

The allometry of egg size and number in insects

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I describe the interspecific scaling of egg size, egg number, and ovary volume in three insect orders; Diptera, Hymenoptera, and Coleoptera. Egg number is correlated with body size in Diptera but not in the Hymenoptera or Coleoptera, whereas egg size and ovary volume are correlated with body size in all three orders. Egg volume shows strong negative allometry in all three taxa whereas ovary volume scales isometrically in the Diptera and Hymenoptera and with negative allometry in the Coleoptera. In all three orders there was a strong negative correlation between the residual values of egg size and number from plots of these parameters versus body size. This is evidence that there is a tradeoff between egg size and number. I argue that the proximate cause of the isometric or negatively allometric scaling of ovary volume and body size is to maintain functionally equivalent levels of locomotor performance. These results are also similar to the results of arguments based on the analysis of direct measurements of energy intake and energy required for maintenance.

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It is widely believed that both potential and realized fecundity increase with size in the females of many plant and animal taxa (but see Leather 1988). Reiss (1987) argues that reproductive effort should be a power function of body weight with an exponent between 0.5 and 1.0. This argument is based on the observation that the energy available for reproduction is the difference between energy intake and energy required for non-reproductive functions (Ware 1980, Roff 1983, Reiss 1987). There is considerable evidence documenting this pattern in vertebrates (reviewed in Lavigne 1982, Reiss 1987). However, there are relatively little data concerning the interspecific allometry of reproductive effort in insects (but see Leather and Wellings 1981, Llewellyn and Brown 1985, Wickman and Karlsson 1989, O'Neill and Skinner 1990).

Recent work on Lepidoptera (Wickman and Karlsson 1989, Marden and Chai 1990), Odonata (Marden 1989), and Diptera (Berrigan 1990) suggests that a proximate explanation for inter- and intraspecific patterns of mass allocation to reproductive effort might involve the maintenance of functionally equivalent levels of flight performance. Muscle mass specific lift production is constant in many flying animals and muscle mass scales isometrically with body mass in interspecific analyses

(Marden 1987). Animals with disproportionately heavy abdomens would suffer decreased levels of flight performance through a reduction in their net lift capacities. One consequence of a constraint on the total abdomen mass is a tradeoff between egg size and number (Smith and Fretwell 1974). This observation has also been made in the context of observations that migratory insects may exhibit an inverse relationship between flight ability or propensity and ovarian development (e.g. Johnson 1969, Walters and Dixon 1983).

In this paper I describe the scaling of egg size, egg number, and ovary volume in three insect orders. I argue that in conjunction with previous work (Marden 1987, Berrigan 1990), these data provide evidence for the hypothesis that the scaling of reproductive effort is constrained by locomotor performance in flying insects.

Materials and methods

Origin of the data

The data used in this study were collected from the literature with the exception of information from four species of Hawaiian *Drosophila*. For these four species

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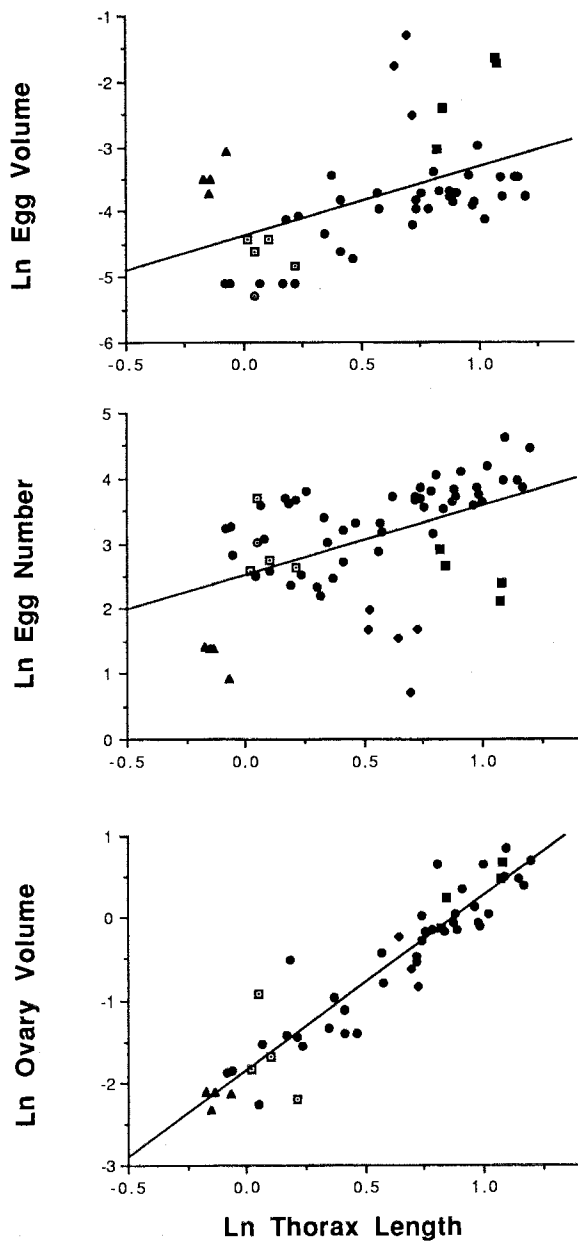


Fig. 1. Ln thorax length versus ln egg volume, egg number, and clutch volume, for species in the family Drosophilidae. Regression statistics are given in Table 1 and the data are listed in Appendix 1. The symbols represent different subgenera; *Antopocerus* (■), *Engioscaphomyza* (◆), *Dorsilopha* (○), *Drosophila* (●), and *Sophophora* (□) in the genus *Drosophila*, and four species of *Scaptomyza* in the subgenus *Exalloscaphomyza* (▲). The lines are the ordinary least squares regression lines.

(see Appendix 1), mature female flies were dissected and their ovariole number, egg number and egg size were recorded. Sample sizes were $n = 14$ (*D. crucigera*), $n = 16$ (*D. grimshawi*), $n = 14$ (*D. heteroneura*), and $n = 8$ (*D. hirtipalpus*). Egg size is reported as the

volume of the egg (mm^3) assuming it is a prolate spheroid and using the formula, $V = 1/6 \pi w^2 L$, where w is the egg width and L is the egg length. Ovary volume is calculated as the product of eggs number and egg volume. Egg number is the product of ovariole number and the average number of eggs per ovariole. Many authors report a range for the number of eggs per ovariole (particularly Kambysellis and Heed 1971). In these cases I use the average of the two extremes to calculate ovary volume. This measure of reproductive effort is a slight underestimate of females' instantaneous allocation to reproductive tissue because I neglect the volume of the nurse cells and the tissue composing the ovariole itself.

Body size is measured as thorax length for the Diptera, body length for the Hymenoptera, and elytra length for the Coleoptera. These linear measures of size are strongly correlated with weight and in many cases are known to be proportional to weight cubed (e.g. Montague et al. 1981). In the following analysis I assume that this is true. However, different linear measures of size may have different intercepts despite having the same exponent in the power function relating length and size. The absence of a uniform measure of body size makes it possible to compare the slopes of the regression equations but not their intercepts.

Taxonomic coverage

I analyze data from three orders of insects; Diptera, Hymenoptera, and Coleoptera. The Diptera are represented by four species of *Scaptomyza* and 58 species of *Drosophila* from five subgenera. Appendix 1 contains the list of sources for the data. A subset of this data containing 35 species was previously analyzed with respect to the tradeoff between egg size and number with similar results (Montague et al. 1981 and see discussion below). The Hymenoptera analyzed include 31 species in 26 genera from 11 families in the superfamily Chalcidoidea. The data on egg size and number was taken from Iwata (1962, 1966a) and the body lengths were collected from various sources in the taxonomic and biocontrol literature (Appendix 2). The Coleoptera included are 39 species of curculionids from 35 genera in 4 families (Iwata 1966b) and 17 species of scarabids from 17 genera in four families (Iwata 1966c). Iwata's papers on Coleoptera list both reproductive parameters and elytra length so the original data are not reported here. Iwata recorded the egg size and number of an enormous number of insect species; this neglected resource has not been fully exploited (but see Price 1973).

Data analysis

All the data were ln transformed before analysis. I calculated ordinary least squares regression coefficients

Table 1. Regression equations describing the relationship between body size and egg number, egg volume, and ovary volume for three orders of insects. All the data were ln transformed prior to analysis. The values in parentheses are the standard errors of the means. Slopes marked by different letters are significantly different from one another ($P < 0.05$). Note that I give two regression slopes, the ordinary least squares regression slope and the reduced major axis regression slope (Pagel and Harvey 1988, and LaBarbera 1989 for discussion). Regression slopes that are not significantly different from zero are indicated by (n.s). The remaining slopes are significantly different from zero with $p < 0.05$.

Order	N (Species)	Slope	RMA Slope	Intercept	r^2
Egg volume (mm³)					
Diptera	48	0.94a (0.28)	2.16	4.27 (0.21)	0.19**
Hymenoptera	31	2.66b (0.28)	3.07	-8.78 (0.34)	0.75
Coleoptera	56	2.07c (0.15)	2.44	-4.35 (0.32)	0.72**
Egg number					
Diptera	62	1.86a(0.42)	3.80	1.80(0.28)	0.24**
Hymenoptera	31	0.21b (0.31)	1.48	3.10 (0.39)	0.02 (n.s)
Coleoptera	56	0.31b (0.18)	1.40	2.08 (0.34)	0.05 (n.s)
Ovary volume (mm³)					
Diptera	48	2.99a (0.25)	3.45	-2.54 (0.19)	0.75
Hymenoptera	31	2.87a (0.27)	3.21	-5.68 (0.33)	0.80
Coleoptera	56	2.38b (0.15)	2.63	-2.27 (0.27)	0.82**

** Regression slope significantly different from isometry (3.00) with $P < 0.05$.

and reduced major axis regression slopes to estimate the scaling relationship between body size and the reproductive parameters analyzed. I chose to report ordinary least squares regression statistics as well as reduced major axis regression statistics because the measurement error for body size is likely to be small compared with the measurement error of these indices of reproductive effort. If the measurement error of the X variable is smaller than the Y variable than ordinary regression procedures are more appropriate (Ricker 1973, LaBarbera 1989). For comparative purposes, (e.g. with Wickman and Karlsson 1989) note that the slope of the reduced major axis regression is b/r , where b is the slope of the ordinary regression and r is the absolute value of the correlation coefficient. Finally, note that because a linear measure of body size was used, $b = 3.0$ represents isometry for the plots of ovary and egg volume versus body size, with $b < 3.0$ negative allometry and $b > 3.0$ positive allometry.

Related taxa do not constitute independent data points for statistical purposes (reviewed in Pagel and Harvey 1988, LaBarbera 1989). I do not attempt any of the sophisticated forms of analysis designed to ameliorate this problem for two reasons. First, the taxonomic coverage of the data described here is extremely spotty and second, the higher level taxonomy of all three insect orders discussed here is very poorly worked out. Nevertheless, the results obtained here are robust to the examination of similar relationships using subgeneric (in the Drosophilidae) or family (in the Chalcidoidea) means rather than treating each species as an independent observation (see below).

Results

Egg volume and ovary volume were significantly correlated with body size in all three taxa, whereas egg number was significantly correlated with body size only in the Diptera (Figs 1–3, Table 1). Notice that body size accounts for around 80% of the variation in ovary volume in all three orders (Table 1). Ovary volume scales isometrically with body size in Diptera and Hymenoptera and with negative allometry in the Coleoptera. Thus, the allocation to reproductive effort based on this instantaneous measure is proportionally similar in flies and wasps but shows a relative decrease in beetles. Egg volume shows strong negative allometry in all three taxa. This indicates that larger insects lay absolutely larger but proportionally smaller eggs. The functional or reduced major axis slopes do not lead to qualitatively different observations. Notice also that they are always higher than the ordinary least squares regression slopes and that the magnitude of the difference depends on the strength of the correlation between body size and the dependent variable.

I calculated the same set of regression statistics for each of the three traits and three taxa using average values for subgeneric groups in the Diptera and families in the Hymenoptera. There was no reasonable way to aggregate the data on the Coleoptera that gave sufficient numbers of means to perform additional analyses. The results were very similar to those obtained in the analysis (above) treating each species as an independent observation. I do not report the regression coefficients because in the Diptera data were only available for five subgenera one of which is represented by a single species (Appendix 1) and similarly in the Hymenoptera several families were represented by one or two species. Detailed analysis of the consequences of phylogenetic relatedness for the allometry of reproductive effort in

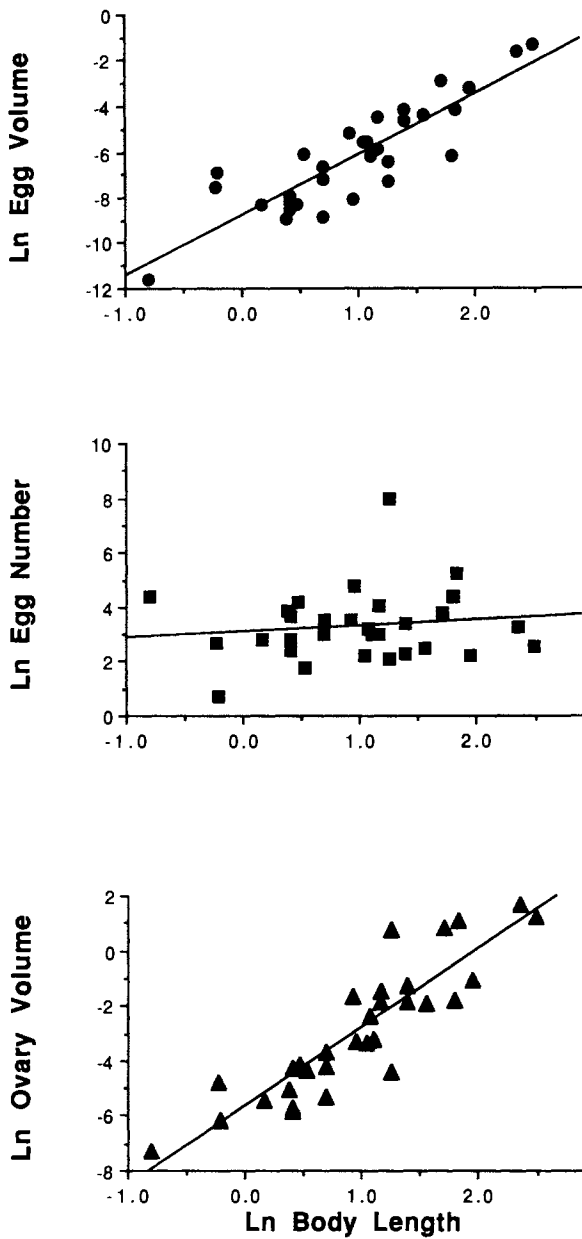


Fig. 2. Ln body length versus ln egg volume, egg number, and clutch volume, for species in the superfamily Chalcidoidea. Regression statistics are given in Table 1 and the data are listed in Appendix 2. The lines are the ordinary least squares regression lines.

insects awaits the collection of data with adequate taxonomic depth and breadth to utilize recent advances in statistical methods (Pagel and Harvey 1988, LaBarbera 1989).

I tested the hypothesis that there is a tradeoff between egg size and number by plotting the residuals of egg size and egg number from regressions versus body size for each of the three orders. The strong negative

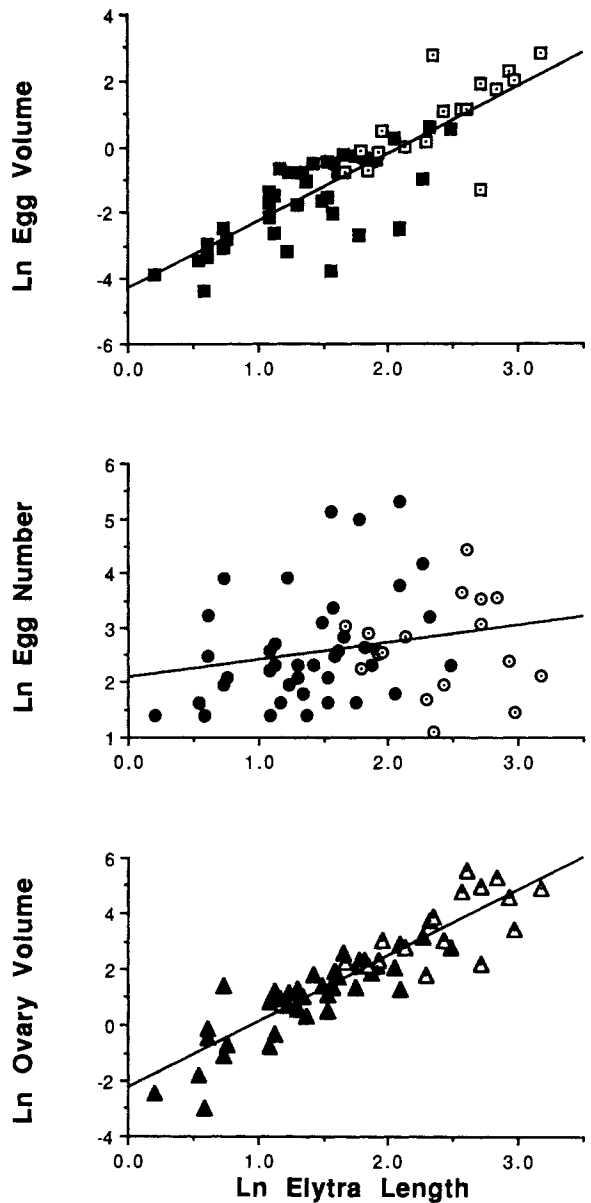


Fig. 3. Ln elytra length versus ln egg volume, egg number, and clutch volume, for species in the order Coleoptera. Regression statistics are given in Table 1. The data are taken from Table 1 of Iwata (1966b) and Table 1 of Iwata (1966c). The solid symbols are curculionid and the open symbols are scarabid beetles. The lines are the ordinary least squares regression lines.

correlations between residual egg size and number indicate that animals with relatively more eggs have relatively smaller eggs: for Diptera; $r^2 = 0.76$, $b = -0.53$ (0.04), and $P < 0.001$, for Hymenoptera; $r^2 = 0.36$, $b = -0.53$ (0.13), and $P < 0.001$, and for Coleoptera; $r^2 = 0.44$, $b = -0.63$ (0.10), and $P < 0.001$, where b is the slope of the regression and p is for $H_0: b = 0$.

Discussion

Scaling of ovary volume

This study brings together an extensive data set describing interspecific variation in the allocation of resources to reproductive effort in insects. The scaling of ovary volume with body size described here in Diptera, Hymenoptera, and Coleoptera are similar to previous results for Diptera and Lepidoptera. Wickman and Karlsson (1989) found that clutch volume scaled with body weight with an exponent of 1.08, not significantly different from one among seven species of butterflies and Gilbert (1982) measured an exponent of $0.95 + 0.10$ for the relationship between clutch volume and body weight among 30 species of hoverflies.

Instantaneous measures of reproductive effort are likely to scale with body weight with exponents ranging from 0.5 to 1.0 (Ware 1980, Lavigne 1982, Roff 1983, Reiss 1987). This observation is based on the idea that the energy available for reproduction is the difference between the energy intake per unit time and the energy necessary for other functions. Simply calculating this difference on the basis of measured energy intake and energy requirements for non-reproductive functions in animals of different sizes gives an exponent relating reproductive effort and body weight between 0.5 and 1.0. A more mechanistic explanation for the upper limit to this interspecific pattern of reproductive effort can be derived from the consideration of locomotor performance. Flight muscle mass is proportional to $W^{1.0}$ across a wide range of insect species, including representatives of the Diptera, Hymenoptera and Coleoptera (Marden 1987). Muscle mass specific lift production is constant in these species and in an extensive survey of age and size specific variation in one species of fly (Marden 1987, Berrigan 1990). If these observations hold more generally, then females which had proportionally higher levels of reproductive effort would have reduced flight capacity (e.g. Leather et al. 1983). In butterflies, flight capacity is strongly related to individual females' vulnerability to aerial predators (Marden and Chai 1990). Therefore it seems likely that the upper limits to reproductive effort could be imposed by the requirement to maintain functionally equivalent levels of locomotor performance (see Wiklund et al. 1987 for a discussion of limits to egg number imposed by a minimum viable egg size).

Intraspecifically, Wickman and Karlsson (1989) found that abdomen weight scaled with positive allometry in 7 species of butterflies and one species of fly. The interspecific exponent relating abdomen size and body weight was not significantly different from one. There are at least two possible explanations for the difference in scaling observed at the inter and intraspecific levels. First, abdomen mass and ovary volume may scale differently with body size. This seems unlikely because the abdomen of a gravid female insect is den-

sely packed with eggs. Second, the constraints on clutch volume may be different at different taxonomic levels (Clutton-Brock and Harvey 1979). We do not know enough about the comparative aspects of reproductive effort and flight requirements in insects to determine the nature of these constraints (Wickman and Karlsson 1989). Furthermore, the arguments I have made here for the role of flight performance in the evolution of reproductive effort depend largely on relating patterns of interspecific correlation (but see Marden 1989, Berrigan 1990). Interspecific correlations can arise in many ways and it seems clear that only experimental studies can identify the causal basis of correlation between body size and reproductive performance at both the inter- and intraspecific levels (Emerson and Arnold 1989). Further studies of the relationship between flight performance, reproductive effort and predation induced mortality are required to determine whether the allometry of reproductive effort is determined by selection acting through variation in flight ability.

Relationship between egg size and number

It is widely argued that a tradeoff between egg size and egg number is an inevitable consequence of a fixed level of resource availability (Smith and Fretwell 1974). Montague et al. (1981) pointed out that in a study of 35 species of Hawaiian *Drosophila*, there was a strong negative correlation between egg size and number. In this study I obtained identical results on an expanded data set including a number of additional species of *Drosophila* and data from two additional orders of insects.

The major factors influencing the particular size and number of eggs in *Drosophila* and in parasitic wasps appears to be the size and distribution of host resources (Kambyzellis and Heed 1971, Price 1973, O'Neill and Skinner 1990). It is not clear what determines the interspecific scaling of egg size and number. For example, in this study the dipteran species examined appear to have radiated with respect to both egg size and egg number's relationship to body size. In contrast, in both the Hymenoptera and Coleoptera, egg size and body size are strongly correlated. Thus, large Diptera may have many small eggs or a few large ones, whereas large chalcid wasps and these Coleoptera always have large eggs. Wiklund and Karlsson (1984) have suggested that egg size in satyrid butterflies may be determined by historical patterns of phylogenetic relatedness. At present it is impossible to assess the relative importance of adaptive and phylogenetic causes for life history variation in the taxa discussed here.

Conclusion

Insects are model systems for the study of adaptation and constraint because of their taxonomic and ecological diversity and because of the fact that there is an enormous amount of both inter- and intraspecific size variation in many insect taxa. For example there may be as much as a 27-fold variation in size in the wasp *Nasonia vitripennis* (O'Neill and Skinner 1990). We need comparative studies of the scaling of reproductive effort at diverse taxonomic levels among insects with known

behavioral and ecological traits and a theoretical framework which attempts to make explicit predictions about scaling relations between body size and life history traits in insects if we are to understand the allometry of reproductive effort.

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Appendix 1. Egg size, ovariole number, and thorax length of 4 species of *Scaptomyza* and 58 species of *Drosophila*. The species are divided into subgenera (Wheeler 1981), and the egg number refers to the average number of mature eggs per ovariole.

Species	Thorax length (mm)	Ovariole number	Egg number	Egg volume (mm ³)	Reference ¹
Antopocerus					
<i>D. diamphidiopoda</i>	2.28	18.44	0.64	0.048	1
<i>D. spp. near tanythrix</i>	2.33	14.30	0.90	0.090	1
<i>D. villosus</i>	2.92	8.40	0.50	0.192	1
<i>D. aduncus</i>	2.94	11.00	0.63	0.178	1
Engioscaptomyza					
<i>D. reducta</i>	1.68	5.33	0.20	-	1
<i>D. inflatus</i>	1.69	7.25	0.17	-	1
<i>D. nasalis</i>	1.90	4.68	0.22	0.170	1
<i>D. undulata</i>	2.00	2.00	0.50	0.270	1
<i>D. crassifemur</i>	2.06	5.36	0.19	0.080	1
Exalloscaptomyza					
<i>S. throckmortoni</i>	0.84	4.07	0.25	0.030	1
<i>S. oahuensis</i>	0.86	4.05	0.25	0.024	1
<i>S. mauiensis</i>	0.87	4.00	0.25	0.030	1
<i>S. caliginosa</i>	0.93	2.50	0.33	0.047	1
Dorsilopha					
<i>D. busckii</i>	1.05	20.60	0.53	0.005	2
Drosophila					
<i>D. mojavensis</i>	0.92	25.46	-	0.006	5
" "	0.94	25.83	-	0.007	5
<i>D. putrida</i>	0.95	16.80	-	-	4
<i>D. recens</i>	1.04	12.51	-	-	4
<i>D. tripunctata</i>	1.04	12.20	-	-	4
<i>D. mettleri</i>	1.07	36.21	-	0.006	5
<i>D. testacea</i>	1.08	21.70	-	-	4
<i>D. falleni</i>	1.11	13.18	-	-	4
<i>D. preapicula</i>	1.20	37.50	1	0.016	1
<i>D. nigrospiracula</i>	1.18	39.81	-	0.006	5
" "	1.24	39.72	1-4	-	5
<i>D. palustris</i>	1.21	10.51	-	-	4
<i>D. pectinatus</i>	1.26	12.42	0.75	0.017	1
<i>D. spenceri</i>	1.29	44.81	-	-	5
<i>D. trichetosa</i>	1.35	10.33	0.22	-	1
<i>D. prodita</i>	1.37	9.00	0.33	-	1
<i>D. funebris</i>	1.41	20.40	0.61	0.013	2
<i>D. disticha</i>	1.45	11.79	0.33	0.032	1
<i>D. hydei</i>	1.51	24.80	0.89	0.010	2
<i>D. kambysellisi</i>	1.51	15.00	0.33	0.022	1
<i>D. immigrans</i>	1.59	27.60	0.58	0.009	2
" "	1.39	30.00	1	-	4
<i>D. petalopeza</i>	1.75	17.75	0.71	-	1
<i>D. picticornis</i>	1.77	27.44	1-2	0.024	1
<i>D. mimica</i>	1.78	23.85	0.9-1	0.019	1
<i>D. gibberosa</i>	1.86	41.38	-	-	5
<i>D. grimshawi</i>	2.05	39.40	1-2	0.015	3
<i>D. crucigera</i>	2.05	41.50	1-2	0.015	3
" "	2.09	40.00	1-3	0.019	1
<i>D. villosipedis</i>	2.09	47.00	1-2	0.022	1
<i>D. setosimentum</i>	2.13	35.61	1	0.024	1

Species	Thorax length (mm)	Ovariole number	Egg number	Egg volume (mm ³)	Reference ¹
<i>D. pilimana</i>	2.19	45.00	1	0.019	1
<i>D. hirtipalpus</i>	2.20	23.67	1-2	-	3
<i>D. sejuncta</i>	2.24	56.83	1-3	0.034	1
<i>D. punulua</i>	2.30	34.00	1	0.025	1
<i>D. ochracea</i>	2.40	38.00	1-3	0.025	1
<i>D. adiastrata</i>	2.41	45.92	1	0.023	1
<i>D. murphyi</i>	2.43	41.57	1-2	0.021	1
<i>D. engyochracea</i>	2.48	59.73	1-3	0.024	1
<i>D. heteroneura</i>	2.61	35.79	1-3	0.032	3
<i>D. fasciculisetae</i>	2.65	47.22	1-2	0.020	1
<i>D. attigua</i>	2.67	43.00	1	0.021	1
<i>D. clavisetae</i>	2.71	38.17	1-2	0.050	1
<i>D. sproati</i>	2.78	65.55	1-3	0.016	1
<i>D. nigribasis</i>	2.98	53.33	1	0.031	1
<i>D. primaeva</i>	3.00	101.33	1	0.023	1
<i>D. silvestris</i>	3.16	52.38	1-3	0.031	1
<i>D. truncipenna</i>	3.22	48.00	1	0.031	1
<i>D. melanocephala</i>	3.31	86.60	1-2	0.023	1
Sophophora					
<i>D. simulans</i>	1.02	13.20	0.42	0.012	2
<i>D. melanogaster</i>	1.05	40.10	-	0.010	6
" "	1.11	15.40	0.47	0.012	2
<i>D. subobscura</i>	1.24	13.90	0.70	0.008	2

¹ 1) Kambysellis and Heed 1971, 2) Atkinson 1979, 3) This study, 4) Grimaldi 1983, 5) Mangan 1984, Mangan and Heed 1983, 6) David and Legay 1977, Carton and David 1983.

Appendix 2. Egg size, ovariole number and body length for 31 species of Chalcidoidea. The egg data was obtained from Iwata (1962,1966) and the body length data from miscellaneous sources in the literature. Egg number is the average number of eggs found in the abdomen.

Family	Species	Body length (mm)	Ovariole number	Egg number	Egg volume (mm ³)
Torymidae					
	<i>Megastigmus aculeatus</i>	3.20	6.0	57.00	0.00279
	<i>Megastigmus spp.</i>	3.20	6.0	20.00	0.01169
	<i>Monodontomerus japonicum</i>	4.00	20.0	30.00	0.00966
Chalcididae					
	<i>Brachymeria fonscolombeii</i>	6.25	6.0	185.00	0.01559
	<i>B. obscurata</i>	4.00	6.0	10.00	0.01513
	<i>Dirhinus luzoniensis</i>	4.70	6.0	12.00	0.01204
Leucospidae					
	<i>Leucospis japonica</i>	12.00	6.0	13.00	0.25656
	<i>L. okinawensis</i>	10.50	6.0	27.00	0.19927
Podagrionidae					
	<i>Podagrion chinensis</i>	3.50	6.0	8.00	0.00157
Eurytomidae					
	<i>Ailomorpha rhopaloides</i>	7.00	6.0	9.00	0.03929
	<i>Harmolita phyllostachitis</i>	5.50	6.0	43.00	0.05304
Perilampidae					
	<i>Perilampus japonicus</i>	3.50	160.0	3000.00	0.00069
Encyrtidae					
	<i>Anagyrus schonherri</i>	1.50	6.0	17.00	0.00019
	<i>Achrysopterus nagasakiensis</i>	1.50	4.0	40.00	0.00036
	<i>Anicetus beneficus</i>	1.50	6.0	11.00	0.00026
	<i>Callipteroma kiushiuense</i>	1.70	6.0	6.00	0.00212
	<i>Cheiloneurus japonicus</i>	2.00	6.0	20.00	0.00126
	<i>Cheiloneurus sp.</i>	2.00	8.0	35.00	0.00014
	<i>Clausenia purpurea</i>	2.60	6.0	120.00	0.00032
	<i>Comperiella bifasciata</i>	1.17	6.0	17.00	0.00025
	<i>C. unifasciata</i>	1.45	6.0	48.00	0.00013
	<i>Homalotylus flaminus*</i>	2.00	32.0	21.00	0.00072
Pteromalidae					
	<i>Nasonia vitripennis</i>	3.00	8.0	20.00	0.00199
	<i>Spalangia sp.</i>	2.50	6.0	35.00	0.00548

Family	Species	Body length (mm)	Ovariole number	Egg number	Egg volume (mm ³)
Eupelmidae					
	<i>Anastatus bifasciatus</i>	2.85	6.0	9.00	0.00389
Eulophidae					
	<i>Aphytis cylindratu</i>	0.80	6.0	15.00	0.00055
	<i>Aspidiotiphagus citrinus</i>	0.45	4.0	80.00	0.00001
	<i>Coccophagus yoshidae</i>	1.60	10.0	65.00	0.00025
	<i>Marietta carnesi</i>	0.81	4.0	2.00	0.00104
	<i>Tetrastichus hagenowi</i>	6.00	24.0	80.00	0.00209
Elasmidae					
	<i>Elasmus japonicus*</i>	2.90	36.0	25.00	0.00369

*From Iwata (1966), the remaining points are from Iwata (1962).

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