent to which point they reached along the line of slope -1 . This is not the case; when given complementary food pairings, they regulate to one target point (Raubenheimer and Simpson 2003). Partial substitutability, however, allowed us to provide a geometric fit to the data. Again fixing $W = 1$, the best fit using the Euclidean metric, with $b = 0.760$, does an excellent job of fitting the data (fig. 6B). In this case, b cannot be estimated accurately. A large range of values of b produced similarly good fits. The residual for the best fit was 6.647, but values of less than 7.0 were found for values of b ranging from 0.6

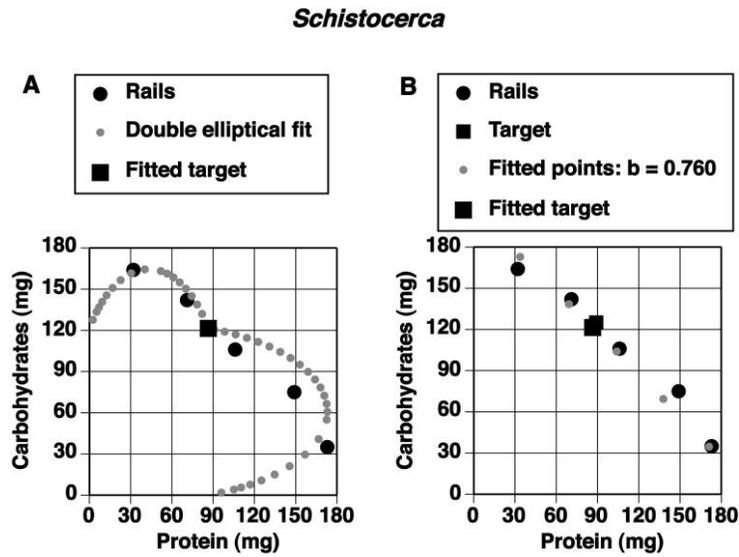


Figure 6: Euclidean fit of data from *Schistocerca*. The data set contained a target point and five points on nutritional rails. The rail data were fitted with a straight line that minimized the square of distances between data and fitted points along each nutritional rail (not shown). The fitted target was determined from this fitted line in both panels. A, Two different ellipses were drawn through the fitted target, one to account for rails with protein deficit and one to account for rails with protein excess. The rails with protein excess are not well fitted by the ellipse. B, Fitted points were derived with the assumption that proteins and carbohydrates are partially substitutable for one another, with b representing the degree (proportion) of substitutability in both the protein-carbohydrate and the carbohydrate-protein directions. This model fitted the rail data well.

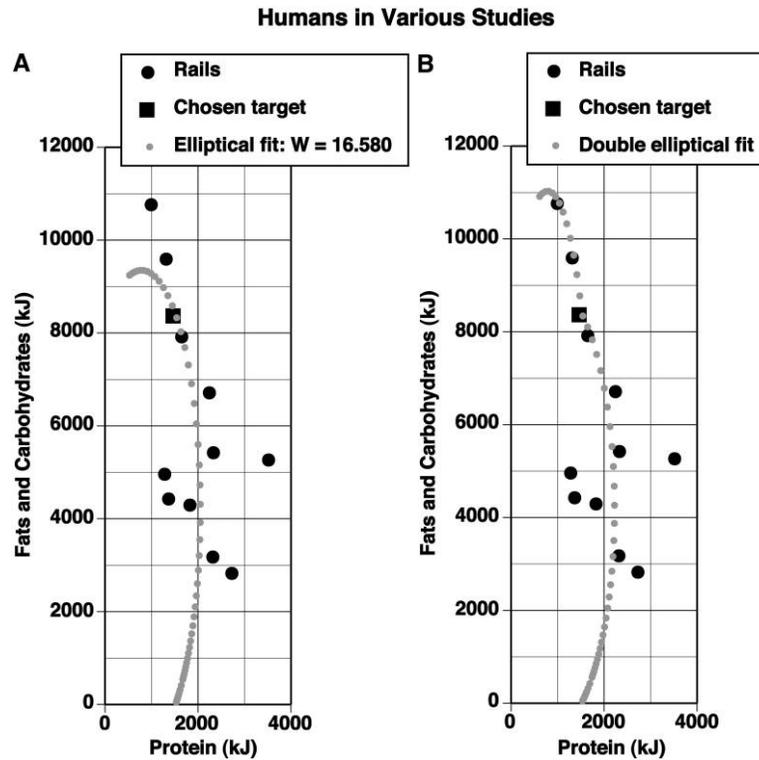


Figure 7: Euclidean fit of humans from various studies. Each data point represents one condition in one study. The data point closest to 15% protein was chosen as the target. The data were first fitted with a single ellipse (A). Because errors in the fit were systematic for data points representing protein deficit, the data were then fitted with a double ellipse, with $W = 11.427$ for protein excess and $W = 53.489$ for protein deficit (B). Humans in this cross-studies analysis weight protein heavily, especially in the case of protein deficit.

to 1.0. The city-block metric can also be used to fit the data, with a best-fitting residual error of 6.233, measured as city-block distance. But the best-fitting value for b was 1. This value is biologically unrealistic because it would imply indifference between the two nutrients and predict that the locusts would not regulate to a single target point.

The fact that the size of b was greater for *Schistocerca* than for *Locusta* is supported by results indicating that *Schistocerca* has a greater capacity to retain protein for growth on low-protein, high-carbohydrate diets than does *Locusta*, and it appears to possess a greater ability to utilize excess protein as an energy source under conditions in which carbohydrate is limiting but protein is in excess (Raubenheimer and Simpson 2003).

Humans, Protein (kJ) vs. Carbohydrates and Fats (kJ): Double Ellipse

The final data set came from a collage of studies (taken from Simpson and Raubenheimer 2005, with addition of subsequently published data from Weigle et al. 2005) in which subjects were both given free choice and forced onto

rails. One data set had subjects consuming 15% protein, which is close to the population average from many studies (see Simpson and Raubenheimer 2005), and this was chosen as the target (fig. 7). This data set is somewhat noisy, probably because the data came from multiple studies with different sample populations and different methodologies.

For the city-block metric, the best fit (not shown) would be a vertical line through the target point for all points except the topmost data point. When measured along rails, this last point is closer to the horizontal line through the target than to the vertical line through the target. The fit is not good as the mean error is large; measured as city-block distance along rails, it is 1,964.9 kJ, or 0.200 of the target distance from (0, 0), also measured in city-block fashion. More pertinently, the errors are systematic. On the rails with protein excess, the consumption of protein exceeds the target protein consumption, whereas the prediction from using a city-block metric is that they should equal the target level of protein consumption. In kJ of protein consumed, the 95% confidence interval about the mean of the rails with protein excess exceeds the target value of 1,475.9 kJ.

Turning to the Euclidean metric, a fit with a single ellipse (fig. 7A) was poor, with systematic underprediction in the case of protein deficits. This suggests that the costs of protein deficits versus excesses are different, a theoretical possibility raised by Simpson et al. (2004; see their fig. 2C), calling for a fit with two separate ellipses, one for protein excess and one for protein deficits. Indeed, a double-elliptical fit provided a much better fit to the data (fig. 7B; table 1). For protein excess, $W = 11.427$, not too far from the corresponding value in the single-elliptical fit (16.580). This is not surprising, because most of the data points are on rails with protein excess. For protein deficits, $W = 53.489$, a much larger figure. Hence, this cross-study compilation shows that humans weight protein heavily, especially in the case of protein deficits. The results and analysis support the claim that protein acts as a strong lever in human energy intake (Simpson and Raubenheimer 2005).

Discussion

We have developed a geometry for characterizing the interactions between nutrient components of feeding regulatory systems and compared for several data sets different metrics of multidimensional minimization. To summarize the curve fitting, of the six data sets, only two—*Locusta*, salt versus protein and carbohydrates, and *Schistocerca*, protein versus carbohydrates—can be fitted well with the city-block metric, whereas all six can be fitted well, without systematic errors, with the Euclidean metric. One data set in particular, from *Schistocerca*, required an assumption of partial substitutability between the two nutrients. That is, excesses in one nutrient can make up in part a deficit in the other nutrient. Four of the data sets (chickens; mink; *Locusta*, protein vs. carbohydrates; and humans) show the signature elliptical or double-elliptical patterns of the Euclidean metric, although in the case of *Locusta*, protein versus carbohydrates, we found that the assumption of a small degree of intersubstitutability led to a better Euclidean fit. The two other cases approximated straight lines. None of the data sets show the signature pattern for the city-block metric, that is, a pattern of data forming two straight lines perpendicular to one another. Empirically then, the Euclidean metric provides a much better fit for the extant data.

We can find a good theoretical reason why the Euclidean metric fits the data from studies imposing nutritional rails on animals. It arises from the fact that the Euclidean distance measures deviations as sums of squares, with different dimensions appropriately weighted (our weighting factor W). We suppose that any distance from the target point represents a cost and that an animal will have evolved mechanisms to eat available foods to minimize this cost.

The question that then arises is how the cost relates to distance from the target point. What is the function that relates discrepancies along each dimension to the total cost? City-block and Euclidean metrics deliver different answers to this question. The city-block metric represents a weighted sum or linear combination of the discrepancies along each dimension. Implicit in the city-block metric, then, is the assumption that costs rise linearly with discrepancy in each dimension. Under the Euclidean metric, on the other hand, the animal attempts to minimize the sum of squares of discrepancies, again in a weighted fashion. Implicit in the Euclidean metric, then, is the assumption that costs rise in an accelerating curve characteristic of quadratic functions with a positive quadratic term, that is, with a positive parameter for the x^2 term.

Minimizing discrepancies as measured by a Euclidean metric, then, makes sense if the cost rises in an accelerating fashion with discrepancies from a target or ideal level. Therefore, we suggest that such an accelerating cost structure in patterns of nutritional discrepancies leads to the good fits according to a model of the minimization of Euclidean distance from the target. Although we have not shown the data, other metrics representing accelerating cost structures can also fit the data well (app. A).

Might this geometric approach be extended to other behavioral choices? A similar conception of a regulatory target has been proposed for animal learning in discussions concerning what a reinforcer is (Timberlake and Allison 1974; Mazur 1975; Staddon 1979; Hanson and Timberlake 1983). The concept of the reinforcer changed from a set of drive-reducing items (food, water, etc.) to an equilibrium in the allocation of behaviors. This is analogous to a shift from considering the reinforcer as belonging to the “causal factor space” to its existing within the “behavioral tendency” space in McFarland and Sibly’s state-space models of motivation. A major step in the history of this change came with Premack’s principle that a behavior of higher probability can serve as a reinforcer for a behavior of lower probability (Premack 1959). This means that the same behavior can be a reinforcer or an instrumental response, depending on which behavior was more probable. Premack (1962) demonstrated that rats can be trained to run in a wheel for the opportunity to drink or drink for the opportunity to run in a wheel, depending on which behavior was deprived before a session. The deprived behavior became the more probable behavior and thus served as a reinforcer.

The notion of a behavioral equilibrium, variously called set point or bliss point, extends Premack’s principle (Staddon 1979; Hanson and Timberlake 1983). The behavioral equilibrium is analogous to the target intake point in the Geometric Framework. In fact, our intake target point can be taken as an instance of a behavioral equilibrium. Sim-

ilarly, a training schedule or contingency of reinforcement can be thought of as a behavioral rail. An animal must do too much (more than ideal) of one behavior (the operant) in order to obtain optimum amounts of another behavior (the reinforcer). Premack's principle is extended because even the less probable behavior can reinforce (increase the amount of) the more probable behavior under the right circumstances. If the schedule requires higher than ideal levels of the more probable behavior in order to obtain ideal levels of the less probable behavior, then the less probable behavior would serve as a reinforcer for the more probable behavior. This was demonstrated experimentally in drinking and wheel running in rats (Mazur 1975). Even though the rats drank more than they ran, when the drinking requirements were high enough, the rats would drink more than they would under unconstrained conditions in order to obtain more running.

The principle of minimizing Euclidean distance to the target point has been proposed for operant conditioning by Staddon (1979), who did not consider any other formulas of distance. And Hanson and Timberlake's (1983) regulatory model can lead to predictions close to Staddon's (1979) model under special circumstances. Some data sets do turn out to have nearly elliptical shapes, two examples of which are shown in figure 8.

However, operant data contain complications that can make the model we have proposed for nutritional choices unsuitable. One factor identified and modeled by Staddon (1979) is other behaviors, which we have ignored. A typical behavioral rail in operant conditioning requires significant amounts of operant behavior to obtain items to consume. This reduces time for all other behaviors, which might also have a nonzero equilibrium or target level. Incorporating constraints from other behaviors can skew the ellipse to the left (Staddon 1979). The data points in figure 8B might well be showing this systematic skew. We have ignored other behaviors in the cases of nutritional rails for good reason. Nutritional targets are usually defended against dilution of caloric density—sometimes to an extraordinary degree, such as the fivefold increase in consumption shown by locusts in response to an equivalent dilution of the diet with indigestible fiber (Raubenheimer and Simpson 1993). Such dilution forces the animal to literally eat into time for other activities in order to reach the target point. Data show that the target is nevertheless well defended (Raubenheimer and Simpson 1997; Simpson and Raubenheimer 2000; Mayntz et al. 2005; Raubenheimer and Jones 2006), suggesting that under the experimental conditions in which the data are gathered, other behaviors can be neglected in modeling.

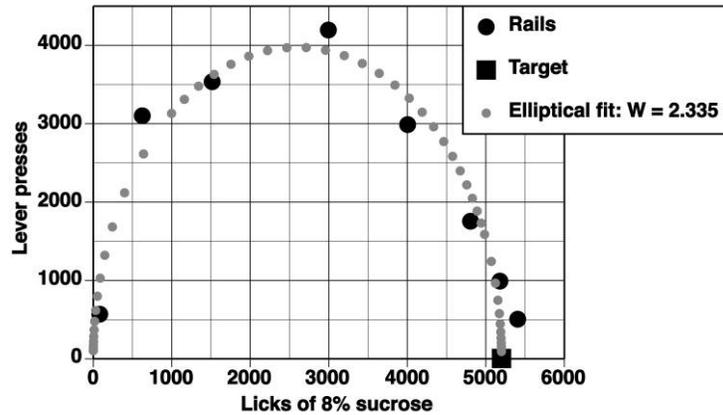
Another complication is the relation between the equilibrium levels of behaviors obtained under unconstrained conditions and the locking of behaviors into fixed allot-

ments of time or numbers in behavioral rails. For instance, Mazur (1975) forced rats on behavioral rails to drink for so many seconds and then run for so many seconds and then go back to drinking, and so on. Such locking of behaviors can make them less attractive than under unconstrained conditions, so that the animals end up doing less-than-target levels of both behaviors, as exhibited by Mazur's (1975) rats.

Given the size of the operant literature, it would take at least a full article to apply our geometric approach to a reasonable sample of data sets. Here we simply want to point out the connections between the geometric approach to nutrition and equilibrium models of operant conditioning. Our approach has the appeal of mathematical simplicity, and it points out the connection between the function of minimization and cost structures. The operant literature takes a distinctly mechanistic approach to accounting for data, and an integrative approach taking in both function and mechanism is desirable. The operant data sets that are fitted well by ellipses suggest that accelerating cost structures sometimes apply to domains beyond nutrition and perhaps have some generality. What their full extent is remains to be explored.

We see potentially exciting prospects for integrating the kind of analysis described here into the fields of ecology and evolution. For example, ethologists have long been interested in evolutionary aspects of how animals integrate conflicting demands in their decision making (McFarland and Houston 1981), but lack of an operationally tractable metric forestalled development in this area. The parameter W from our geometric models provides a simple metric that can be related to the evolutionary ecology of animal cognition (Dukas 1998). Likewise, over recent years there has been a growing awareness of the need to incorporate information on the properties and actions of individuals into ecological models (Elser and Hamilton 2007). This approach has been explicitly taken in the field of ecological stoichiometry (ES), where physiological regulation of the elemental composition of organisms forms the platform for modeling ecosystem processes (Sturner and Elser 2002). Although the importance of behavioral (feeding) regulation has been acknowledged in ES, current models cannot readily incorporate this central aspect because in most cases the regulatory systems of animals respond to macromolecular nutrients (e.g., sugars, fatty acids, amino acids) rather than their elemental components (e.g., carbon, nitrogen, phosphorus), as modeled in ES (Frost et al. 2005). Given the centrality of food selection and feeding behavior in ecosystem trophodynamics, the importance of these behaviors in mediating animal body composition (Raubenheimer et al. 2007), and the fact that nutrient-specific regulation is now known to occur at all trophic levels >1 (Mayntz et al. 2005, forthcoming), we see an

A. Rats Barpressing for Sugar Water



B. Chicks Pecking for Heat

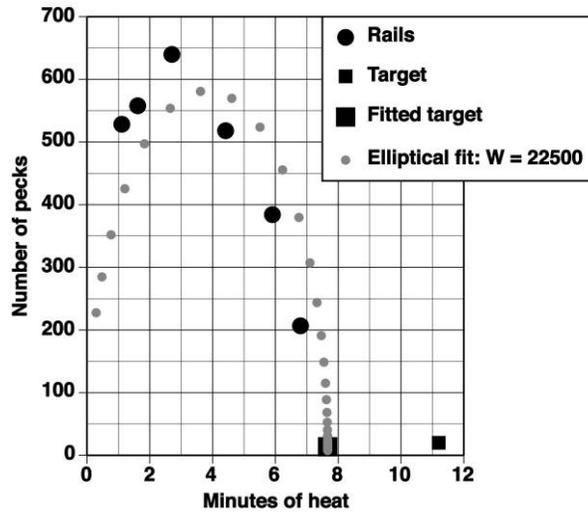


Figure 8: Euclidean fits of two sets of data from operant conditioning. Data were estimated using graphics software from figures 3A and 5B of Hanson and Timberlake (1983). *A*, Data stemming originally from Kelsey and Allison (1976), in which rats were trained to press a lever to obtain sugar water to drink. The target point, displayed in Hanson and Timberlake’s graph, was estimated by Staddon (1979). Other conventions and procedures were the same as in figures 2 and 3. *B*, Data stemming originally from an unpublished manuscript by G. Lucas in which 6 chicks were pecking to obtain heat. The fitted target was found by intersecting the target rail with a quadratic fit of the rail data (not shown). The ellipse was fitted by eye because the errors along rails were large for the two leftmost data points, and using our standard minimization procedures, the leftmost data points dominate the curve fitting at the expense of the other data points. For these two cases, a single ellipse provides a good fit.

urgent need for a parameter such as W that abstracts the key components of this complex phenomenon for use in ecosystem models.

Conclusions

We have taken a number of nutritional data sets, each of which contains a target point consisting of the amounts of two different nutrients, a point that is defended by the

subject animals. The data sets also contain data from diets (nutritional “rails”) in which the proportions of the two nutrients are not ideal, that is, do not intersect the intake target, such that the animals are forced to consume too much of one and/or too little of the other nutrient. We have found that in all cases, these rail data can be seen as attempts to minimize the Euclidean distance from the rail to the target point. The distance includes a suitable weighting factor representing the relative costs of deviations in

the levels of the two nutrients. We suggest that the minimization of Euclidean distances accounts for data well because the costs rise in an accelerated fashion with deviations from the target state. This analysis may well be suitable to some cases of behavioral choices beyond the domain of nutrition. An important issue that arises is the extent to which minimization of Euclidean distances is a general property of regulatory systems. The challenges ahead are to extend the comparison more broadly in a search for patterns (Radinsky 1985) across regulatory systems and animals and explore these patterns in ecological and evolutionary contexts.

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