2000. The Journal of Arachnology 28:241–242

RESEARCH NOTE

ESTIMATING FORAGING INTAKE: A COMMENT ON TSO AND SEVERINGHAUS (1998)

Keywords: Energy intake, allometry, digestible biomass

Tso & Severinghaus (1998) have recently drawn attention to the problems of using Schoener's (1980) length-weight equations for insects as a means of estimating foraging intake by spiders. They pointed out that a biomass estimate calculated from Schoener's equations includes all tissues irrespective of whether they are digestible or not. As predators do not utilize largely indigestible material (e.g., the exoskeleton—but note that at least some spider species can produce chitinase (Collatz 1987)) this will inevitably lead to inaccuracies in determining digestible biomass acquisition by a foraging spider. Tso & Severinghaus (1998) therefore measured the actual biomass removed from a variety of prey items of different sizes and taxonomic groups by caged female *Argiope trifasciata* (Forskål 1775). They did this by simply subtracting the weight of the discarded exoskeleton from the initial wet weight of the prey. Dry weights of the prey items used were estimated by inserting prey lengths into Schoener's (1980) equations for each of the various taxonomic groups. Plots of ingested biomass and of dry weights of prey against prey length yielded curves that increasingly diverged towards higher prey lengths. Tso & Severinghaus assume dry weight is composed of digestible biomass + exoskeleton; ingested biomass is composed of digestible biomass + water; the relative proportions of these three components are constant and the absolute contribution of each is a function of size. This being so, because water comprises a large proportion of the wet weight (and therefore, ingested biomass) the absolute difference between ingested biomass and dry weight will be a positive function of size—the plotted curves will diverge with increasing body length. The conclusion is that because many large spiders take a great range of prey sizes ''. . . the relative energy content of large prey would be greatly underestimated if determined by dry weight alone.'' They recommend that ''future studies should consider using ingestible biomass of prey in estimating the foraging intake of spiders.''

Tso & Severinghaus (1998) argue that using dry weights will tend to underestimate the ingested biomass, and disproportionally so with increasing prey sizes. However, the ingested biomass they suggest measuring is still not a good estimate of the energy derived from the prey because a large proportion of this biomass will be the water responsible for the divergence of the plotted curves; water is not a source of metabolic energy. In very dry habitats, the water content of the biomass ingested from a prey item may indeed be of great importance, and the total volume of liquified food ingested will certainly be a factor in determining satiation level in situations where prey is not limiting. Wet biomass ingested will only be proportional to energy intake if the separate components of water and digestible biomass are in constant proportions (as assumed by Tso & Severinghaus) in different sized prey. This will only be the case if water content and digestible biomass both scale with size in exactly the same way. One might expect both to be approximately proportional to volume (i.e., $\propto$ length^3) but the exact exponents would have to be determined empirically (see Schoener 1980), and their coefficients (0.7 for water and 0.1 for digestible macromolecules in the equation of Tso & Severinghaus) checked for constancy across prey size range.

An appropriate measure that is likely to be a direct function of energy intake from a prey item is total dry weight (= digestible dry weight + exoskeleton) less the weight of the dry exoskeleton rejected after feeding. The absolute intake of digestible dry weight must, of necessity, always be less than the total dry weight of the prey and will therefore fall below the lower curves in Tso & Severinghaus's fig. 1. Within this constraint, the shape of the digestible dry weight curve will depend on its allometric relationship with absolute size. Although digestible dry weight probably scales approximately $\propto$ length^3 (but, again, see Schoener 1980) exoskeleton probably reflects more closely surface area (i.e., $\propto$ length^2). As total dry weight increases with size, one would therefore expect a greater proportion to be represented by digestible material in larger prey items. Some evidence for this is provided by Rees (1986) who investigated the relationship between the fraction of total (wet) mass attributable to dry skeletal mass and total wet mass across taxa within six beetle families. The slopes of all six plots were negative (two-tailed sign test, $P = 0.03$), although only one was individually significant. Total mass was measured as wet rather than dry weight, but if the degree of tissue hydration is constant or, if variable, not a function of beetle size, these data suggest that skeletal mass decreases and, as a consequence, the remainder (digestible mass) increases with total beetle mass (size). This is in direct contrast to the conclusions of Tso & Severinghaus quoted above—the use of total dry weight as a surrogate for energy availability will produce an underestimate that decreases with increasing prey size. If energy intake is the currency of interest when investigating spider foraging, ingested dry weight is the appropriate, and direct, measure to use.

I would like to thank Peter Mayhew and Chris Rees for discussion.

LITERATURE CITED

Collatz, K.-G. 1987. Structure and function of the digestive tract. Pp. 229–238, *In* Ecophysiology of Spiders (W. Nentwig, ed.). Springer-Verlag, Berlin.

Rees, C.J.C. 1986. Skeletal economy in certain herbivorous beetles as an adaptation to a poor dietary supply of nitrogen. Ecol. Entomol., 11: 221–228.

Schoener, T.W. 1980. Length-weight regression in tropical and temperate forest-understory insects. Ann. Entomol. Soc. America, 73:106–109.

Tso, I-M. & L.L. Severinghaus. 1998. Ingested biomass of prey as a more accurate estimator of foraging intake by spider predators. J. Arachnol., 26:405–407.

G.S. Oxford: Department of Biology, University of York, P.O. Box 373, York YO10 5YW, U.K.

Manuscript received 6 March 1999, revised 3 November 1999.