

Body sizes of hosts and parasitoids in individual feeding relationships

Joel E. Cohen^{*†}, Tomas Jonsson^{*§}, Christine B. Müller^{¶||}, H. C. J. Godfray[¶], and Van M. Savage^{**}

^{*}Laboratory of Populations, The Rockefeller University and Columbia University, Box 20, 1230 York Avenue, New York, NY 10021; [†]Laboratory of Populations, Rockefeller University, Box 20, 1230 York Avenue, New York, NY 10021; [§]Department of Natural Science, University of Skövde, Box 408, S-541 28 Skövde, Sweden; [¶]Centre for Population Biology, Department of Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY, United Kingdom; ^{||}Institute of Environmental Sciences, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland; and ^{**}Bauer Center for Genomics Research, Harvard University, 7 Divinity Avenue, Sherman, Bauer Laboratory, Cambridge, MA 02138

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In a natural community of 49 species (12 species of aphids and 37 species of their parasitoids), body lengths of 2,151 parasitoid individuals were, to an excellent approximation, related to the body lengths of their individual aphid hosts by a power law with an exponent close to 3/4. Two alternative models predict this exponent. One is based on surface area to volume relationships. The other is based on recent developments in metabolic ecology. Both models require a changing ratio (in both host and parasitoid) of length to diameter with increasing body length. These changing ratios are manifested differently in the two models and result in testably different predictions for the scaling of body form with increasing size. The estimated exponent of 3/4 for the relationship between individual host body size and individual parasitoid body size degrades to an exponent of nearly 1/2, and the scatter in the relationship between aphid and parasitoid body length is substantially increased, if the average length of a parasitoid species is examined as a function of the average length of its aphid host species instead of using measurements of individuals.

allometry | aphids | development | metabolism | weight-length relations

Explaining the size of organisms is an enduring challenge to ecologists and evolutionary biologists (1, 2) to cellular and developmental biologists (3). Ecological studies of the relationship between consumer and resource body sizes (4–8) usually assume that the average body size of a species is an adequate approximation to the size of the individuals taking part in a particular trophic interaction. However, individuals of different size within one resource species may be selectively consumed by different consumer species or individuals of different size within a given consumer species. Vice versa, individuals of different size within one consumer species may selectively consume resource species of different average size or individuals of different size within a given resource species. To understand the relationship between consumer and resource body sizes, it is important that the data correctly represent the body sizes of the consumers and resources involved in the trophic interactions. What are the consequences of focusing on body sizes of consumer and resource individuals vs. average sizes of taxonomic species for understanding feeding relations in natural communities? To answer this question, here we report quantitative field data on body sizes in individual events of parasitism.

Animal consumers are often considerably larger than their prey (4), whereas parasites and pathogens are generally much smaller than their resources (5). Solitary insect parasitoids that complete their larval development on or in the body of other living insects, and require just a single host to complete development, lie between these extremes: they are often similar in size to their insect hosts. Parasitoid and host body sizes are well suited to shed light on the role of individual differences in consumer-resource body size relations because the variations in both parasitoid and host body sizes are likely to be of comparable magnitude.

Parasitoids are important components of all terrestrial ecological communities. Probably 1–2 million species are parasitoids (9), and they are thus a significant fraction of all species on this planet. As potentially important regulators of their host populations, parasitoids are intensively used in biological control (10). Most prior studies of the body sizes of hosts and parasitoids consider only a single species of host. The few studies (11–14) that consider host–parasitoid size relationships of multiple species have only one data point per species.

We studied quantitatively the relationship between final individual aphid host and parasitoid body length in a natural aphid-parasitoid community with multiple species of hosts and parasitoids. The objectives of the study were to (i) describe the relationship between final aphid host and parasitoid body size, (ii) analyze the consequences of focusing on body sizes of consumer and resource individuals vs. average sizes of taxonomic species for the apparent relationship between final aphid host and parasitoid body size, and (iii) offer two alternative explanations for the relationship between final aphid host and parasitoid body size. We hope that future studies will discriminate between these alternative explanations.

Methods

Aphid mummies that contained developing parasitoid larvae were collected from May to September 1994, in an abandoned field at Silwood Park. Müller *et al.* (15) described the aphid-parasitoid community at this site. Mummies were kept at room temperature in the laboratory until the parasitoids emerged. The mummies with diapausing parasitoids were kept in an outside insectary from the beginning of November 1994 to the beginning of February 1995. The samples were then brought back to the laboratory.

The aphid mummy and newly emerged parasitoid were pinned and later measured (length, reported in millimeters) and identified to species (Table 1). The lengths of the aphid mummy and the parasitoid were measured from the front of the head to the end of abdomen. The cauda of aphids was excluded because it is pronounced only in adult stages and some of the mummies were in the fourth-instar stage. Specimens that had been pinned in a distorted position were excluded. The data (listed in full in Data Set 1, which is published as supporting information on the PNAS web site) consist of 2,151 individual observations of the length of individual parasitoids emerging from aphid hosts and the length of their aphid mummy hosts.

All of the parasitoids in this study are solitary Hymenoptera (parasitoid wasps): that is, only one parasitoid individual develops within one host individual. In primary parasitoids (Braconidae: Aphidiinae, Aphelinidae), the female usually attacks nymphal instars of a living unparasitized aphid and lays one egg within the aphid. The developing parasitoid larva

[†]To whom correspondence should be addressed. E-mail: cohen@rockefeller.edu.

Table 1. The species and number of observations of each link

Wasp species	Aphid species											
	1	2	3	4	5	6	7	8	9	10	11	12
13	2	1	0	0	0	0	0	0	2	0	29	0
14	0	0	0	0	0	0	0	0	0	0	1	0
15	76	0	0	0	0	0	0	1	0	0	0	0
16	99	0	0	0	0	0	2	0	0	0	2	0
17	0	0	0	0	0	233	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	288	0	0
19	4	0	0	0	0	0	0	0	0	6	2	0
20	0	0	0	0	0	0	0	0	28	0	42	0
21	0	4	0	0	0	0	41	0	0	14	0	0
22	0	0	68	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	94	0
24	0	0	101	0	0	0	0	0	0	0	0	0
25	10	10	1	0	0	0	9	2	0	22	3	3
26	0	0	0	0	0	0	0	0	0	0	12	0
27	0	0	0	0	0	3	0	0	0	0	0	0
28	2	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	1	0	0	2	0	0	0
30	0	0	0	0	0	0	0	0	0	0	10	1
31	0	0	0	0	0	0	0	0	1	0	0	0
32	0	0	0	0	0	0	0	0	0	31	0	0
33	42	0	0	0	0	0	0	0	0	4	0	2
34	0	0	0	0	0	24	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	4	0
36	17	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	1	0	0	0	2	0
38	0	0	0	0	0	170	0	0	0	0	0	0
39	6	0	0	0	0	0	0	0	3	2	45	0
40	0	0	0	0	0	2	0	0	14	0	20	0
41	0	2	0	0	0	0	0	0	0	0	0	0
42	4	0	0	0	0	0	0	0	0	1	1	1
43	8	0	0	0	0	3	0	0	29	0	9	0
44	18	0	0	1	0	7	1	0	41	55	33	1
45	78	1	3	0	0	0	2	0	1	10	23	5
46	2	0	0	0	0	26	1	0	1	1	3	0
47	16	0	0	0	3	18	0	0	0	18	78	0
48	5	0	0	0	0	9	0	0	1	8	0	1
49	0	0	0	0	0	0	0	0	1	0	0	0

Species: 1, *Acyrtosiphon pisum*; 2, *Amphorophora rubi*; 3, *Aphis grossulariae*/*Aphis epilobii*; 4, *Aulocorthum solani*; 5, *Brachycaudus cardui*; 6, *Capitophorus carduinis*; 7, *Macrosiphum funestum*; 8, *Megoura viciae*; 9, *Metopolophium albidum*; 10, *Microlophium carnosum*; 11, *Sitobion fragariae*/*Sitobion avenae*; 12, *Sitobion ptericolens*; 13, *Aphelinus abdominalis*; 14, *Aphelinus varipes*; 15, *Aphidius eadyi*; 16, *Aphidius ervi*; 17, *Aphidius matricariae*; 18, *Aphidius microlophii*; 19, *Aphidius picipes*; 20, *Aphidius rhopalosiphii*; 21, *Aphidius urticae*; 22, *Binodoxys acalephe*; 23, *Ephedrus plagiator*; 24, *Praon abjectum*; 25, *Praon dorsale*; 26, *Praon volucre*; 27, *Alloxysta brachyptera*; 28, *Alloxysta circumscripta*; 29, *Alloxysta cursor*; 30, *Alloxysta fulviceps*; 31, *Alloxysta fuscicornis*; 32, *Alloxysta halterata*; 33, *Alloxysta macrophadna*; 34, *Alloxysta brevis*; 35, *Alloxysta ramulifera*; 36, *Alloxysta ruficollis*; 37, *Alloxysta semiaperta*; 38, *Alloxysta tscheki*; 39, *Alloxysta victrix*; 40, *Phenoglyphis villosa*; 41, *Phenoglyphis xanthochroa*; 42, *Syrphophagus mamitus*; 43, *Asaphes suspensus*; 44, *Asaphes vulgaris*; 45, *Coruna clavata*; 46, *Dendrocerus aphidum*; 47, *Dendrocerus carpenteri*; 48, *Dendrocerus dubiosus*; 49, *Dendrocerus laevis*. Species: 1–12, aphids; 13–26, primary parasitoids; 27–41, hyperparasitoids; 43–49, mummy parasitoids; Species 42 is both a hyperparasitoid and a mummy parasitoid. Primary parasitoid genus *Aphidius* belongs to Aphidiinae (Ichneumonoidea, Braconidae), and genus *Aphelinus* belongs to Aphelinidae (Chalcidoidea). Secondary parasitoid genera split into (family number 1) Alloxystinae (Cynipoidea, Charipidae) for genera *Alloxysta* and *Phenoglyphis*, (family number 2) Pteromalidae (Chalcidoidea) for genera *Asaphes* and *Coruna*, (family number 3) Megaspilidae (Ceraphronoidea) for genus *Dendrocerus*, and (family number 4) Encyrtidae (Chalcidoidea) for genus *Syrphophagus*.

feeds on the aphid. When the aphid contains more than one larva of the same (superparasitism) or different (multiparasitism) species, the larvae fight until one remains. Normally, the larva kills the aphid when the aphid is in the last-instar or adult stage. At this point, the aphid is transformed into a mummy in which the parasitoid larva pupates.

The primary parasitoids may be parasitized by secondary parasitoids that may attack the primary parasitoid larva inside

the still-living aphid (true hyperparasitoids, Charipidae: Alloxystinae) or after the aphid has mummified (mummy parasitoids, Pteromalidae, Megaspilidae, and Encyrtidae). The development of the hyperparasitoid egg(s) and their consumption of the primary parasitoid host are delayed until the primary parasitoid has killed and mummified its aphid host (16). Primary parasitoids and hyperparasitoids can potentially influence the final size of the aphid host, whereas mummy parasitoids cannot.

The major part of the interaction (searching, decision to attack a host, and final oviposition by female wasps, and growth of the primary parasitoid larvae) took place in the field. The aphid host is mummified just before the primary parasitoid larva pupates so growth of the primary parasitoid ceases at host mummification. Thus, the data represent the relationship between host and primary parasitoid body size under field situations (not in the laboratory). Larvae of secondary parasitoids grow within the aphid mummies so that some growth of secondary parasitoids may have occurred under laboratory conditions.

A link is a pair consisting of one host species and one parasitoid species known to feed on the host species. Link averages refer to the geometric mean body size of the host and parasitoid individuals actually observed in each link. Species averages are the geometric mean body size of all individuals of a species. Analyses using arithmetic means instead of geometric means lead to entirely parallel conclusions.

Analysis of covariance in combination with Tukey's honestly significant difference criterion (17) was used to analyze the effect of species identity on the regression slope. All individual data points are treated as statistically independent in calculating P values. Further details are given in *Supporting Text*, which is published as supporting information on the PNAS web site.

Results

Across individuals of all species, the sizes of emerging parasitoids were strongly positively related to final aphid size for primary, hyper-, and mummy parasitoids (Fig. 1A and Table 2). On a log-log scale, there was no significant difference in regression slope between primary and secondary parasitoids ($P = 0.16$), but the intercepts and overall regressions were both significantly different ($P < 0.001$). The slope of the relationship was significantly less than 1 ($P < 0.001$) and was close to $3/4$ for both primary ($b = 0.77$, $r^2 \approx 0.85$) and secondary ($b = 0.76$, $r^2 \approx 0.72$) parasitoids (Table 2). The regression slopes for individual species differed extensively among themselves and differed widely from the regression slopes of 0.76 or 0.77 over all individuals. The slopes 0.76 or 0.77 represented the interspecific trend over a wider range of body sizes than the species-specific clouds of points. The minimum and maximum lengths of all 2,151 aphids were 0.69 and 3.97 mm, respectively, whereas the aphid hosts of individual species of parasitoids covered a narrower range of body sizes (Table 3, which is published as supporting information on the PNAS web site).

When link averages were used instead of body sizes of individuals, the intercept and slope of the relationship between aphid host and parasitoid body sizes were similar to those obtained when using individual data (Fig. 1B and Table 2) for both primary and secondary parasitoids. The slopes were significantly less than 1 ($P < 0.001$) but not significantly different from $3/4$ ($P > 0.077$). On a log-log scale, a significant amount of the variation in average parasitoid size was explained by the average size of the aphid mummy ($r^2 \approx 0.87$ for primary parasitoids, $r^2 \approx 0.68$ for secondary parasitoids collectively, $r^2 \approx 0.92$ for hyperparasitoids, and $r^2 \approx 0.78$ for mummy parasitoids).

Using the geometric-average body size of all of the individuals of a species (i.e., species averages) instead of body sizes of individuals or link averages markedly affected the relationship between aphid host and parasitoid body size (Fig. 1C and Table 2). For primary parasitoids and hyperparasitoids, the intercepts increased, whereas the slopes decreased to the neighborhood of $1/2$. The slopes were significantly less than both 1 ($P < 0.001$) and $3/4$ ($P < 0.008$). Much less of the variation in parasitoid size was explained by the size of the aphid mummy ($r^2 \approx 0.54$ for primary parasitoids and $r^2 \approx 0.51$ for hyperparasitoids). For mummy parasitoids, the relationship between final aphid size and parasitoid size was no longer statistically significant ($P >$

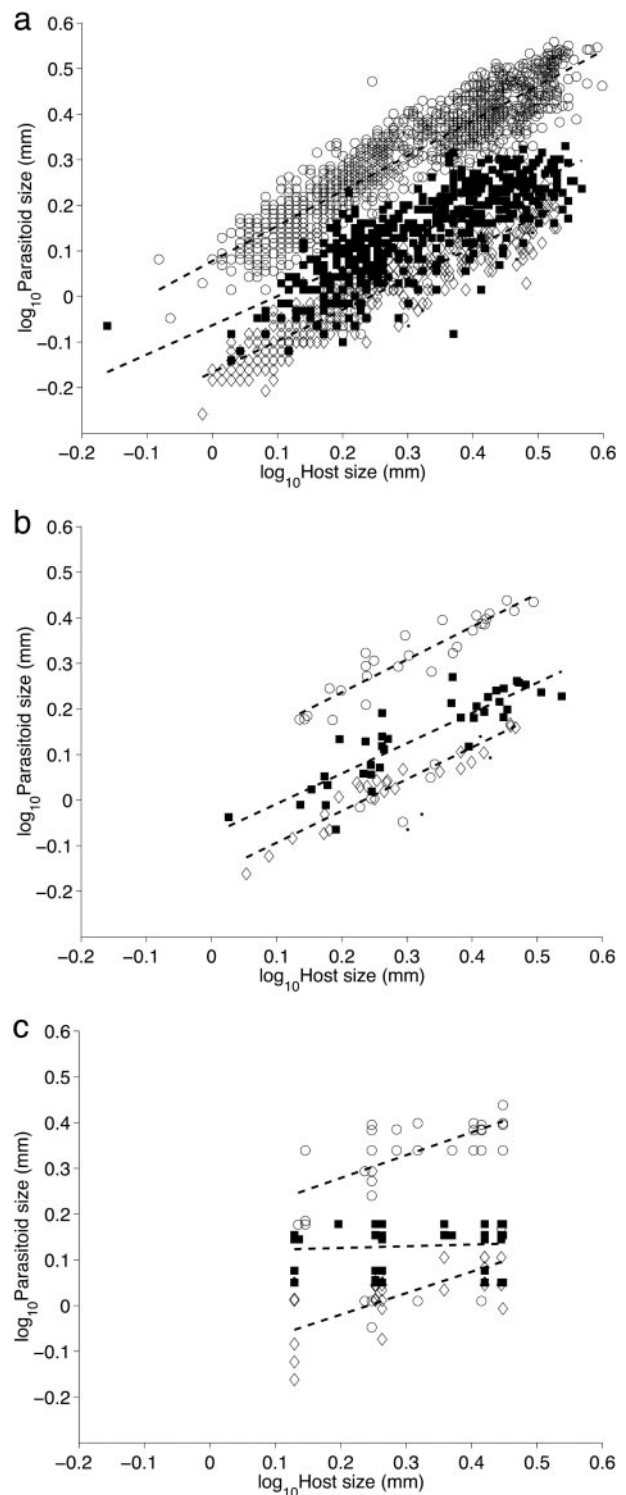


Fig. 1. The relationship between aphid host body size and parasitoid body size. (A) Individual data. Each marker represents the body size of a parasitoid individual and the body size of the individual aphid host from which the parasitoid emerged. (B) Link-average data. Each marker represents the geometric-average body size of the individuals of the host and parasitoid involved in one trophic link. (C) Species-average data. Each marker represents the geometric-average body size of the host and parasitoid species. \circ , primary parasitoids; \diamond , hyperparasitoids; \blacksquare , mummy parasitoids; \blacktriangledown , secondary parasitoid *Syrphophagus mamitus* (see *Methods*). Dashed lines in A–C are the ordinary least-squares regression lines of \log_{10} (lengths) after excluding observations of *Aphelinus abdominalis*, *Aphelinus varipes*, and *Syrphophagus mamitus* (see *Supporting Text*).

Table 2. Ordinary least square regressions of log parasitoid length as a function of log aphid host length using body size data of individuals (A), the geometric mean body size of the individuals involved in each link (B), and the geometric mean body size of all individuals of each species (C)

Relationship	Data type	a (\pm 95% c.l.)	b (\pm 95% c.l.)	r	n	P
$\log_{10}(PP) = a + b\log_{10}(H)$	A	0.0780 \pm 0.0061	0.7694 \pm 0.0182	0.9239	1,177*	<0.001
	B	0.09218 \pm 0.0379	0.7208 \pm 0.1149	0.9326	27*	<0.001
	C	0.1759 \pm 0.0643	0.5056 \pm 0.1922	0.7349	27*	<0.001
$\log_{10}(SP) = a + b\log_{10}(H)$	A	-0.1405 \pm 0.0096	0.7644 \pm 0.0305	0.8493	939	<0.001
	B	-0.1291 \pm 0.0400	0.7171 \pm 0.1215	0.8274	66	<0.001
	C	0.0157 \pm 0.0535	0.2292 \pm 0.1636	0.3302	66	0.0034
$\log_{10}(HP) = a + b\log_{10}(H)$	A	-0.1665 \pm 0.0070	0.6862 \pm 0.0255	0.9339	411	<0.001
	B	-0.1632 \pm 0.0271	0.6972 \pm 0.0910	0.9571	27	<0.001
	C	-0.1135 \pm 0.0628	0.4685 \pm 0.1982	0.7140	27	<0.001
$\log_{10}(MP) = a + b\log_{10}(H)$	A	-0.0632 \pm 0.0141	0.6374 \pm 0.0409	0.8026	521	<0.001
	B	-0.0746 \pm 0.0412	0.6644 \pm 0.1197	0.8854	39	<0.001
	C	0.1185 \pm 0.0476	0.0373 \pm 0.1428	0.0892	39	0.2999

H , aphid host size; PP , primary parasitoid size; SP , secondary parasitoid size; HP , hyperparasitoid size; MP , mummy parasitoid size (all in millimeters). The correlation coefficient is denoted by r , n is the number of observations, and P is the probability that the slope is not different from 0. For the intercept a and the slope coefficient b , 95% c.l. gives the 95% confidence limits. For example, in the first line, the 95% confidence interval of the estimate $b = 0.7694$ is from 0.7512 to 0.7876.

*Observations involving primary parasitoids *Aphelinus abdominalis* and *Aphelinus varipes* excluded (see Supporting Text).

0.29). The average size of a mummy parasitoid species was unrelated to the average size of the aphid species.

Further details of the results, such as a comparison of the relationship between hyper- and mummy parasitoids, as well as a description of species-specific relationships, are given in *Supporting Text*.

Discussion

This analysis of data on body sizes of individual aphids and parasitoids in a natural community of 49 species led to three conclusions. First, the relationship between emerging parasitoid body size and final aphid host body size depended on the type of parasitoid (primary, hyper-, or mummy parasitoid) as well as on the species identity of the parasitoid. Second, using the average size of a species to study the relation between consumer and resource body sizes generated a misleading picture of the real feeding interactions between an individual host and an individual parasitoid. Third, the body lengths of parasitoid individuals were related to the body lengths of aphid host individuals by a power law with an exponent close to 3/4. We discuss these conclusions and conclude by suggesting their implications for community dynamics.

Effects of Aggregation to Species Averages and of Species Identity. In the data analyzed here, going from individuals' body lengths to species-average body lengths dramatically lowered the estimated exponent (from nearly 3/4 to nearly 1/2 for primary parasitoids) of an allometric relationship, and lowered the proportion of variance that the relationship explains. According to Jensen's inequality, the average of differing individual body masses, each raised to a power $b < 1$, is less than the species-average body mass raised to the power b (18). Allometric functions may be corrected to allow for averaging, and the corrections matter when averaging over systems where the range in body size is large compared with the average body size (19). The statistical literature on the pitfalls of averaging nonlinear functions is extensive (19).

The close adjustment between the body sizes of individual aphid hosts and their individual primary parasitoids suggested that parasitoids developed under the joint influence of the host and the primary parasitoids, and that secondary parasitoids were influenced by both their hosts and their primary parasitoids. These mutual influences may include indirect influences of the genes of the individual aphid, primary parasitoid, and secondary

parasitoid (3). Both the type of parasitoid (primary, hyper-, or mummy parasitoid) and the species identity of the plant, aphid, or parasitoid affected the relationship between the emerging parasitoid body size and the final aphid host body size. To accurately predict the body size of an emerging parasitoid, it was not sufficient to know the body size of the attacked host individual and the type of parasitoid. The species identities of the aphid and parasitoid also mattered.

Within each type of parasitoid (primary, hyper-, and mummy parasitoid), the relationship between parasitoid and aphid body size was different for different plant and aphid species. Aphid species identity did not seem to matter much for the slope of the relationship within any given parasitoid species. The explanation of this apparent contradiction is that most parasitoid species in this community were very host-specific and mainly attacked one aphid species. The slope of the relationship differed for different aphid species mainly because they were attacked by different parasitoid species. For the few parasitoid species where the data allowed the effect of aphid species identity on the regression slope to be analyzed within a parasitoid species, the effects of aphid species identity were, with one exception, insignificant. The type and species identity of the parasitoid seemed to matter most for the relationship between parasitoid and aphid body size. Plant and aphid species identities were important through the association with different parasitoid species and because different aphid species had different body sizes.

Two Models of Allometric Length Scaling in Parasitoid and Host. The conclusion that the body lengths of emerging parasitoid individuals were related to the body lengths of aphid host individuals by a power law with an exponent close to 3/4 raises the question: what explains 3/4? We propose two testable explanations. In summary, the first model assumes that emerging parasitoid mass scales in proportion to the host's surface area. This model must be rejected if observations indicate that the parasitoid gets relatively fatter, whereas the host gets relatively thinner, with increasing length. The second model assumes that parasitoid metabolic rate scales in proportion to host metabolic rate. Contrary to the first model, this second model must be rejected if the parasitoid gets relatively thinner and the host gets relatively fatter as they get longer.

As a preliminary to the first model, an overly simple physical model may be constructed from the observation that the aphid host breathes through tracheae. For biological background and

interesting observations on insect tracheal systems, see Kozłowski and Konarzewski (ref. 20, p. 287). Suppose that the rate of oxygen supply to the host's tissue is limited by its surface area, or by a quantity proportional to its surface area. Savage *et al.* (ref. 19, p. 258) traced this "surface-area rule" as well as the basic ideas in the rest of this paragraph back to a paper by Rubner in 1883 (40). Suppose the parasitoid body density (weight per unit of volume) is independent of size, so that parasitoid volume is proportional to parasitoid mass, and suppose that emerging parasitoid mass is limited by the rate of oxygen supply within the host, i.e., by the host's surface area. Let L be the length of the host and A be the surface area of the host. Let λ be the length of the parasitoid and let μ be the mass of the parasitoid (proportional to volume by assumption). If the parasitoid body form is the same at all lengths (an assumption of geometric similarity), so that its mass or volume is proportional to the cube of its length, then $\lambda^3 \approx \mu \approx A$ (where \approx means proportionality). If the host body form is the same at all lengths (geometric similarity), so that $A \approx L^2$, then $\lambda^3 \approx L^2$ or $\lambda \approx L^{2/3}$. The exponent $2/3$ is nearly $3/4$, but not near enough to describe our data accurately.

Our first model refines this classic model by abandoning either or both of the assumptions that the parasitoid and the host body forms are the same at all body lengths. Suppose, for example, that the host body form may be approximated by a cylinder with basal diameter D and length L perpendicular to the base, so that $A = \pi D(D/2 + L)$, and that the parasitoid body form may also be approximated by a cylinder of basal diameter Δ and length λ perpendicular to the base, so that $\mu \approx \Delta^2 \lambda$. Suppose that $\Delta \approx \lambda^{1-\delta}$ and that $D \approx L^{1+\varepsilon}$, for some δ and ε . If $\delta > 0$, then parasitoid body form is predicted to become relatively thinner with increasing length. Here, "relatively thinner" means that Δ does not increase by as large a proportion as λ increases, whether or not Δ increases absolutely as λ increases absolutely. Likewise, if $\varepsilon > 0$, then host body form is predicted to become relatively fatter with increasing length. Here, "relatively fatter" means that D increases by a higher proportion than L increases. However, we do not assume that $\delta > 0$ and $\varepsilon > 0$.

If parasitoid mass is proportional to the host surface area, $\mu \approx A$, then $\mu \approx \Delta^2 \lambda \approx \lambda^{3-2\delta} \approx A \approx D(D/2 + L) \approx L^{2+\varepsilon}(L^\varepsilon/2 + 1)$. If ε is small enough that, for the relevant range of variation in values of L , the proportional variation in $L^{2+\varepsilon}(L^\varepsilon/2 + 1)$ is largely accounted for by the proportional variation in $L^{2+\varepsilon}$ (an assumption that will be checked below), then approximately $\lambda^{3-2\delta} \approx L^{2+\varepsilon}$ or $\lambda \approx L^{(2+\varepsilon)/(3-2\delta)}$. Any combination of values of δ and ε such that $3/4 = (2+\varepsilon)/(3-2\delta)$, or equivalently $4\varepsilon + 6\delta = 1$, will reproduce the estimated $3/4$ slope of the linear relationship between log parasitoid body length and log host body length. The constraint $4\varepsilon + 6\delta = 1$ can be satisfied by $\delta > 0$ and $\varepsilon > 0$, for example, $\delta = \varepsilon = 1/10$. To satisfy $4\varepsilon + 6\delta = 1$ and $\delta > 0$ and $\varepsilon > 0$ requires that $\varepsilon \leq 1/4$ and $\delta \leq 1/6$.

We now check the intermediate assumption that the proportional variation in $L^{2+\varepsilon}(L^\varepsilon/2 + 1)$ is largely accounted for by the proportional variation in $L^{2+\varepsilon}$. Because we are estimating slopes on log scales, what matters is the ratio of changes in $L^{2+\varepsilon}(L^\varepsilon/2 + 1)$ over the range in our data (Table 3) from minimum $L_{\min} = 0.69$ mm to maximum $L_{\max} = 3.97$. Recall that $1/4$ is the largest value of ε compatible with the measured exponent of $3/4$ if $\delta > 0$ and $\varepsilon > 0$. With $\varepsilon = 1/4$, $L_{\min}^{2+\varepsilon}(L_{\min}^\varepsilon/2 + 1) = 0.63$ and $L_{\max}^{2+\varepsilon}(L_{\max}^\varepsilon/2 + 1) = 37.95$. The ratio of the latter to the former is ≈ 60.1 . By using the power-law approximation with $\varepsilon = 1/4$, $L_{\min}^{2+\varepsilon} = 0.43$, and $L_{\max}^{2+\varepsilon} = 22.27$. The ratio of the latter to the former is ≈ 51.3 . The ratio of these ratios, $60.1/51.3 = 1.17 = (L_{\max}^\varepsilon/2 + 1)/(L_{\min}^\varepsilon/2 + 1)$, is not grossly different from 1. Even if $\varepsilon = 1/2$, $(L_{\max}^\varepsilon/2 + 1)/(L_{\min}^\varepsilon/2 + 1) = 1.41$. The intermediate assumption, then, is reasonable for the observed range of L .

In addition to the case where $\delta > 0$ and $\varepsilon > 0$, the constraint

$4\varepsilon + 6\delta = 1$ can be satisfied in other ways, for example, by $\varepsilon = -1/2$, $\delta = +1/2$, so that both the parasitoid and the host are predicted to become relatively thinner (and, moreover, because $\varepsilon = -\delta$ in this instance, the host and parasitoid get relatively thinner at the same rate). Alternatively, the constraint $4\varepsilon + 6\delta = 1$ can be satisfied, for example, by $\varepsilon = +3/4$, $\delta = -1/3$, so that now the parasitoid is predicted to get relatively fatter (unlike before), whereas host body form is predicted to become relatively fatter with increasing length (as when $\delta > 0$ and $\varepsilon > 0$). Only the combination $\delta < 0$ and $\varepsilon < 0$ is incapable of satisfying the constraint $4\varepsilon + 6\delta = 1$. The model must be rejected if observations indicate that the parasitoid gets relatively fatter, whereas the host gets relatively thinner with increasing length.

In a second model, instead of assuming that emerging parasitoid body mass scales in proportion to host surface area, an alternative approach assumes that emerging parasitoid metabolic rate β scales in proportion to host metabolic rate B . This assumption follows if the emerging metabolic rate (rate of oxygen consumption) for the parasitoid is limited by the rate of nutrient supply from the host, which in turn is determined by the metabolic rate of the host. The metabolic rate of the host may be proportional to its surface area, in which case B and A may be used interchangeably in these derivations. If metabolic rate scales with body mass according to $\beta \approx \mu^\eta$ and $B \approx M^\eta$ for the parasitoid and host, and if body mass scales with length according to $\mu \approx \lambda^\sigma$ and $M \approx L^s$ for the parasitoid and host, then $\beta \approx B$ implies that $\lambda \approx L^{s/(\sigma\eta)}$. If $\eta = y$, whether their common value be $2/3$ or $3/4$ or any other non-zero value, then $\lambda \approx L^{s/\sigma}$. Geometric similarity of body form requires $s = \sigma = 3$, leading to the prediction that $\lambda \approx L$, which is not consistent with the data unless the assumption that $\eta = y$ is abandoned. However, the relation $\eta = y$ can be maintained if, as in the previous model, body diameters scale with increasing body lengths according to $\Delta \approx \lambda^{1-\delta}$ for parasitoids and $D \approx L^{1+\varepsilon}$ for hosts. Then, instead of geometric similarity, one has $\sigma = 3 - 2\delta$ and $s = 3 + 2\varepsilon$. Imposing agreement with the observed $3/4$ slope of log parasitoid body length as a function of log aphid length, i.e., $3/4 = s/\sigma = (3 + 2\varepsilon)/(3 - 2\delta)$, leads to $6\delta + 8\varepsilon = -3$. Possible solutions of this constraint include $\delta = +1/2$, $\varepsilon = -3/4$ (the parasitoid and host both get relatively thinner as they get longer), $\delta = -2/3$, $\varepsilon = +1/8$ (the parasitoid and host both get relatively fatter as they get longer), and $\delta = -1/3$, $\varepsilon = -1/8$ (the parasitoid gets relatively fatter, whereas the host gets relatively thinner as they get longer). If $\varepsilon = -\delta$, then $\delta = 3/2$ and $\Delta \approx \lambda^{-1/2}$ for parasitoids and $D \approx L^{-1/2}$ for hosts. In this case, both parasitoids and hosts thin absolutely (their diameters decrease with increasing length) as well as thinning relatively. Only the combination $\delta > 0$ and $\varepsilon > 0$ is excluded. Contrary to the previous approach, this model (on the assumption that $\eta = y$) must be rejected if the parasitoid gets relatively thinner and the host gets relatively fatter as they get longer.

The system of simultaneous constraints $6\delta + 4\varepsilon = 1$ and $6\delta + 8\varepsilon = -3$ has a unique solution $\delta = 5/6$ and $\varepsilon = -1$. Only for these values of δ and ε would it be impossible to distinguish the two models on the basis of the body-form scaling exponents alone. Both models assumed that $\Delta \approx \lambda^{1-\delta}$ and that $D \approx L^{1+\varepsilon}$. If $\delta = 5/6$, $\varepsilon = -1$, then $\Delta \approx \lambda^{1/6}$, and $D \approx L^0$, i.e., the diameter of the parasitoid would increase very slowly with increasing parasitoid length, whereas the diameter of the aphid would not increase at all with increasing aphid length. Otherwise, if power-law scaling of body form were a good approximation to the data for both parasitoid and host, the estimated values of δ and ε would reject one or both models. Thus, these models are readily testable with appropriate data for parasitoids and aphids on how body diameter scales with body length.

In several temperate and tropical habitats, for a variety of insect taxa at various levels of taxonomic resolution, linear regressions of log body dry mass as a function of log length had

ERRATUM

J. E. Cohen, Tomas Jonsson, Christine B. Müller, H. C. J. Godfray and Van M. Savage 2005. Body sizes of hosts and parasitoids in individual feeding relationships. *Proceedings of the National Academy of Sciences* 102(3):684-689. 2005 www.pnas.org/cgi/doi/10.1073/pnas.0408780102

On page 687, left column, next to last paragraph, the correct article for Reference (19) is:

Van M. Savage (2004). Improved approximations to scaling relationships for species, populations, and ecosystems across latitudinal and elevational gradients. *J Theor Biol* 227(4), 525-534.

Elsewhere in this article, reference to (19) is as shown on page 689.

Table 3. The slope, intercept, and degrees of freedom (df) of the linear least square regressions of \log_{10} (parasitoid size) as a function of \log_{10} (aphid size) for different species of parasitoid

Parasitoid species	Slope	Intercept	df	Minimum aphid length, mm	Maximum aphid length, mm
<i>Aphelinus abdominalis</i>	0.7039	-0.1702	32	1.31	2.52
<i>Aphidius eadyi</i>	0.4292	0.2081	75	1.52	3.62
<i>Aphidius ervi</i>	0.5961	0.1346	101	1.31	3.38
<i>Aphidius matricariae</i>	0.8927	0.0563	231	0.83	1.97
<i>Aphidius microlophii</i>	0.7744	0.0873	286	1.83	3.79
<i>Aphidius picipes</i>	0.6170	0.1383	10	1.76	3.28
<i>Aphidius rhopalosiphi</i>	0.5343	0.1510	68	1.31	3.03
<i>Aphidius urticae</i>	0.4272	0.2222	57	1.76	3.97
<i>Binodoxys acalephe</i>	0.7507	0.0701	66	1.03	1.83
<i>Ephedrus plagiator</i>	0.7936	0.0827	92	1.21	2.45
<i>Praon abjectum</i>	0.7495	0.0746	99	1.14	1.93
<i>Praon dorsale</i>	0.3684	0.2111	58	1.41	3.31
<i>Praon volucre</i>	0.8938	0.0628	10	1.14	2.10
<i>Alloxysta fulviceps</i>	0.4664	-0.0835	9	1.38	2.41
<i>Alloxysta halterata</i>	0.4708	-0.0484	29	2.34	3.34
<i>Alloxysta macrophadna</i>	0.4595	-0.0854	46	1.69	3.38
<i>Alloxysta brevis</i>	0.8478	-0.1978	22	1.00	1.52
<i>Alloxysta ruficollis</i>	0.2038	0.0017	15	2.00	3.21
<i>Alloxysta tscheki</i>	0.8478	-0.1893	168	0.97	1.83
<i>Alloxysta victrix</i>	0.4489	-0.0812	54	1.38	3.28
<i>Phenoglyphis villosa</i>	0.5143	-0.1244	34	1.45	2.48
<i>Asaphes suspensus</i>	0.5053	-0.0537	47	0.69	3.21
<i>Asaphes vulgaris</i>	0.7648	-0.1100	155	1.21	3.55

<i>Coruna clavata</i>	0.4626	0.0033	121	1.45	3.59
<i>Dendrocerus aphidum</i>	0.7332	-0.0934	32	1.07	3.21
<i>Dendrocerus carpenteri</i>	0.5675	-0.0272	131	1.21	3.69
<i>Dendrocerus dubiosus</i>	0.6950	-0.0785	22	1.28	3.34

Linear least square regression was performed on primary parasitoid *Aphelinus abdominalis* and is reported above, but this species was not included in the analysis of covariance reported in the text (see *Supporting Methods*). The df for each species is the number of data points minus 2. Summing the df column in the table yields 2,070, which, with 27 species in this table, corresponds to $2,070 + (27 \times 2) = 2,124$ data points. Data for 10 species of parasitoids (representing 27 data points) in the community reported in this study were not included in the regressions reported above due to fewer than 10 data points (see *Supporting Methods*). $2,124$ (represented in the table above) + 27 (not represented in the table above) = 2,151, the total number of data points. The minimum and maximum lengths of all 2,151 aphids (including those omitted from the list above) were 0.69 and 3.97 mm, respectively.

Supporting Text

Supporting Methods

The relationship between host and parasitoid body length was slightly curvilinear on linear scales of body length, but more or less linear on log-log scales. On linear scales, the variance in parasitoid size increased with increasing host size, but not on log-log scales. Thus, log-log scales were used for analyzing the relationship between host and parasitoid body lengths.

Primary parasitoid species belonging to the genus *Aphelinus* were generally much smaller than, and different in shape from, members of the other primary parasitoid genera analyzed here. They tended to attack small stages of the aphids and also took much longer to develop than parasitoids within the Braconidae. By visual inspection of Fig. 1, observations involving the genus *Aphelinus* were outliers with respect to the other primary parasitoids (circles located in the lower part of the scatter of secondary parasitoid observations in Fig. 1). Therefore, we excluded 34 observations involving primary parasitoid *Aphelinus abdominalis* and one observation involving primary parasitoid *Aphelinus varipes* from the regression analyses of the data in Fig. 1a. We also excluded four links involving *A. abdominalis* and one link involving *A. varipes* from the regression analyses of the data in Fig. 1 b and c. Secondary parasitoid species *Syrphophagus mamitus* sometimes behaved as a hyperparasitoid and sometimes as a mummy parasitoid; seven observations involving this species (dots in Fig. 1) were excluded from the regression analyses in Fig. 1, where hyperparasitoids were distinguished from mummy parasitoids, but were included in the analyses of all secondary parasitoids.

For the reasons mentioned above, we excluded 34 observations involving primary parasitoid *Aphelinus abdominalis* from the analyses of the effect of primary parasitoid species identity on the regression slope. Only species with >10 data points (individual observations of a parasitoid emerging from an aphid) were included in the analysis.

Supporting Results

Comparison of Secondary Parasitoids: Hyperparasitoids Vs. Mummy Parasitoids. The biologically important distinction between secondary parasitoids, called hyperparasitoids, that attack the still living aphid before mummification (in this web, members of the Alloxystinae genera *Alloxysta* and *Phaenoglyphis*) and the other secondary parasitoids, so-called mummy parasitoids, that attack the aphid after mummification (see *Methods*) influenced the relation between final aphid host size and the size of the emergent parasitoid. The slope was significantly <1 ($P < 0.001$) for hyperparasitoids ($b = 0.6862$, $r^2 \sim 0.87$) and mummy parasitoids ($b = 0.6374$, $r^2 \sim 0.64$) analyzed separately. These slopes were also significantly less than 3/4 and were significantly different ($P = 0.025$) from one another.

Comparison of Primary and Secondary Parasitoids. Overall, individual body length measurements presented this picture. When emerging from aphids of similar final size, primary parasitoids were, with a few exceptions, larger than secondary parasitoids and similar in size to their hosts. Small aphid mummies gave rise to primary parasitoids slightly longer than themselves, and large aphid mummies produced primary parasitoids slightly shorter than themselves. Emerging secondary parasitoids were smaller than their aphid hosts. Parasitoids emerging from larger aphids were larger absolutely but smaller relative to their aphid hosts than parasitoids emerging from smaller aphids.

Effects of Parasitoid Type and of Species of Plant, Aphid, and Parasitoid. Within each type of parasitoid (primary, hyper-, and mummy parasitoid), analysis of covariance showed that the relationship between parasitoid log body length and aphid log body length was affected by the species identity of the plant ($P < 0.001$ for both slope and intercept among primary, hyper-, and mummy parasitoids), aphid ($P < 0.001$ for both slope and intercept among primary, hyper-, and mummy parasitoids), and parasitoid species ($P < 0.001$ for both slope and intercept among primary, hyper-, and mummy parasitoids). Table 3 gives the slope, intercept, and degrees of freedom of the linear least square regressions of $\log_{10}(\text{parasitoid size})$ as a function of $\log_{10}(\text{aphid size})$ for different species of parasitoid. Among different species of primary parasitoids, the slopes ranged from 0.3684 to 0.8938 (a mean of 0.6523). A multiple comparison showed that the slopes of 8 of 12 species of primary parasitoids were significantly different from the slope of at least one other primary parasitoid and no single species was responsible for the difference among species. Among hyperparasitoids, the slopes ranged from 0.2038 to 0.8478 (a mean of 0.5324), and one species (*Alloxysta tscheki*) was the main contributor to the overall significant difference among slopes. The slope for this species was significantly different from the slopes of five (species *Alloxysta halterata*, *Alloxysta macrophadna*, *Alloxysta ruficollis*, *Alloxysta victrix*, and *Phenoglyphis villosa*) of the other seven hyperparasitoid species. In addition, the slope of *Alloxysta brevis* was significantly different from that of species *Alloxysta ruficollis*. Among mummy parasitoids, the slopes ranged from 0.5053 to 0.7648 (a mean of 0.6214), and one species (*Asaphes vulgaris*) was the only contributor to the overall significant difference among slopes. The slope for this species was significantly different from the slopes of three (species *Asaphes suspensus*, *Coruna clavata*, and *Dendrocerus carpenteri*) of the other five mummy parasitoid species, and no other slopes were significantly different from any other.

The effect of aphid species identity on the regression slope within different parasitoid species was difficult to analyze. Most individuals in any given species of parasitoid emerged from only one species of aphid (not necessarily the same species of aphid for different parasitoid species), preventing an analysis of differences in regression slopes among different aphid species within one species of parasitoid. For the few parasitoid species (*Asaphes vulgaris*, *Coruna clavata*, and *Dendrocerus carpenteri*) where individuals emerged in sufficient numbers from several species of aphids, an analysis of covariance in combination with a multiple comparison showed that only for parasitoid species *Coruna clavata* did aphid species identity significantly affect the slope of the relationship between aphid and parasitoid size ($P = 0.0474$). For this parasitoid species, the slope of aphid species *Microlophium carnosum* was significantly different from the slope of aphid species *Sitobion fragariae/Sitobion avenae*.

Effect of Aphid Life Stage and Parasitoid Sex. Female parasitoids tended to be larger than male parasitoids, and parasitoids emerging from adult aphid mummies were larger, on average, than those emerging from nymphal aphid mummies. Specifically, within primary parasitoids, hyperparasitoids, and mummy parasitoids, the relationships between log size of aphid host and log size of emerging parasitoid were in most cases significantly different among female and male parasitoids emerging from nymphal and adult aphid mummies (F-test of four regression lines, against the null hypothesis of no difference, within primary parasitoids: $P_{\text{slope}} = 0.0037$, $P_{\text{intercept}} < 0.001$, $P_{\text{overall}} < 0.001$; within hyperparasitoids: $P_{\text{slope}} = 0.0018$, $P_{\text{intercept}} < 0.001$, $P_{\text{overall}} < 0.001$; and within mummy parasitoids: $P_{\text{slope}} = 0.08534$, $P_{\text{intercept}} < 0.001$, $P_{\text{overall}} < 0.001$). Within each category of parasitoids (primary, hyper-, and mummy parasitoids), the slope was different ($P < 0.05$, Tukey's test) between female parasitoids emerging from nymphal aphids and female parasitoids emerging from adult aphids. The slope tended not to be different between female and male parasitoids emerging from nymphal aphids (with the exception of hyperparasitoids, $P = 0.049$) and between female and male parasitoids emerging from adult aphids (with the exception of mummy parasitoids, $P = 0.041$).

When the intercepts, but not the slopes, differed significantly between female and male parasitoids emerging from nymphal aphids and/or between female and male parasitoids emerging from adult aphids, then the sexual size dimorphism in parasitoids was constant for hosts of any length. For example, the difference in intercepts yielded a ratio of male primary parasitoid body length to female primary parasitoid body length of 0.88 (for primary parasitoids emerging from nymphal aphids) and 0.87 (for primary parasitoids emerging from adult aphids).

Hyperparasitoid species developed differently. Female hyperparasitoids emerging from nymphal aphids had a significantly steeper slope than males (but not a significantly different intercept). The ratio of male hyperparasitoid body length to female hyperparasitoid body length was close to 1 for a 1-mm nymphal aphid mummy and decreased as the size of the nymphal aphid mummy increased. For hyperparasitoids emerging from adult aphid mummies, neither slope nor intercept differed significantly between males and females, implying a constant sex ratio of body length close to unity.

Intercepts, but not slopes, differed significantly between male and female mummy parasitoids emerging from nymphal aphid mummies, yielding a constant ratio of male parasitoid body length to female parasitoid body length of ≈ 0.88 . For mummy parasitoids emerging from adult aphid mummies, both slope and intercept differed significantly between males and females, yielding an increasing ratio of male parasitoid body length to female parasitoid body length (because males showed a significantly steeper slope than females).

In summary, the relationship (across species of parasitoids) between aphid host and emerging parasitoid body length was affected by the life stage of the aphid when mummified (nymph or adult) and the sex of the emerging parasitoid, in addition to being affected by the species identity of the plant, aphid and parasitoid. Within parasitoid species, the relationship between host and parasitoid body length was in general too weak (because of too few data points) to allow an analysis of the effect of life stage of the aphid when mummified and of the sex of the emerging parasitoid.

Few parasitoid species had 10 or more observations of a parasitoid emerging from a particular aphid species in each of the four categories: (i) female parasitoid emerging from larval host, (ii) male parasitoid emerging from larval host, (iii) female parasitoid emerging from adult host, and (iv) male parasitoid emerging from adult host. In three of the four combinations of aphid and primary parasitoid species with enough observations (≥ 10), the intercepts were significantly different but not the slopes. Among hyperparasitoid species, the intercepts were significantly different, but not the slopes in the one combination of aphid and parasitoid species with enough observations. Among mummy parasitoids, no combinations of aphid and parasitoid species had enough observations to allow an analysis of the effect of life stage of the aphid when mummified and the sex of the emerging parasitoid.

Discussion of Results. Previous studies found a relationship between the size of the aphid and the size of the emerging parasitoid and inferred that developing parasitoid larvae were resource limited. Parasitoid-host choice models assumed that female wasps selectively placed fertilized eggs (i.e., daughters), in large (i.e., high-quality) hosts, and unfertilized eggs (i.e., sons), and in small (i.e., low-quality) hosts. If parasitoid larvae were resource-limited, female parasitoids should be larger than male parasitoids because the aphid size of emerging female parasitoids would be larger, on average, than the aphid size of emerging male parasitoids. However, whether female parasitoids were larger than male parasitoids, on average, when emerging from hosts of similar size, this would imply that female parasitoid larvae used resources more efficiently than male parasitoid larvae. The latter alternative

appears to hold in the data analyzed here because female primary parasitoids were larger, on average, than male parasitoids when emerging from hosts of similar size.

In most species of parasitoid wasps, females are larger than males, although the range of male and female sizes overlaps in many species (reviewed by Hurlbutt; ref 1). In a few groups of parasitoid wasps, the sexual size dimorphism was reversed: males were larger than females. The ratio of male parasitoid body length to female parasitoid body length ranged from 0.56 to 1.56, with a mean of 0.89, across all 361 species analyzed by Hurlbutt (1). In two species of parasitoid wasps, the size ratio changed with the size of the host. The size ratio Hurlbutt (1) found was remarkably close to the values found here. The data analyzed here suggested that the ratio of male parasitoid body length to female parasitoid body length changed with the length of the host in hyperparasitoids and mummy parasitoids, but not in primary parasitoids. Female hyperparasitoid and mummy parasitoid larvae may use resources more efficiently than male hyperparasitoid and mummy parasitoid larvae, respectively.

1. Hurlbutt, B. (1987) *Biol. J. Linn. Soc.* **30**, 63-89.