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RESEARCH NOTE

INGESTED BIOMASS OF PREY AS A MORE ACCURATE ESTIMATOR OF FORAGING INTAKE BY SPIDER PREDATORS

Spiders have became more and more important as model organisms of foraging ecology (Uetz 1992; Wise 1993). Their foraging intake, especially that of orb-weaving spiders, can be easily estimated. These are sit-and-wait predators whose prey intake can be measured by examining insects trapped on webs. Furthermore, all spiders exhibit external digestion by injecting into the prey digestive juices which liquefy the inner soft parts. The spider retrieves the liquefied material by its sucking stomach, then discards the indigestible exoskeleton (Foelix 1982). Therefore, the spider's foraging intake can be accurately investigated by comparing biomass of prey before and after consumption.

This advantage has not been fully exploited in most spider foraging studies. Instead, dry weight of trapped prey calculated from length-weight equations given by Schoener (1980) is frequently used to estimate the spider's foraging intake. For example, Craig (1989) estimated the foraging intake between sympatric orb-weavers of different size; Cangialosi (1990) accessed the relative foraging intake of social spider hosts and kleptoparasites, and Higgins & Buskirk (1992) examined how prey intake affects foraging strategies of *Nephila clavata* L. Koch 1878. However, the biomass calculated from equations of Schoener (1980) includes both digestible soft parts and the indigestible exoskeleton, which does not seem to be appropriate considering how most spiders ingest food. Therefore, I estimated the biomass of temperate zone insects available for spider ingestion by comparing the weight of prey before and after spider consumption to provide a length-ingested biomass equation for future foraging studies. Moreover, I also evaluated total dry weight as an estimator of ingestible biomass by examining if those two variables associated with prey correlate well with each other.

This study was conducted in Matthaei Botanical Gardens of the University of Michigan in Ann Arbor, Michigan, USA in August 1995. Twenty cages (40 × 40 × 20 cm) were built from foam board and nylon screen, and each cage housed one female banded garden spider (*Argiope trifasciata* (Forskål 1775)) collected from the Gardens. During the study, insects were collected daily from the prairie at the Gardens by sweep netting. Before being given to spiders, insects were kept in vials then placed in a freezer for 5 minutes. After being removed from the vial and wiped dry with tissue paper, the insect body length was measured to the nearest 0.1 mm and weighed to the nearest 0.1 mg. Insects were placed on the webs of caged *A. trifasciata* before recovering from cooling. Each spider was given one insect each day, and size and taxa of prey each spider consumed were documented to ensure that all spiders received a similar array of prey, both in type and size. After 24 hours I collected the discarded exoskeletons from the cage bottoms then weighed the remains. I gave spiders new prey only after they dropped the consumed insect from their webs. The insect's weight after being consumed was subtracted from its original weight to give the ingested biomass.

I estimated body length–ingested biomass relationship by the following equation used by Schoener (1980):

$$\text{(a)} \qquad W = aL^b$$

In equation (a), W stands for ingested biomass, L for body length of prey, and a and b are parameters to be estimated. To estimate parameters a and b, (a) was log-transformed into:

$$\text{(b)} \qquad \log W = \log a + b \log L$$

A linear regression was calculated between log W and log L to generate statistics of parameters a and b (Schoener 1980). To examine the relationship between dry weight and ingested biomass of various insect taxa and size, body length data were transformed into dry weight using equations given by Schoener (1980). Schoener (1980) did not provide a temperate zone orthopteran dry weight equation, so I used the equation generated from orthopterans of Canas, Costa Rica (dry forest). I then plotted ingested biomass and dry weight values generated from body length of collected insects to examine the relationship between those two variables (Fig. 1).

Ingested biomass data were collected from 25 hymenopterans (ranging from 5–24 mm), 46 orthopterans (ranging from 6–28 mm), 13 dipterans (ranging from 5–10 mm), and 19 homopterans (ranging from 4–9 mm). Coleopterans were not included in the analysis because I could not collect sufficient insects. The ingested biomass - body length relationship of temperate zone prairie insects can be expressed as Hymenoptera: $W = 0.120L^{2.226}$, Orthoptera: $W = 0.382L^{1.972}$, Diptera: $W = 0.008L^{3.678}$ and Homoptera: $W = 0.014L^{3.233}$ (Table 1). Insect dry weight and ingested biomass did not correlate well with each other (Fig. 1). The deviation between estimated ingested biomass and dry weight widened as insect body length increased.

The increase in discrepancy between dry weight and digestible biomass as insect size increases can be explained by the following. Suppose the weights of three major components of an insect—water, digestible macromolecules and indigestible exoskeleton—can be described as functions of the insect size (S). Assume that a given type of insect is composed of 70% water, 20% exoskeleton and 10% macromolecules, and assume that this ratio is more or less constant for all size classes, then the total biomass of an insect of the size S can be described as:

$$\text{Total biomass} = f(S) = 0.7\ f(S) + 0.2\ f(S) + 0.1\ f(S).$$

The dry weight estimated from Schoener (1980) is composed mainly of exoskeleton and digestible macromolecules, and therefore can be described as $0.1\ f(S) + 0.2\ f(S) = 0.3\ f(S)$. However, the ingestible biomass of an insect is composed of both water and digestible macromolecules, therefore can be described as: $0.7\ f(S) + 0.1\ f(S) = 0.8\ f(S)$. The discrepancy between the dry weight and ingestible biomass of a given insect then is: 0.8

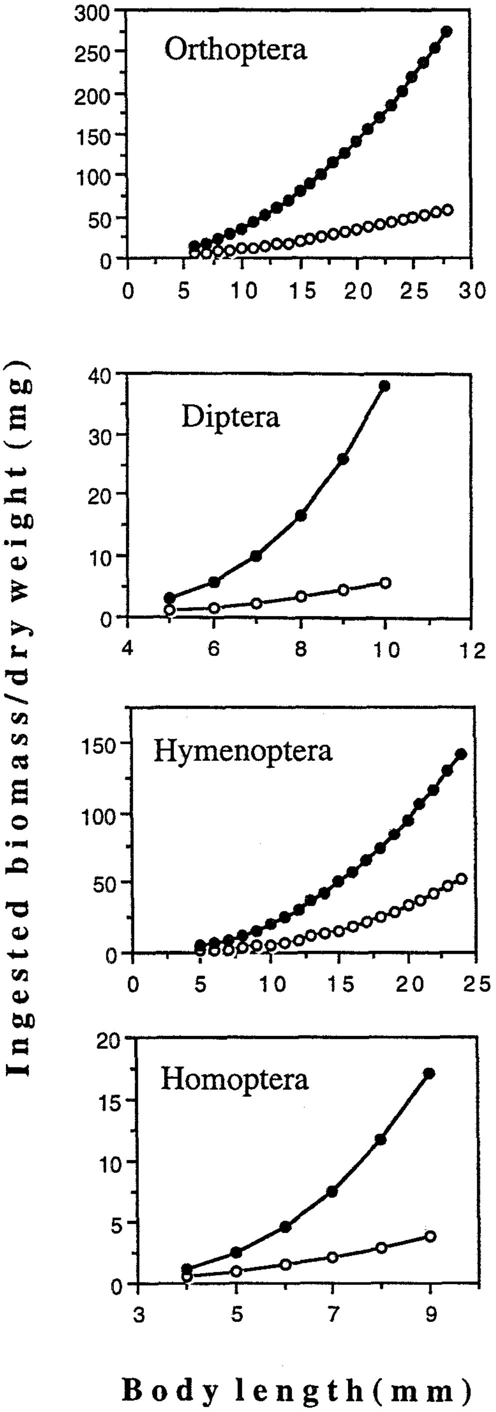

Figure 1.—Estimated ingested biomass (●) and dry weight (○) of temperate zone prairie insects. Length-weight equations used for dry weight estimation were Hymenoptera: $W = 0.016L^{2.55}$, Orthoptera: $W = 0.240L^{1.65}$, Diptera: $W = 0.022L^{2.42}$ and Homoptera: $W = 0.024L^{2.31}$, where W is the dry weight (mg) and L the body length (mm) of the insects.

Table 1.—Regression statistics for ingested biomass (mg) on body length (mm) of temperate prairie insects. Equation is $\log W = \log a + b \log L$, r is the regression coefficient.

	n	r	P	log a ± SE	b ± SE
Hymenoptera	25	0.796	<0.001	−0.921 ± 0.400	2.226 ± 0.353
Orthoptera	46	0.883	<0.001	−0.417 ± 0.178	1.972 ± 0.158
Diptera	13	0.841	<0.001	−2.094 ± 0.617	3.678 ± 0.713
Homoptera	19	0.894	<0.001	−1.868 ± 0.316	3.233 ± 0.394

$f(S) - 0.3 f(S) = 0.5 f(S)$. Therefore, the larger the size of an insect, the larger the value of $f(S)$, and consequently generates a larger discrepancy between that insect's dry weight and digestible biomass.

The results of this study suggest that the length-weight equation provided by Schoener (1980), although traditionally used as a standard way of generating foraging intake of spiders, is not an accurate estimator. This is true especially since many spiders, such as *Nephila* (see Nentwig 1985) and *Argiope* (Murakami 1983), have a great range in prey size, thus the relative energy content of large prey would be greatly underestimated if determined by dry weight alone. The equations given by Schoener (1980) may be a good estimator of foraging intake if predators ingest whole prey. However, the unique food ingestion mode exhibited by spiders makes the length-weight equations provided by Schoener (1980) not entirely suitable for estimating their foraging intake. Future studies should consider using ingestible biomass of prey in estimating the foraging intake of spiders. To allow better and more accurate estimation of spider foraging gain in future studies, similar data for temperate zone coleopterans and various taxa of tropical insects are needed.

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