



Nordic Society Oikos

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Author(s): Alois Honěk

Reviewed work(s):

Source: *Oikos*, Vol. 66, No. 3 (Apr., 1993), pp. 483-492

Published by: [Wiley-Blackwell](#) on behalf of [Nordic Society Oikos](#)

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Accessed: 18/08/2012 05:44

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Intraspecific variation in body size and fecundity in insects: a general relationship

Alois Honěk

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. – *Oikos* 66: 483–492.

The relationship between intra-specific variation in female body size and potential fecundity was investigated using the published literature on 57 oviparous species of Coleoptera, Diptera, Ephemeroptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, and Trichoptera, and 11 species of larviparous Aphidina and Diptera. Female body sizes were converted to dry body weight. Variation in body weight and fecundity was expressed as percentage deviation from the median values. The increase in fecundity with body weight was similar in most taxa, with only a few important exceptions. The common regression for oviparous and larviparous species predicts a 0.95% increase in median fecundity for each 1% increase in dry body weight. The number of ovarioles (in 10 species of Coleoptera, Diptera, Hymenoptera and Orthoptera) also increased with body weight. The general relationship predicted a 0.81% increase in ovariole number for each 1% increase in dry body weight. The slope of ovariole number versus weight relationship was greater in species with many ovarioles than in species with few. The common slope of the fecundity/size relationship is close to 1 and this indicates that female size is a principal constraint on insect potential fecundity.

A. Honěk, *Research Inst. of Plant Production, CS-161 06 Praha 6, Ruzyně 507, Czechoslovakia.*

Fecundity in most insects varies with body size of the female. This fact is well recognized but there have been few attempts to generalize the size/fecundity relationship (Reiss 1989). The reluctance originates partly from the low reliability of body size when predicting the fecundity achieved under natural conditions (Leather 1988). Size and fecundity are influenced by genetic factors and development conditions, and fecundity is also dependent on the environmental conditions prevailing during oviposition. Therefore it is not possible to predict the number of eggs that will be laid from the size of the female. However, under constant environmental conditions fecundity is positively correlated with female size (e.g. Evans 1982, Gilbert 1984). It would be interesting to know whether there is a general relationship between size and fecundity, i.e. one independent of actual size and fecundity. Logarithmically transforming

data and calculating the allometric exponent b enables one to compare the slopes of regressions of fecundity on body size. Data transformed in this way, however, cannot be used to provide a common equation for several species. The difficulty may be overcome by expressing the intraspecific variation in terms of deviations from the median size or fecundity of a species. Data for different species may then be plotted on one figure, and a common regression of fecundity on body size calculated.

Recent literature (Tables 1 and 2) provides several examples of correlations between variation in body size and fecundity or ovariole number. These data were used to calculate a general relationship. The ovariole number/size relationship in aphids, which includes the problem of morph specific variation, has already been investigated by several authors (e.g. Walters et al.

Accepted 23 July 1992

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Table 1. List of species used in calculating the fecundity vs body size relationship, slope of the regression, and selected information on data elaboration.

Species	Slope	N	M	C	Reference
Coleoptera					
<i>Brachinus lateralis</i> Dejean	0.603	3	T+D	—	Juliano 1985
<i>Labidomera clivicollis</i> (Kirby)	0.675	4	T	—	Palmer 1985
Diptera					
<i>Aedes punctator</i> (Kirby)	0.968	6	D	G	Packer and Corbet 1989
<i>Aedes sierrensis</i> (Ludlow)	0.985	5	T	—	Hawley 1985
<i>Aedes triseriatus</i> (Say)	0.356	8	L	—	Jalil 1974
<i>Agromyza frontella</i> (Rondani)	1.145	5	L	—	Quiring and McNeil 1984
<i>Anopheles claviger</i> Meigen	0.788	9	L	—	Kühlhorn 1964
<i>Anopheles messae</i> Falleroni	1.031	8	L	—	Kühlhorn 1981
<i>Boettcherisca formosensis</i> Kirner & Lopes	1.169	5	L	—	So and Dudgeon 1989b
<i>Ceratitis capitata</i> (Wiedemann)	1.203	5	T	G	Krainacker et al. 1989
<i>Culicoides melleus</i> (Coquillett)	1.164	7	L	—	Linley and Hinds 1973
<i>Culicoides variipennis</i>	1.614	3	T	—	Akey et al. 1978
<i>Dacus dorsalis</i> Hendel	0.624	5	T	G	Krainacker et al. 1989
<i>Eucelatoria bryani</i> Sabrosky	1.297	6	L+D	—	Mani and Nagarkati 1983
<i>Hemipyrellia ligurriens</i> (Wiedemann)	0.612	5	D	F	So and Dudgeon 1989a
<i>Hilara</i> sp.n.	0.942	4	D	G	Marden 1989
<i>Lucilia cuprina</i> (Wiedemann)	0.759	6	D	—	Vogt et al. 1985
<i>Metasyrphus corollae</i> (F.)	0.862	4	L	—	Scott and Barlow 1984
<i>Musca autumnalis</i> DeGeer	0.666	2	L	F	Cilek and Knapp 1989
<i>Musca vetustissima</i> Walker	0.951	5	D	G	Vogt and Walker 1987
<i>Thecodiplosis japonsis</i> Uchida	1.004	6	L	—	Sone 1985
Ephemeroptera					
<i>Ephemerella dorothea</i> Needham	1.403	6	L	—	Svensson 1980
Heteroptera					
<i>Dysdercus fasciatus</i> Signoret	1.289	2	L	—	Clarke and Sardesai 1959
<i>Lygaeus equestris</i> (L.)	1.012	6	L	F	Solbreck et al. 1989
<i>Podisus maculiventris</i> (Say)	1.323	5	T	—	Evans 1982
Homoptera – Aphidina					
<i>Acyrtosiphon pisum</i> Harris	0.392	4	L	—	Murdie 1969
<i>Aphis fabae</i> Scopoli	0.407	6	L	—	Dixon and Dharma 1980
<i>Brevicoryne brassicae</i> (L.)	0.821	6	L	—	Raworth et al. 1984
<i>Drepanosiphum platanoidis</i> (Schrank)	0.431	6	D	—	Leather and Wellings 1981
<i>Masonaphis maxima</i> (Mason)	1.004	5	L	—	Gilbert 1980
<i>Metopolophium dirhodum</i> (Walker)	0.903	6	L	—	Wratten 1977
<i>Metopolophium festucae</i> (Theobald)	0.661	8	L	—	Dent and Wratten 1986
	0.255	6	L	—	Dent and Wratten 1986
<i>Myzus persicae</i> (Sulzer)	0.638	7	D	—	Kempton et al. 1980
	1.247	4	L	—	Hayamizu 1984
<i>Rhopalosiphum padi</i> (L.)	0.643	4	D	—	Wellings et al. 1980
	0.964	5	T	—	Leather 1982
	0.491	4	T	—	Leather 1982
	0.381	4	T	—	Leather 1985
	0.544	7	T	—	Leather 1989
<i>Sitobion avenae</i> (F.)	1.105	7	L	—	Wratten 1977

cont.

1988). The factors limiting the variation in the slopes of fecundity vs size and ovariole number vs size relationships are also discussed.

Material and methods

The data used in calculating the fecundity/size and ovariole number/size relationships are listed in Tables 1 and 2. Data selected were for fecundity established under standard conditions, either as lifetime fecundity, fecundity over a significant part of the oviposition pe-

Table 1. Continued.

Species	Slope	N	M	C	Reference
Homoptera – others					
<i>Nephotettix cincticeps</i> Uhler	3.947	4	L	–	Valle et al. 1987
<i>Nephotettix nigropictus</i> Stål	5.145	5	L	–	Valle et al. 1987
<i>Nephotettix malayanus</i> Ishihara & Kawasa	4.089	5	L	–	Valle et al. 1987
<i>Nephotettix virescens</i> Distant	4.736	4	L	–	Valle et al. 1987
<i>Prokelisia marginata</i> (Van Duzee)	1.252	4	L	–	Denno and McCloud 1985
Hymenoptera					
<i>Aphidius sonchi</i> Marshall	0.812	4	D	–	Liu 1985
<i>Aphytis lingnanensis</i> Compere	1.391	5	D	–	Opp and Luck 1986
<i>Aphytis mellinus</i> DeBach	1.365	5	D	–	Opp and Luck 1986
<i>Diprion pini</i> (L.)	2.296	2	T	–	Geri et al. 1985
<i>Lariophagus distinguendus</i> Forster	1.165	4	T	–	Bellows 1985
<i>Pteromalus puparum</i> (L.)	0.782	3	L	–	Takagi 1985
Lepidoptera					
<i>Agriphila plumbifimbriella</i> Dyar	1.020	4	D	–	Crawford 1971
<i>Antheraea polyphemus</i> (Cramer)	0.664	4	D	G	Miller et al. 1982
<i>Cadra cautella</i> (Walker)	1.066	5	L	G	Hagstrum and Tomblin 1975
<i>Callosamia promethea</i> (Drury)	1.072	4	D	G	Miller et al. 1982
<i>Choristoneura fumiferana</i> (Clements)	1.590	8	D	–	Thomas et al. 1980
	1.041	5	L	G	Lorimer and Bauer 1983
<i>Choristoneura conflictana</i> (Walker)	1.153	5	L	F	Beckwith 1970
<i>Cnephasia jactatana</i> (Walker)	1.654	5	L	F	Ochieng-Odero 1990
<i>Crambus harpipterus</i> Dyar	1.306	4	D	–	Crawford 1971
<i>Heliconius charithonia</i> (L.)	0.985	4	T	–	Dunlap-Pianka 1979
<i>Laspeyresia pomonella</i> (L.)	1.199	6	D	G	Boreyko 1972
<i>Malacosoma disstria</i> Hübner	1.151	7	D	G	Lorimer 1979
<i>Mythimna convecta</i> Walker	0.698	5	D	G	Smith 1986
<i>Mythimna pallens</i> (L.)	0.784	4	L	G	Hill and Hirai 1986
	1.485	4	L	F	Hill and Hirai 1986
<i>Mythimna separata</i> Walker	1.909	7	L	–	Hill and Hirai 1986
	1.396	5	L	–	Hill and Hirai 1986
<i>Operophtera brumata</i> (L.)	1.486	8	D	G	Holliday 1977
	1.431	4	D	F	Roland and Myers 1987
<i>Pararge aegeria</i> (L.)	1.854	6	L	G	Karlsson and Wickman 1990
<i>Platyrepia virginalis</i> Boisduval	1.204	5	D	F	Harrison and Karban 1986
<i>Pieris rapae</i> Boisduval	1.619	6	L	–	Gilbert 1984
	1.394	4	L	G	Kimura and Tsubaki 1986
<i>Rheumaptera hastata</i> (L.)	1.004	3	L	F	Werner 1979
<i>Spodoptera frugiperda</i> (Smith)	1.312	5	L	F	Pencoe and Martin 1982
<i>Taraka hamada</i> Druce	1.206	6	L+D	–	Banno 1990
Trichoptera					
<i>Potamophylax cingulatus</i> (Stephens)	0.880	5	D	–	Svensson 1975

N – number of intervals into which the range of body size was divided; M – the method how the fecundity was established; D – dissection; L – lifetime fecundity under standard conditions; T – fecundity established for a part of oviposition period only; C – the species used for comparing effects of genetic and random variation of body size (G) and food (or population density) elicited variation of body size (F) (see Discussion).

riod, or number of eggs at the adult moult, ascertained by dissection. It was assumed that the proportion of the eggs actually laid under standard conditions does not vary with female size.

Body size was expressed as dry weight. Dry weight was calculated as 0.3 wet weight, adult weight as 0.6 pupal weight (e.g. Banno 1990, Ochieng-Odero 1990). When body size was given as length, it was converted to weight using the formula of Rogers et al. (1976), which has been verified by Jarošík (1989):

$$\text{Mass} = 0.0305 (\text{length})^{2.62}$$

The length part of the body (head, thorax, tibia) was sometimes given instead of total body length. The size of various body parts was assumed to vary isometrically, i.e. the variation in the size of distal or proximal body parts is equal to the variation in total body length. In order to estimate the dry weight of an adult insect one needs to know its body length, which was assumed to be

Table 2. List of species used in calculating the ovariole number vs. body size relationship, slope of the regression, and number of intervals into which the range of body size was divided (N).

Species	Slope	N	Reference
Coleoptera			
<i>Aulacophora nigripennis</i> Motschulsky	0.536	5	Suzuki 1976
<i>Pseudodera xanthospilla</i> Baly	1.060	6	Suzuki 1976
Diptera			
<i>Aedes aegypti</i> (L.)	0.888	5	Steinwascher 1984
<i>Aedes punctator</i> (Kirby)	1.479	9	Packer and Corbet 1989
<i>Dacus jarvisi</i> (Tryon)	0.824	5	Fitt 1990
<i>Dacus tryoni</i> (Froggat)	0.721	4	Fitt 1990
<i>Metasyrphus corollae</i> (F.)	0.835	2	Scott and Barlow 1984
<i>Winthemia fumiferanae</i> Totham	0.713	6	Hebert et al. 1989
Hymenoptera			
<i>Encarsia formosa</i> Gahan	0.313	10	Vianen and Lenteren 1986
Orthoptera			
<i>Calliptamus barbarus</i> (Costa)	0.425	3	Hugueny and Louveaux 1986

equal to wing length, or 1.5 elytron length, 3.5 thorax length, or 5 times the width of the head. This gave a crude estimate of adult dry weight. Ovariole number is the total number of ovarioles per female. Data for one ovary was multiplied by 2. Some species may have uneven numbers of ovarioles but no author reports that he deliberately selected smaller or larger ovaria.

For each data set (Table 1) the median value of the size and the median fecundity were used as marker values. The original data can then be presented in standard graphical form in the x (size) axis and y axis (fecundity or ovariole numbers) divided into equal intervals. The mean y value for each size class was calculated and

both the y and x values expressed as a percentage of the marker values. The median values are calculated as half the minimum plus the maximum values. The values for each species were presented as percentages of the median values:

$$[(\text{actual size} - \text{median size})/\text{median size}] \times 100$$

Regressions of these transformed data were calculated for each species. The number of points from which a regression was calculated was equal to the number of size classes, which varied between species. The slope of the regression indicates the magnitude of the effects of

Table 3. The slope of linear regression of fecundity on dry weight of adult female (% deviation from median value). Common slope for all data of a taxon, coefficient of determination R^2 , maximum and minimum slopes of particular species and range of body weight (mg) and fecundity data from which the calculations were made.

Taxon	Slope						
	N	Common	R^2	Minimum	Maximum	Body weight	Fecundity
Oviparous							
Coleoptera	2	0.652	93.1	0.603	0.675	6.6–7.8	59.6–161.6
Diptera	18	0.880	82.7	0.612	1.614	0.2–30.2	25.1–376.0
Ephemeroptera	1	1.403	97.3	1.403	1.403	140.0	595.3
Heteroptera	3	1.058	92.4	1.012	1.323	12.0–35.8	24.4–746.0
Homoptera	1	1.252	70.1	1.252	1.252	0.56	8.8
Hymenoptera	6	1.098	82.7	0.782	2.296	0.02–27.9	5.2–263.0
Lepidoptera	21	1.221	87.3	0.664	1.854	4.9–578.0	40.0–2469.0
Trichoptera	1	0.880	99.2	0.880	0.880	70.0	222.3
Total	53	1.038	76.8	0.603	2.296	0.02–578.0	5.2–2469.0
Larviparous							
Aphidina	10	0.685	79.2	0.255	1.247	0.12–0.90	8.7–74.1
Diptera	1	1.169	99.3	1.169	1.169	8.5	53.0

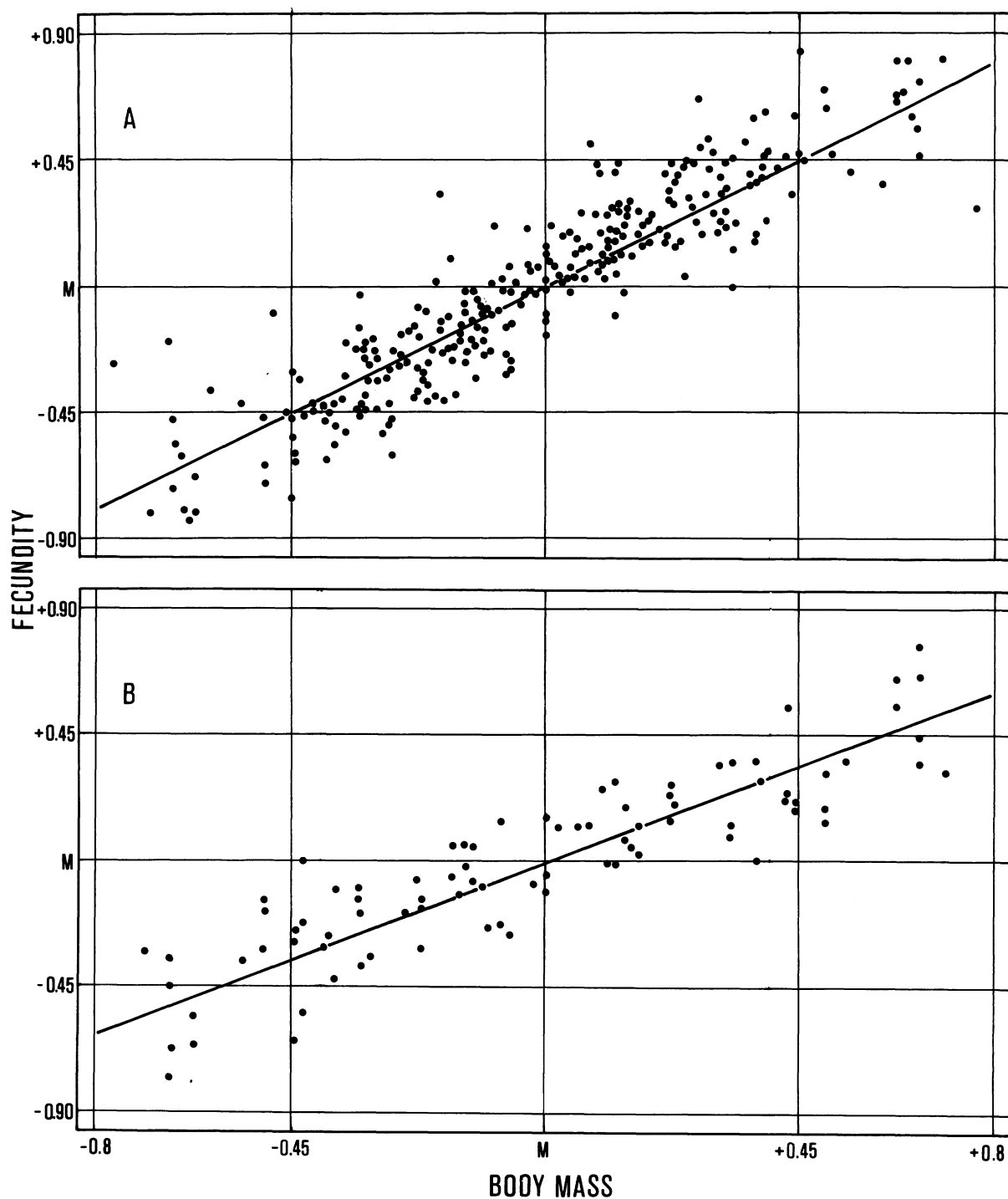


Fig. 1. The relationship between female body weight and fecundity (number of eggs or larvae). The variation is expressed as a proportion of median (M) value: difference = (actual value - median value) / median value. A: oviparous species, all taxa combined (genus *Nephotettix* excluded). Regression: fecundity = 1.038 body weight + 1.617, $r^2 = 83.2\%$, $p < 0.05$. B: viviparous aphids. Regression: fecundity = 0.685 body weight + 0.938, $r^2 = 79.4\%$, $p < 0.05$.

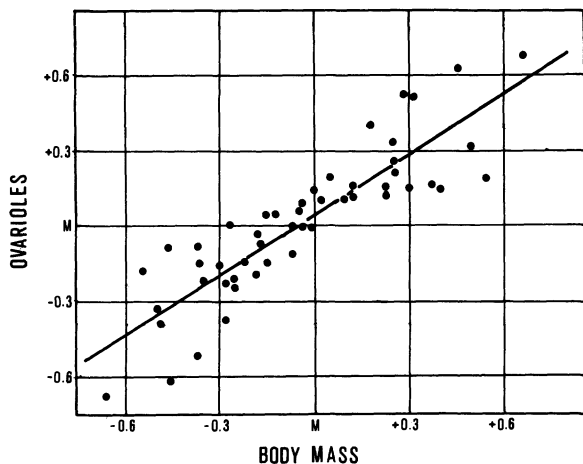


Fig. 2. The relationship between variation in female body weight and ovariole numbers, in oviparous species. Regression: ovariole number = 0.805 body weight + 4.613, $r^2 = 76.5\%$, $p < 0.05$.

body weight on fecundity. The differences between groups of species were tested using the means and variances of the slopes for individual species in each group. The common slopes of the pooled data for groups of species (orders, oviparous or viviparous species) were also calculated.

Results

Body size and fecundity

The slopes of the regression of fecundity on body weight for well represented (>5 species) oviparous orders ranged from 0.88 to 1.22 (Table 3). The slopes for individual species varied between 0.60 and 2.30. The common slope for 53 oviparous species was 1.04 (Fig. 1A). Individual species of the homopteran genus *Nephotettix* are exceptional in having slopes that varied between 3.95 and 5.15 (Valle et al. 1987) and the common slope 4.62. The clearly outlying values of this genus were not considered when calculating the common fecundity/weight relationship. The common slope thus applies to 53 (93%) of the total of 57 species included in this study.

The common slope for viviparous aphids (Fig. 1B) was 0.69, and the value for individual species varied between 0.26 and 1.25 (Tab. 3). The lower slope of the fecundity/weight relationship in aphids was perhaps not a consequence of viviparity. The slope for a viviparous dipteran, *B. formosensis*, was 1.17. The difference in the average slopes for oviparous species (1.14 ± 0.36 , *Nephotettix* excluded) and aphids (0.68 ± 0.29) was significant ($t = 4.605$, $p < 0.01$).

The common regression for all data

$$\text{fecundity} = 0.954 \text{ weight} + 0.867$$

was highly significant ($r^2 = 74.9\%$, $p < 0.001$). In general, the increase in fecundity was directly proportional to the increase in female body mass and the allometric exponent was therefore close to 1.

The well represented orders Lepidoptera, Diptera, and Homoptera-Aphidina, were markedly different in size. The slope of regression of the fecundity/weight relationships of individual species on their average female weights for each of these orders declined with size being 1.27 in Lepidoptera (average weight 74.9 mg), 0.94 in Diptera (7.2 mg) and 0.90 in aphids (0.23 mg). The differences, however, were not statistically significant as the slopes for individual species were very variable. Median egg productions were not correlated with the slopes of the fecundity/weight regressions.

Ovariole number

The fecundity/size relationship may be determined by several factors including an increase of ovariole number with female body size. This was investigated for 10 oviparous species, mostly Diptera. There was a relationship between ovariole number and body weight (Fig. 2). The slope of the regression was similar to that for the fecundity/weight relationship. For Diptera (6 species) it was 1.05 ($r^2 = 85.6\%$), for all species combined it was 0.81 ($r^2 = 76.5\%$).

The increase in the slopes of ovariole number/size regressions for individual species was in direct proportion to the median ovariole numbers of these species (Fig. 3). This means that the increase in ovariole num-

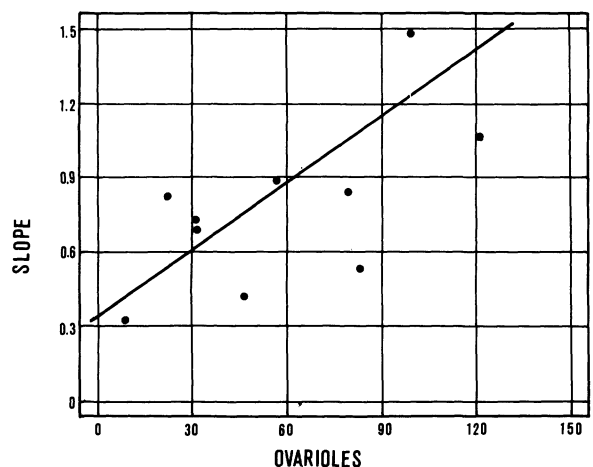


Fig. 3. The relationship between the median number of ovarioles and the slope of body weight/ovariole number regression in oviparous species of Diptera, Hymenoptera and Orthoptera. Regression: slope = 0.00585 ovariole number + 0.441; $r^2 = 42.0\%$, $p < 0.05$.

ber and body size is greater in species with many ovarioles than in species with few. The correlation between slopes and body mass was not significant ($r^2 = 9.5\%$).

Discussion

For the calculation of a fecundity/size relationship an appropriate measure of body size is needed. Body weight is a convenient measure, however, its use raises statistical difficulty. The egg mass represents a considerable part of a female's weight. Fecundity (in the ideal case of constant egg size) is a particular fraction of body mass expressed in units of egg weight. Therefore, both the independent and dependent variables include female weight. It is desirable to select an independent measure of body size. However, the results would not change very much because other measures of size like body length are correlated with weight ($r > 0.97$; Rogers et al. 1976, Jarošík 1989) as are the lengths of distal parts of the body such as antennal segments ($r = 0.63$ to 0.78 ; Alpatov and Boschko-Stepanenko 1928). In practice, the selection of an alternative measure of body size was impossible due to absence of such data in the source literature.

The number of eggs (of a constant size) per female is a linear function of the space available within the mother's body. This space should be proportional to female weight. No study of the relationship between internal abdominal volume and weight of egg-free female body is available. If fecundity is constrained only by the size of the female we should expect a linear fecundity/weight relationship, whose allometric exponent is equal to 1. The slope of fecundity/size relationship after transformation of data to percent deviation from median value should also be equal to 1. A positive deviation from this value of the slope of allometric exponent will indicate that the fecundity per unit body weight is greater in large than small females. A negative deviation indicates the reverse relationship (Sibly and Calow 1986). Such deviations would indicate physiological constraints on fecundity that are different in small and large females. In fact, the common slope of fecundity/size relationship is close to 1. Size is thus apparently the most important constraint on fecundity. The slopes of individual species or their groups may differ from this average, and this variation may have an ecological significance. This variation is partly a consequence of the different methods used by the various authors when estimating fecundity and body size (Table 1). A comparative study of fecundity/size relationship using a uniform method for several species may decrease the variation substantially.

An underlying assumption of the above conclusion is that egg size does not vary much with mother size. This is true for some species (Hawley 1985, Juliano 1985, Krainacker et al. 1989, Solbreck et al. 1989, Fitt 1990), in others egg size may increase with female weight (Re-

isen 1975, Richards and Myers 1980, Dodson and Marshall 1984, Kimura and Tsubaki 1985, Dixon 1985, Larsson 1990, McLain 1991). The slopes of egg size/female size regressions are generally smaller than the slopes of fecundity/size regressions. Two papers (Wiklund and Karlsson 1984, Palmer 1985) which permitted the recalculation of the egg size increase as a percentage of the median value (similar to the fecundity data) provided the egg size/female size slopes 0.2–0.3. Individual egg sizes vary largely, and the average weights vary also with female age (Harvey 1977, Wiklund and Karlsson 1984, Karlsson and Wiklund 1984, 1985, Kimura and Tsubaki 1985, Boggs 1986, Forrest 1986, Karlsson 1987, Moore and Singer 1987, Wickman and Karlsson 1987, Svård and Wiklund 1988, Kasule 1991) and temperature (Beckwith 1982, Brittain et al. 1984, Wall 1990). The latter factors influence egg size more than the size of the mother (Kimura and Tsubaki 1985). The variation of egg size with female size may contribute to the variation in the fecundity/size slopes, but the significance of this variation is small.

Adult body size in insects is determined genetically and modified by environmental conditions during larval development, and each of these factors might influence the fecundity in different ways. This means that the slope of the fecundity/size regression for a species may differ when the variation in size was produced by the genetic constitution, growing larvae at different temperatures, on a variety of diets, etc. In fact, in some species the fecundity/size relationship differed when the variation in size was caused by different environmental factors (Carroll and Hoyt 1986), and the magnitude of these effects vary greatly even between closely related species (Hill and Hirai 1987). A one-way analysis of the variance of a group of 16 species (Table 1) from the orders: Diptera, Lepidoptera, and Heteroptera selected on the basis that the size was affected by unspecified factors (i.e. genetic or random variation), and a group of 10 species (Table 1) in which size was affected by food availability or population density revealed virtually no difference between the two groups ($F = 6.15 \times 10^{-4}$). The slopes of the size/fecundity relationships showed a similar range of variation, regardless of the nature of factors that caused the variation.

In some species larval resources determine both adult size and fecundity (the maximum number of eggs is present at the adult moult). In others, larval conditions affect adult size but egg mass and number are largely determined by resources available to adults. In the former group, egg mass is a part of the adult body and therefore should be highly correlated with female size. In the latter group, size is an indicator of the potential egg production, which depends on physiological and environmental constraints. The slopes of the fecundity/size relationships may differ for both groups. In fact, the average slope was 1.2 for a group consisting of Ephemeroptera, Lepidoptera and Trichoptera. In most species included in this group, fecundity is determined in the

larval stage. This slope was greater than the average slope 0.9 for a group consisting of Coleoptera, Diptera, Heteroptera, Homoptera, and Hymenoptera, in which oogenesis occurs in adult stage. Large size may confer greater advantage to females of the first group than of the second group. However, the difference in timing of egg maturation was paralleled by difference in average body size of the groups (Table 3), which also may affect the fecundity/size relationship.

Female size is usually a good predictor of potential fecundity and cases of no relationship are scarce (Slansky 1980, Boggs 1986, Johnson 1990). Using the laboratory estimated fecundity/size relationship for prediction in the field is difficult, since the achieved fecundity is modified by many factors (Leather and Burnand 1987, Leather 1988). However, an impact of body size on fecundity cannot be denied, and variation in body size may be a part of a species, adaptive strategy. In most oviparous species, maternal control of the size of the progeny is minimal, and variation in size is caused by unpredictable developmental factors (temperature, food) or are associated with changes in population density. In these species decrease in adult size is an emergency solution, which enables the insect to overcome the constraints on larval development. In species where there is maternal control of offspring size, changing offspring size may anticipate the needs of the progeny. The regulation of progeny size may become a part of the adaptive strategy of the species (Dixon 1985, Walters et al. 1987).

Acknowledgement – I thank A. F. G. Dixon for reading the manuscript, helpful comments and improving my English.

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