

Use of Geometric Forms to Estimate Volume of Invertebrates in Ecological Studies of Dietary Overlap

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Studies of diet overlap of insectivores, especially lizards, have been important for the development of much ecological theory. However, measures of overlap, usually based on dietary volumes, vary widely among studies. Most researchers estimated the volumes of prey in stomach contents subjectively or attempted to reconstruct the volume of individual prey items from linear measurements of length (L), width (W) and/or height (H), or from mass. We studied the relationship between indices of volume based on indirect measures and direct measures of volume by fluid displacement for a collection of arthropods that simulated the diet of a generalist lizard. For each individual arthropod, we calculated the proportional error [(measured volume—estimated volume)/measured volume] for each estimation method. For individual large insects, there were significant differences between orders in the proportional error for all methods. The methods based on linear measurements had only weak relationships ($r^2 \leq 0.4$ in all cases) with measured volume. Mass had a stronger ($R^2 = 0.9$), but curvilinear relationship with measured volume. For the combined masses of all arthropods in each diet category from stomach contents of four species of lizards, there were also significant differences in the proportional error between arthropod orders for all methods ($P \leq 0.018$ in all cases), except for mass ($P = 0.126$). Because most indices of overlap are based on proportions, errors in estimation for any one category affect the degree of overlap for all other categories found in that stomach. Cluster analysis of different indices based on the same data indicated differences of up to 10% in proportional overlap. Such large differences for identical diets mean that it is extremely difficult to compare studies that used different methods of volume estimation. We conclude that the use of general formulas to reconstruct the volumes of arthropods are not appropriate for most studies of diet overlap and that extreme care should be exercised in attempts to perform meta-analyses on studies that purportedly measured prey volumes.

STUDIES of diet overlap of insectivores, especially lizards, have been important for the development of much ecological theory (e.g., Schoener, 1977; Pianka, 1980; Caldwell, 1996). However, overlap may be inferred from a variety of measures, including number of items (e.g., Forstner et al., 1998), frequency of occurrence (e.g., Durtsche, 1995), mass (e.g., Lima and Magnusson, 1998), volume (e.g., Anderson and Mathis, 1999), or compound indices of “importance” (e.g., Gadsen and Palacios-Orona, 1997).

It is unlikely that researchers would attempt to compare studies that used different measures, but even where studies have purportedly used the same measure, differences in techniques can lead to different conclusions. Most studies of dietary overlap in insectivores have reported relative volumes but few researchers measured volumes directly. Most researchers attempted to reconstitute volumes of invertebrates from linear measures using formulas for geometric shapes. Even for eggs, which show ra-

dial symmetry, this process is inexact (Maritz and Douglas, 1994).

In this paper, we will show that indices based on volume reconstruction methods do not correspond to any physical quantity and that differences in errors for different taxonomic groups of arthropods make detailed comparisons between studies difficult, even when researchers used the same technique.

MATERIALS AND METHODS

To compare indices of volumes with measured volumes of individual arthropods, we collected three or four species of arthropods from each of the following categories: Blattaria, Coleoptera, Diplopoda, Diptera, Hemiptera, Hymenoptera (only Formicidae), Lepidoptera (adults), Lepidoptera (larvae), Odonata and Orthoptera. The collection of orders is similar to that which might be found in a large (> 5 cm SVL) generalist lizard, and the categories correspond to those used in most studies of diet overlap in arthropodi-

vores. We measured one individual per species, and only specimens that we considered were large enough (> 1 cm in length) to confidently measure by volumetric displacement (Milstead, 1957; Itamies and Koskela, 1970; Sproston et al., 1999). Insects were preserved in alcohol for 1–2 weeks before analysis.

Prey items were blotted dry and introduced into a measuring cylinder graduated in intervals of 0.1 ml. Taking care to avoid air bubbles, water was added from a pipette graduated in intervals of 0.01 ml until the prey item was completely covered and the water was at the level of one of the graduations in the measuring cylinder. The volume of the prey was taken as the level of water in the cylinder minus the amount added from the pipette.

We estimated the volume of invertebrates using the formula for a “prolate spheroid” (e.g., Martori and Aun, 1994; Parmalee, 1999; Vitt et al., 1999), also called an “ellipsoid” (Colli and Zamboni, 1999). We refer to this formula as “Ellipsoid-1.” The formula used was $V = 4/3 \times \pi \times L/2 \times 2 (W/2)^2$, where V = volume, L = length, and W = width. We also used the mean of width and height as W in the equation (ellipsoid-2) because this approximated some of the subjective methods used by other researchers. Maximum measurements for width, height, and length of the body, were used in these and all subsequent formulae. We considered the width to be the maximum dimension orthogonal to length when viewed from above with the animal lying on its ventral surface. Using the maximum of width or height gives similar results to using width as defined above. We excluded appendages from measurements for this and other forms.

We also estimated volume from the formula for a parallelepiped ($V = L \times W \times H$) (e.g., Schoener, 1967; Bergallo and Rocha, 1994; Vrcibradic and Rocha, 1996; Bergallo and Magnusson, 1999), and a cylinder, $V = \pi \times (W/2)^2 \times L$ (e.g., Werner et al., 1995; Forstner et al., 1998).

We used mass in grams as an index of volume in milliliters (e.g., Pianka, 1994) and as a direct index of diet composition (e.g., Lima and Magnusson, 1998). Individual freshly caught insects, and all identifiable prey items in stomachs, including those represented only by disarticulated parts, were grouped into prey categories, blotted with absorbent paper towel to remove excess fluids, and weighed on a balance with a limit of reading of 0.001 g.

Because most of the estimates based on linear measurements are modifications of the general formula $V = a \times L^b \times W^c \times H^d$, we used the NONLIN program in the SYSTAT 8 statistical

program to estimate values of a , b , c , and d that minimized the squared deviations given the measured values of V , maximum L , maximum W , and maximum H for the arthropods we collected. The resulting equation, $V = 0.55 \times H^{2.03} \times W^{0.16} \times L^{1.14}$, which we refer to as “empirical,” accounted for about 85% of the variance ($R^2 = 0.85$) and should be close to optimum for this dataset. However, extrapolation to other datasets would be unwise.

We calculated the proportional error for each arthropod as the estimated volume minus the measured volume, divided by the measured volume. If there was no bias in the estimate of volume, or if the bias was the same for each group, there would be no significant difference between groups in the proportional error.

Arthropods in stomach contents may be compressed into shapes that are more similar to the geometric forms used as models than the freshly caught arthropods. Also, the objective is usually not to use volume as an index of the size of individual prey but to estimate the total amount of that prey type in the stomach. Therefore, we used data collected for a previous study (Magnusson and Silva, 1993) to evaluate the differences among the methods for stomach-contents data. The lizards used in that study had a variety of inter- and intraspecific ranges in snout–vent lengths (SVL; *Anolis aeneus*: 4.4–5.2 cm, $n = 5$; *Cnemidophorus lemniscatus*: 3.3–6.6 cm, $n = 14$; *Kentropyx striata*: 3.7–10.7 cm, $n = 19$; *Ameiva ameiva*: 4.4–13.2 cm, $n = 29$). The same procedures were used to estimate the volumes of individual insects by the volume reconstruction methods used in the study of freshly caught insects. The sums of estimates of individual relatively intact insects by each method were used to estimate the total volume of each prey type in each stomach. Prey represented only by isolated fragments were not included in analyses. This is the procedure adopted in most studies of diet overlap in arthropodivores. Direct measures of mass and volume were made for all items combined, including disarticulated parts, after blotting off excess liquid, for each prey type in each stomach.

Differences among prey types in proportional error were evaluated by analysis of variance (ANOVA) in the SYSTAT 8 statistical package. ANOVA is useful for describing the magnitude of effects. However, probabilities associated with null hypotheses estimated by ANOVA are sensitive to heteroscedasticity, gross departures from normal distributions, and outliers (Manly, 1997). Although there are no powerful tests for departures from the ANOVA assumptions when there are only three or four observations per

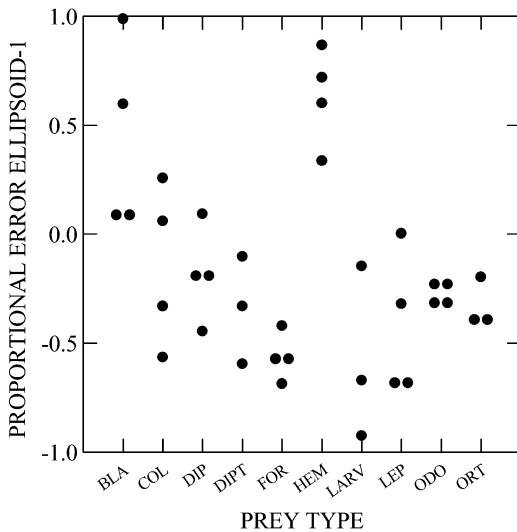


Fig. 1. Proportional error of volume estimates in relation to fluid displacement for the prolate spheroid (ellipsoid-1) model for different categories of arthropods. BLA = Blattaria, COL = Coleoptera, DIP = Diplopoda, DIPT = Diptera, HEM = Hemiptera, FOR = Formicidae, LARV = Lepidoptera (larvas), LEP = Lepidoptera (adults), ODO = Odonata, and ORT = Orthoptera.

cell, stomach-contents data are likely to deviate from the assumptions of the parametric test. Therefore, we also present probabilities based on the nonparametric Kruskal-Wallis test (KST), which is insensitive to these distributional problems.

RESULTS

For individual large insects, there were significant differences between prey categories in the proportional error for all methods (ellipsoid-1: $F_{9,27} = 8.0$, $P < 0.001$, $r^2 = 0.73$, KST $P = 0.007$; ellipsoid-2: $F_{9,25} = 3.8$, $P = 0.004$, $r^2 = 0.58$, KST $P = 0.022$; cylinder: $F_{9,27} = 8.0$, $P < 0.001$, $r^2 = 0.73$, KST $P = 0.007$; parallelepiped: $F_{9,25} = 3.1$, $P = 0.012$, $r^2 = 0.53$, KST $P = 0.05$; mass: $F_{9,22} = 2.38$, $P = 0.047$, $r^2 = 0.49$, KST $P = 0.064$). The estimates for some prey categories had errors centered on zero, which indicates negligible bias. However, estimates for most categories were systematically greater or less than zero (Fig. 1), indicating that the indices do not correspond to the physical measure "volume" for these categories. Even the empirical method, which we expected to minimize differences between estimated and measured volumes for this dataset, showed significant differences in proportional error among categories ($F_{9,25} = 6.2$, $P < 0.001$, $r^2 = 0.69$, KST $P = 0.006$).

The estimated total volume of the insects differed by over 100% among methods. The cylinder (17.6 ml) and the parallelepiped (15.5 ml) were closest to the measured volumes (16.7 ml), and mass (11.1 ml), ellipsoid-1 (11.8 ml) and ellipsoid-2 (8.6 ml) returned much lower estimates. However, these do not necessarily reflect the differences likely to affect interpretations in diet studies, because researchers usually use some proportional index so that they can compare predators with different sizes and stomach volumes (e.g., Winemiller and Pianka, 1990). For example, Pianka's (1974) index gives a proportional measure that ranges from one for complete overlap to zero for no dietary items in common.

To illustrate the magnitude of differences among methods used for estimating volumes on estimates of diet overlap, we applied each method to our dataset for freshly caught insects and calculated the distances among diets (= methods) using the dissimilarity form of Pianka's (1974) index of niche overlap. This gives a measure of proportional differences among diets. The distances were used to construct a dendrogram based on the mean differences (Average-linkage clustering). Because there were no differences between the diets summarized by each method, if the methods measured the same physical dimension, there would be little difference among the categories, and they would be tightly grouped in a single cluster. However, the dendrogram indicates differences of over 10% in diet overlap between the estimates based on measured volume and other indices of volume (Fig. 2). Although the cylinder estimates volumes 50% greater than ellipsoid-1, there was no difference between these techniques when the results were converted to percent overlap.

For the data on lizard stomach contents, the different indices of total quantity of food items in each diet category in each stomach had different relationships to measured volume. The relationship between mass (M , g) and volume (V , ml) was curvilinear ($V = 0.03 + 1.80M - 0.70M^2$, $F_{2,216} = 939.7$, $P < 0.001$, $R^2 = 0.90$) but relatively precise (Fig. 3A). The relationships between the estimates of total quantity (Q) and volume were apparently linear for the ellipsoid ($Q = 0.06 + 0.55V$, $F_{1,217} = 118.4$, $P < 0.001$, $r^2 = 0.35$), the cylinder ($Q = 0.06 + 0.37V$, $F_{1,217} = 118.4$, $P < 0.001$, $r^2 = 0.35$), and the parallelepiped ($Q = 0.06 + 0.40V$, $F_{1,217} = 144.3$, $P < 0.001$, $r^2 = 0.40$), but lacked precision (Fig. 3C–D). Given the great variation around the lines, these quantities capture very little of the information that is in the physical quantity "volume."

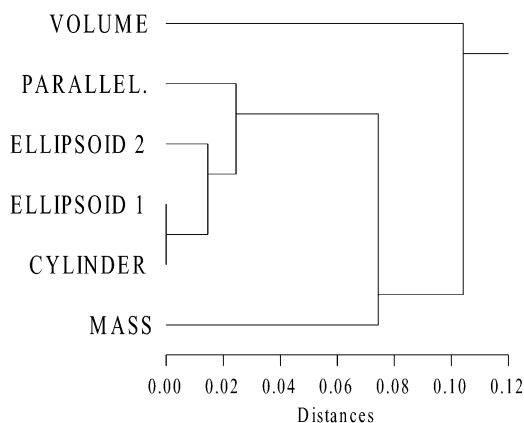


Fig. 2. Dendrogram of mean similarity ("Average" clustering) among different volume-estimation methods for the same sample. The true difference between the samples was zero. Therefore, distances along the horizontal axis, which would be interpreted as proportional dissimilarities in diet studies (max = 1, min = 0), represent only differences induced by the use of different methods to quantify diet.

For the data on lizard stomach contents, there were significant differences in proportional error among prey categories for ellipsoid-1 ($F_{14,204} = 2.02$, $P < 0.018$, $r^2 = 0.12$, KST $P = 0.002$), ellipsoid-2 ($F_{14,204} = 2.23$, $P < 0.008$, $r^2 =$

$= 0.13$, KST $P = 0.003$), cylinder ($F_{14,204} = 2.02$, $P < 0.018$, $r^2 = 0.12$, KST $P = 0.002$) and parallelipid ($F_{14,204} = 2.26$, $P < 0.007$, $r^2 = 0.13$, KST $P = 0.003$), but not for mass ($F_{14,204} = 0.145$, $P = 0.126$, $r^2 = 0.09$, KST $P = 0.44$).

DISCUSSION

The most appropriate measure of diet overlap will depend on the aims of the study. If behavior is being studied, the number of prey ingested may be the most appropriate metric. Much information may be contained in the proportion of lizards with empty stomachs (Huey et al., 2001), and when energy flow is important, digestible energy may provide more insights (e.g., Dimmitt and Ruibal, 1980). However, most studies in the herpetological literature have used indices of volume to estimate diet overlap.

Some researchers have used purely subjective visual estimates of relative volume (e.g., Pianka, 1973; Winemiller and Pianka, 1990; Sheldon and Meffe, 1993), and some researchers reported that they used "average" measurements but not how they calculated the average (e.g., Schoener, 1967; Gadsen and Palacios-Orona, 1997). Other researchers make visual adjustments to approximate the average when making

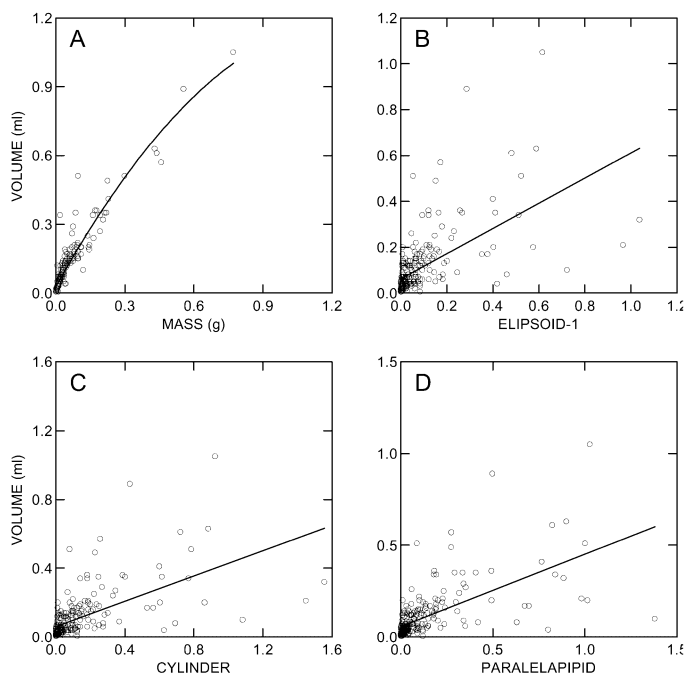


Fig. 3. Relationship between measured volume and volume estimated from mass (A), and geometric models based on an ellipsoid (B), a cylinder (C), and a parallelipid (D), for lizard stomach-contents data. Each point represents one category of prey in one lizard stomach.

measurements (L. Vitt, pers. comm.). Because we could not replicate the methodology, we could not evaluate the precision or accuracy of those methods. However, there is no reason to believe that they would have closer relationships to measured volume than the methods based on direct linear measurements. Unless the authors report calibration curves, it will be very difficult to interpret the results of these studies.

The most common geometric form used to represent the form of invertebrates is the “prolate spheroid” (e.g., Martori and Aun, 1994; Parmalee, 1999; Vitt et al., 1999), also called an “ellipsoid” (Colli and Zamboni, 1999). The formula used is $V = 4/3 \times \pi \times L/2 \times (W/2)^2$, where V = volume, L = length, and W = width. Parmalee (1999) reported that width was measured at the midpoint of the prey item, but most authors did not indicate where measurements were made. We used maximum measurements for width, height, and length of the body, because maximum measurements were the only ones that could be defined unambiguously.

No authors indicated how they decided which measurement indicated width or height (H). This depends on the orientation of the prey item. We assumed that they considered the width to be the maximum dimension orthogonal to length when viewed from above with the animal lying on its ventral surface. Using the maximum of width or height gives similar results to using width as defined above. We also used the mean of maximum width and maximum height as W in the equation for an ellipsoid as this approximated some of the subjective methods.

Some authors have used the formula for a parallelepiped ($V = L \times W \times H$). The method was first used by Schoener (1967) with “average” width and height. However, Schoener did not explain how he obtained the average width and did not use the method in more recent publications. Subsequent authors appear to have used maximum rather than mean dimensions (e.g., Bergallo and Rocha, 1994; Vrcibradic and Rocha, 1996; Bergallo and Magnusson, 1999).

The volume of individual prey items has also been estimated from the formula for a cylinder, $V = \pi \times (W/2)^2 \times L$ (e.g., Werner et al., 1995; Forstner et al., 1998). As with the other forms, authors did not define width.

The variety of formulas and interpretations of what constitute “length” and “width” in the equations make comparisons among studies difficult. In this study, none of the indices of volume based on linear measurements were closely

related to volume as estimated by fluid displacement ($r^2 \leq 0.4$ in all cases).

A major problem is that the relative error in volume estimation differs between arthropod categories. Even though some prey types may be estimated accurately, or at least unbiasedly, errors in any one diet category influence the estimated overlap for all categories because data are usually transformed to proportions before analysis. Our cluster analysis of diets indicated differences of up to 10% based only on the method of estimating volumes. Therefore, dissimilarities in diets among studies may often reflect methodological differences rather than the biology of the species.

The dendrogram we constructed represents a best-case situation. There were no differences in the diets summarized by each method. In a real study, the similarities of results obtained by the different methods will also depend on the relative proportions of different orders in the diets. For example, ellipsoid-1 overestimates the quantity of ants (Formicidae) and grubs (Lepidoptera) in the diet by about 50% (Fig. 1). Therefore, volumes reported by this method, need to be discounted by about 33%. In contrast, the volumes of roaches (Blattaria) and bugs (Hemiptera) were underestimated by about 50%. If the simulated diet had consisted of different proportions of these groups, the similarities among the methods would have changed unpredictably, even if the methods analyzed the same sample.

When there are different relationships between the index of volume and measured volumes for different prey categories, the proportions are very difficult to interpret. This is especially important when electivities are calculated based on the total amount of a resource used by the entire community (e.g., Winemiller and Pianka, 1990), or prey availability is based on estimates of volume (e.g., Bergallo and Magnusson, 1999). Even when volumes are measured accurately, much information is lost when diet overlap is reported only as proportions. This is especially important when overlap is asymmetrical. For example, if ants and termites are excluded from the diet, *Bufo marinus* and *Leptodactylus ocellatus* (= *macrosternum*) of the same size eat very similar types, sizes and numbers of prey (Strussmann et al., 1984). As *L. macrosternum* eats few ants or termites, its diet is overlapped almost completely by the diet of *B. marinus*. However, as well as eating similar types, sizes and quantities of other prey to *L. macrosternum*, *B. marinus* eats large quantities of ants and termites. Therefore, the diet of *L. macrosternum* overlaps only part of its diet. This asym-

metry cannot be seen after data are transformed to proportions and information on the absolute ingested quantities is lost.

Volume can be measured directly by fluid displacement, but the process is tedious, difficult to perform for very small arthropods, and it is not clear what volume represents to the predator, even when it is measured directly. It is usually easier to weigh the prey items than measure their volumes, and in this study, prey type was associated with slightly less of the variation in proportional error for mass of freshly caught invertebrates than other indices of volume and was not significantly related to the proportional error for the stomach-contents data. However, when prey are very small, it may be necessary to group a large number of similar sized organisms and take the mean (e.g., Lima et al., 2000), which introduces further error.

All authors excluded appendages from measurements used to estimate volume from linear dimensions. An advantage of the use of measured mass or volume is that all of the material in the stomach can be used to estimate the volume of each diet category. For instance, one of the anoles used in this study had eaten eight legs of a large spider and its stomach was full. We believe that it had tried to eat the whole spider but was unable to swallow the body. One could try to reconstitute the size of the spider before ingestion, but that would exaggerate its contribution to the diet. Alternatively, the volumes of each segment for each leg could be estimated by a geometric model, but that was not done for other prey. Discarding the information from the legs also does not seem appropriate. Use of a direct measure of mass or volume avoids the necessity for making these decisions and, in the case of data collected by other researchers that is available in electronic archives, avoids doubts about what subjective decisions might have been made.

Wet mass could be used as a direct index of the quantity of food in each diet category. However, if the researcher needs an index of volume, the mass data probably have to be transformed. Pianka (1994) stated that "volume and mass are equivalent (e.g., 1 ml of lizard is assumed to weigh approximately 1g)." Although that may be true for lizard prey, it is not necessarily true for invertebrates, which accounted for more than 50% of the reported volumes in some of the varanids he studied. Our data showed a relatively precise, but curvilinear relationship between measured volume and mass for lizard stomach-contents data.

Some researchers have used calibration curves that relate linear measures of different

categories of invertebrates to their dry or wet masses (e.g., Zug and Zug, 1979; Schoener, 1980; Sage, 1982), and these can be used to estimate the amount consumed in diet studies (e.g., Spiller and Schoener, 1994; Durtsche, 1995; Toft, 1995). It would be possible for researchers to develop calibration curves for the types of prey eaten by the species they study. However, it is unlikely that general relationships that are not taxon-specific (e.g., Rogers et al., 1976; Maury, 1995) will be any more successful for mass than they are for volume.

Studies of diet overlap have lead to important insights into the ecology of insectivores. However, combining the results of studies that used subjective methods, indices that have no physical counterparts, or measures of overlap based only on proportions, may induce artifactual patterns. This makes the construction of generalizations and the use of meta-analyses based on the data in ecological texts extremely difficult. There are many other problems with analyses of gut contents (e.g., Magnusson et al., 1987, 2001) and short-term studies of diet may be grossly inaccurate because of seasonal and yearly variations. However, carefully planned studies can reveal subtle patterns among size classes within species and species within feeding guilds (e.g., Lima and Magnusson, 1998). Researchers collecting data that may be made available in public-access databanks, such as those required of National Science Foundation grantees, or in electronic journals such as Ecological Archives, would do well to consider the use of simple direct physical measures, such as mass or volume, even if they persist in the use of geometric models in their own studies.

ACKNOWLEDGMENTS

Financial support was provided by CNPq grants Produtividade de Pesquisa to W. Magnusson and PIBIC to W. Silva. C. Keller gave invaluable help in the preparation of previous drafts of the manuscript.

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