

EXTRINSIC EFFECTS ON FECUNDITY-MATERNAL WEIGHT RELATIONS IN
CAPITAL-BREEDING LEPIDOPTERA

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ABSTRACT. Capital-breeding Lepidoptera depend for reproduction on metabolic resources assembled either entirely or primarily by their larvae, the former termed 'perfect' the latter 'imperfect'. Empirical evidence suggests that maternal size determines capital-breeder fecundity. The fecundity-maternal size relation is usually formulated as $F = bW + a$, where F is fecundity, W is final maternal size in units such as weight of newly transformed pupae, b is the slope, and a the intercept. Exhaustive search yielded 71 fecundity-maternal pupal weight relations for 41 capital breeders in 15 families, 58 of which, including 2 previously unpublished, were based on individual specimens, and 13 on grouped specimens. In 22 individual-specimen relations, cohorts divided into 2 or more subgroups were reared simultaneously at different temperatures, on different diets, or exposed to other extrinsic factors. These 22 'multiform' relations were compared with 36 'uniform' relations, and where possible cohort subgroups were compared. Pupal weights of cohort subgroups were affected much oftener than underlying slopes and intercepts. Individual-specimen slopes based on transformed data ranged 0.52–2.09 with a mean and standard error of 1.13 ± 0.04 , and slopes did not differ significantly among perfect, imperfect, multiform, and uniform categories. Despite the evident similarity, one relation does not apply to all capital breeders. Tradeoffs sometimes occur between fecundity, F , and mean egg weight, E . Reaction norms of fecundity and pupal weight across extrinsic-factor ranges were overwhelmingly congruent, which supports axiomatic status for the dependence of fecundity on capital-breeder maternal size. Cooler rearing temperatures usually produced heavier female pupae and greater fecundities, a phenomenon of population dynamics interest. The two sides of practically all fecundity-maternal weight regressions are not statistically independent, in effect stating $F = b(W + [F \times E]) + a$, which artificially inflates test statistics. Where desirable, the fully independent relation $R = b(W - [F \times E]) + a$ can be used, where R is reproductive bulk, the mathematical product of $F \times E$.

Additional key words: temperature, diet quality, population dynamics

'Capital-breeding' describes Lepidoptera that depend for reproduction entirely or primarily on metabolic resources assembled by their larvae, in contrast to 'income-breeding', which describes those that depend for reproduction primarily or entirely on resources assembled by their adults (Boggs 1992, Miller 1996, Tammaru and Haukioja 1996). The gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), is a capital breeder; the monarch butterfly, *Danaus plexippus* (L.) (Nymphalidae), an income breeder. In four butterfly income breeders in two families, income contributed $\geq 80\%$ to fecundity, and capital $\leq 20\%$ (Boggs 1997, Fischer and Fiedler 2001a). Based on sizes of superfamilies (Kristensen and Skalski 1999) and the extent to which income breeding is phylogenetically limited, probably $\approx 90\%$ of extant Lepidoptera are capital breeders. Most outbreak Lepidoptera also are capital breeders (Miller 1996, Tammaru and Haukioja 1996). Capital breeders have an ovigeny index, OI, of 1 or $\gg 0$, referring to the proportion of lifetime potential fecundity that consists of mature eggs at eclosion, whereas income breeders have an OI of 0 or $\ll 1$ (Jervis and Ferns 2004). Capital breeders with nonfeeding adults and OIs of 1 are here termed 'perfect', whereas those with OIs of $\gg 0$ whose adults may feed, but do so less than income breeders, are termed 'imperfect'.

Maternal size is widely believed to determine fecundity in capital breeders (Leather 1988, Honek 1993). This belief derives not from experimentation but

from long empirical observation. Direct fecundity-size relations occur in the lepidopteran phylogenetic sequence at least as early as Tineidae, the basal-most lineage of Ditrysia (Titschack 1922, Kristensen and Skalski 1999) and are probably part of the ground plan of Ditrysia, if not all Lepidoptera. This dependence implies that whatever influences maternal size may influence fecundity and its associated quality attributes, and thus population fluctuations. Fecundity can be a proxy for net reproductive rate (Carey 1993, Huey and Berrigan 2001) and has been implicated in capital-breeder population fluctuations, as in *Bupalus piniaria* L. (Geometridae) (Klomp 1966), *Bucculatrix pyrivorella* Kuroko (Bucculatricidae) (Fujie 1980), *Leucoptera spartifoliella* (Hübner) (Lyonetiidae) (Agwu 1974), and in capital-breeding Noctuidae (Spitzer et al. 1984).

Traditionally, the relation between fecundity, F , and maternal weight, W , usually has been defined by linear regression as $F = bW + a$, where W refers to newly transformed pupae or newly eclosed adults, b is the slope, and a is the intercept or scaling parameter. Honek (1993) devised a fecundity-maternal weight relation for insects generally, as well as one for Lepidoptera, but he did not segregate capital breeders for special study nor exhaustively seek examples. Honek noted that weight appears on both sides of fecundity-maternal weight regressions, but that statistically independent measures of fecundity and maternal weight are practically

nonexistent. In effect, such relations state that $F = b(W + [F \times E]) + a$, where E is mean egg weight. The resulting nonindependence inflates test statistics and minimizes variation between response and explanatory variables. The practical usefulness of the traditional regressions is not necessarily impaired, but their statistics should not be used where strict independence between the variables is assumed. As discussed further on, a fully independent alternative relation emerged from this study.

In any capital-breeder reared under homogeneous conditions, intrinsic effects alone will produce a direct relation between fecundity and maternal size. If a cohort of eggs or hatchlings is divided into subgroups, and each subgroup reared at a different level of an extrinsic factor, such as a different temperature, or on a different diet, then extrinsic effects are likely to be added to the intrinsic ones. Here I examine extrinsic effects on fecundity-maternal pupal weight relations during rearing of capital breeders. I focus on effects produced by different temperatures—as might occur during anomalous weather, or between microhabitats, or between generations or seasons—and by differing diet quality—as might occur on variably stressed or different kinds of foodplants, or on different kinds or amounts of adult nourishment.

MATERIALS AND METHODS

I assembled as many statistical fecundity-maternal weight relations as possible from a personal reference collection, electronic databases including *Biosis*, *Biological Abstracts*, and the *Zoological Record*, and from citations in references. Most relations were based on observations of specimens individually, a few on means of grouped specimens. Individual-specimen relations were admitted if based on samples numbering ≥ 20 , grouped-specimen relations if based on groups numbering ≥ 5 . No relations were excluded because of non-English text.

In the 58 assembled individual-specimen relations, weights and fecundities were available in numerical form for three published and two unpublished ones (Table 1); weights and fecundities for the remainder were transcribed from enlarged photocopies of published scatterplots. Because transcription creates error—when one point covers another, for instance—I tested slopes of transcribed relations against corresponding slopes given in sources. A few departures were statistically significant, but most were not (F -tests, $P = 0.99\text{--}0.009$; median $P = 0.76$; $n = 35$). If P was < 0.25 , I retranscribed, but in no case did retranscription change the outcome appreciably. I accepted scatterplots at face value despite minor inconsistencies, except that

for *Philosamia ricini* Hutt. (Singh and Prasad 1987), which seemed too anomalous. In the 13 grouped-specimen relations, most weights and fecundities were available in numerical form (Table 2).

Study relations consisted of perfect and imperfect groups and uniform and multiform subsets. 'Uniform' denotes homogeneous conditions of development expected to produce only intrinsic effects, and 'multiform' denotes heterogeneous conditions expected to produce extrinsic as well as intrinsic effects. I examined relations for extrinsic effects first by meta-analysis (Gates 2002) and second by comparing cohort subgroup relations provided in sources or obtained by deconstruction.

A standardized maternal weight was desirable, and I chose fresh pupal weight. By the pupal stage metabolic resources for ovigenesis are in place. Moreover, pupal weight has been most often used in describing fecundity-size relations (42 of 58 relations in Table 1, 12 of 13 in Table 2), and explanatory variables based on weight outnumber those based on lineal dimensions such as forewing length and pupal diameter. I maximized the number of relations for study by converting female adult fresh weight, W_a , to fresh pupal weight, W_p , where $W_p = W_a \times 1.85$, a factor based on four observations: (1) first-day female pupae of *Malacosoma disstria* (Hbn.) (Lasiocampidae) in a previously unpublished study averaged 1.98 times heavier than first-day adults ($n = 30$ weighings, paired); (2) a corresponding value of 1.81 for *Epiphyas postvittana* (Walker) (Tortricidae) ($n > 130$ weighings, unpaired) (Danthanarayana 1975); (3) a corresponding value of 1.74 for *Streblote panda* (Hbn.) (Calvo and Molina 2005); and (4) a corresponding value of 1.67 for *Cnephasia jactatana* (Walker) (Tortricidae) (Ochieng'-Odero 1990).

Fecundity had been estimated in sources by various methods, all internally consistent and all accepted here. Methods included counting unlaied eggs in dissections of newly eclosed females, counting only eggs actually laid, and combining eggs laid with residual eggs in ovaries after death.

For meta-analysis, I transformed fecundities and pupal weights of each relation to percentages of their midranges (Honek 1993) ([individual value/midrange value] $\times 100$, where midrange = $0.5 \times$ [minimum value + maximum value]). This transformation enabled comparison of relations for different species and groups on a single scale, as between large saturniids and small tortricids.

Statistics were generated by SYSTAT (1992) software. Student's t used pooled variances except where noted otherwise. In analyzing and comparing cohort subgroup

relations, I used nontransformed transcribed data when tabulated data were unavailable. In tests of differences among fecundity-maternal weight regressions of cohort subgroups, I included a categorical explanatory variable, as well as a maternal weight \times group interaction term, the latter enabling tests of differences among slopes and the former enabling tests of differences among heights of regression lines. Height tests were used here as tests of intercept differences. Where subgroup relations within multiform relations were not provided in sources and deconstruction was not possible, the fact is noted.

Wherever possible, I report whether reaction norms of fecundity and maternal pupal weight are congruent. A reaction norm is the trajectory of response values across the range of an extrinsic factor (Schlichting and Pigliucci 1998). Congruency signifies that fecundity and female pupal weight peak at the same value of an extrinsic factor. Reaction norms to rearing temperatures are illustrated in Fig. 1a, and those to different diets in Fig. 2a. In sources where it was not possible to evaluate congruency, it is noted as indeterminate.

RESULTS

The 71 assembled fecundity-maternal pupal weight relations represent 41 capital breeders in 15 families (Tables 1 and 2). The 58 individual-specimen relations (Table 1) consist of 35 in perfect and 23 in imperfect groups, 36 of the 58 uniform and 22 multiform. Perfect-uniform and perfect-multiform categories number 23 and 12, and imperfect-uniform and imperfect-multiform categories each number 13. The 13 grouped-insect relations (Table 2) consist of 10 of the perfect kind and 3 of the imperfect, with 5 uniform and 8 multiform. Individual-specimen relations are unaffected by aggregation bias and thus receive more attention here than grouped-specimen relations. In all discussions, attributes and their numerical values appear in parallel sequences. 'Tradeoffs' refer to any change in proportion between fecundity and egg size. Egg size refers to the mean weight of one egg in an egg load.

Individual-specimen relations

Meta-analysis. Midrange maternal pupal weight, which approximates the mean, varied from 12–9435 mg (Table 1), averaging 1401 and 63 mg for perfect and imperfect groups. The difference is highly significant (Student's t [separate variances] = 3.74; df = 34.1; P < 0.001). Range in transformed weights of pupae (greatest % of midrange minus smallest % of midrange) varied from 34–179 (Table 1), averaging 97 and 99 for perfect and imperfect groups. Corresponding uniform and multiform ranges are 34–179 and 48–143 (Table 1), averaging 97 and 100.

Slopes of fecundity-maternal pupal weight relations varied from 0.52–2.09 (Table 1, Fig. 3), with the mean and standard error, SE, 1.13 ± 0.04 . This overall mean significantly exceeds 1.00 (Student's t [one-tailed test] = 3.02; df = 57; P = 0.02). Slopes for perfect and imperfect groups average 1.14 and 1.12; those for uniform and multiform subsets also 1.14 and 1.12. The four slopes for perfect-uniform and perfect-multiform, and imperfect-uniform and imperfect multiform categories average 1.13 and 1.15, and 1.14 and 1.09. Differences among them are not significant (F = 0.08; df = 3, 54; P = 0.97). Pooled slopes are likewise unrelated to midrange pupal weight (Pearson's r = 0.06; df = 56; P = 0.68) or to range (Pearson's r = 0.04; df = 56; P = 0.77). Although a positive correlation among relations between range and number of observations either as n or $\log_e n$ could be expected statistically, it did not materialize (Pearson's r = 0.16; df = 56; P = 0.24). Slope variability as SE_b/b among perfect-uniform and perfect-multiform categories averaged 9.5 and 8.9, and among imperfect-uniform and imperfect-multiform, 13.0 and 15.7. The mean for the entire imperfect group, 14.8, is seemingly higher than that for the entire perfect group, 9.3, but the difference is not strictly significant (Student's t [separate variances] = 1.85; df = 27.4; P = 0.07). So-called funnel diagrams—plots of SE_b/b vs. b —visually suggest greater scatter among imperfect than perfect groups (Fig. 3a, b).

Spatial and temporal effects. Coefficients of fecundity-maternal pupal weight relations for the same species often differ geographically (Table 1), but only those obtained in the same way by the same workers can be meaningfully compared, as in the following examples. Lorimer (1979) found slopes and intercepts of two uniform relations for *Malacosoma disstria* from Indiana and Michigan to differ significantly. Parry et al. (2001) found four of the six *M. disstria* slope comparisons for Michigan, Manitoba, and Louisiana between two years to differ significantly, as well as all of the six intercept comparisons. In *M. disstria*, however, a tradeoff between fecundity and egg size occurs as a geographic NW-SE cline (Parry et al. 2001). At two Quebec locations, slopes of 0.26 and 0.18 for *Lymantria dispar* differed significantly (F = 20.5; df = 1, 111; P < 0.001) (transcribed data) (Madrid and Stewart 1981). Egg size is notably plastic in *L. dispar* (Rossiter 1991). Lorimer and Bauer (1983) found that fecundity-pupal weight slopes for *Choristoneura fumiferana* differed between New Hampshire and Minnesota; atypically, significant correlation was absent in the latter (transcribed data). Harvey (1983) demonstrated a geographic NW-SE cline in *C. fumiferana* egg size, as well as a clear geographic tradeoff between fecundity

TABLE 1. Regressions relating fecundity, F_p , to maternal pupal weight, W_p , in capital breeders based on transformed values for individual specimens.

No.	Species	Family	Pupal weight			Equation ($F_p = bW_p + a$)				Source of data	
			Midrange (mg)	Min. (%)	Max. Range (%)	b, SE	a	r^2	n		
Perfect-uniform											
1.	<i>Callosamia promethea</i> (Drury)	Saturniidae	1488	45	155	110	1.11, 0.06	-18.6	0.94	25	Miller et al. 1983
2.	<i>Antheraea polyphemus</i> (Cramer)	"	2760	46	154	108	0.73, 0.12	14.6	0.62	26	Miller et al. 1982
3.	<i>A. assamensis</i> Helfer	"	7255	83	117	34	1.25, 0.10	-22.5	0.88	24	Yadav & Goswami 1999
4.	<i>A. paphia</i> (L.) ^a	"	9435	74	126	52	1.00, 0.24	-6.4	0.45	23	Yadav et al. 2001
5.	<i>Nudaurelia c. cytherea</i> (F.)	"	5800	59	143	84	1.32, 0.34	-38.0	0.41	24	Geertsema 1975
6.	<i>Latoia viridissima</i> Holland ^a	Limacodidae	562	38	122	84	1.30, 0.07	-40.9	0.79	95	Igbinosa 1992
7.	<i>Epirrita autumnata</i> (Bkh.)	Geometridae	70	46	154	108	1.29, 0.09	-51.5	0.66	100	Haukioja & Neuvonen 1985
8.	<i>Bupalus piniaria</i> (L.) ^b	"	138	65	134	69	0.76, 0.12	0.7	0.19	157	Stahl 1939
9.	<i>B. piniaria</i> ^b	"	115	61	139	78	1.40, 0.12	-48.3	0.67	70	Bevan & Paramonov 1957
10.	<i>Operophtera brumata</i> (L.) ^a	"	49	23	196	173	1.26, 0.09	-22.7	0.76	58	Kikuzawa et al. 1979
11.	<i>O. brumata</i> ^a	"	44	10	189	179	1.22, 0.06	-38.8	0.85	74	Holliday 1977
12.	<i>Lymantria dispar</i> (L.) ^{a, c}	Lymantriidae	1517	62	138	76	1.88, 0.16	-70.2	0.70	55	Madrid & Stewart 1981
13.	<i>L. dispar</i> ^{a, d}	"	1957	47	153	106	1.10, 0.02	-10.5	0.98	60	"
14.	<i>Dendrolimus pini</i> (L.) ^{a, b}	Lasiocampidae	3034	52	154	102	0.81, 0.09	16.2	0.59	58	Eckstein 1911
15.	<i>Malacosoma</i>										
	<i>disstria</i> (Hbn.) IN ^c	"	300	57	143	86	1.24, 0.10	-15.2	0.76	55	Lorimer 1979

16.	"	MI	"	358	58	142	84	1.00, 0.11	-7.0	0.62	55	"
17.	"	MI '98	"	494	53	147	94	0.84, 0.05	15.2	0.74	84	Parry et al. 2001
18.	"	MI '99	"	464	69	130	62	0.85, 0.09	19.1	0.77	29	"
19.	"	MB '98	"	496	47	153	106	1.16, 0.05	-7.9	0.85	86	"
20.	"	MB '99	"	490	61	139	78	1.19, 0.09	1.9	0.83	24	"
21.	"	LA '98	"	435	39	161	122	0.84, 0.05	15.4	0.81	70	"
22.	"	LA '99	"	464	69	131	62	1.08, 0.07	-4.6	0.88	29	"
23.	<i>M. neustria testacea</i> (Mots.)	"	"	468	51	149	98	1.37, 0.11	-26.8	0.74	50	Shiga 1977
Perfect-multiform												
24.	<i>Lymantria monacha</i> (L.)	Lymantriidae	"	480	33	167	134	1.57, 0.07	-64.1	0.88	71	Zwölfer 1933
25.	<i>L. dispar</i> (L.) ^b	"	"	1466	34	166	132	1.20, 0.10	-23.8	0.72	52	Maksimovic 1958
26.	<i>L. dispar</i>	"	"	2180	53	147	94	0.91, 0.05	2.5	0.83	62	Cambini & Magnoler 1997
27.	<i>Orgyia vetusta</i> Bdv.	"	"	533	55	145	90	1.02, 0.22	-21.8	0.44	28	Harrison & Karban 1986
28.	<i>Euproctis chrysorrhoea</i> (L.)	"	"	222	47	153	106	1.38, 0.07	-38.5	0.86	56	Van der Linde & Voüte 1967
29.	<i>Malacosoma neustria</i> (L.)	Lasiocampidae	"	498	58	142	84	1.20, 0.19	-3.4	0.31	90	Mehmet 1935
30.	<i>M. dissitria</i>	"	"	422	62	139	77	1.21, 0.09	-14.0	0.86	32	Original
31.	<i>Streblote panda</i> Hbn.	"	"	2886	59	141	82	0.80, 0.11	22.3	0.50	51	Calvo & Molina 2005
32.	<i>Ennomos subsignarius</i> (Hbn.)	Geometridae	"	214	41	159	118	1.31, 0.06	-34.7	0.92	36	Drooz 1965
33.	<i>B. piniaria</i>	"	"	170	60	140	80	1.10, 0.08	-5.2	0.41	313	Gruys 1970
34.	<i>Quadricalcarifera punctatella</i> (Mots.) ^a	Notodontidae	"	509	29	171	142	1.38, 0.03	-40.1	0.96	77	Kamata & Igarashi 1995
35.	<i>Bombyx mori</i> (L.) ^g	Bombycidae	"	1275	59	141	82	0.73, 0.08	25.4	0.40	146	Mizuta et al. 1969
Imperfect-uniform												
36.	<i>Tortrix viridana</i> L.	Tortricidae	"	40	38	162	124	1.05, 0.05	-26.2	0.83	99	Schütte 1957
37.	<i>Archips fuscocupreanus</i> (Wlsm.)	"	"	62	52	148	96	1.25, 0.07	-20.4	0.81	76	Ohira 1990

continued

TABLE 1. Continued

No.	Species	Family	Pupal weight			Equation ($F_p = bW_p + a$)				Source of data	
			Midrange (mg)	Min. (%)	Max. Range (%)	b, SE	a	r^2	n		
38.	<i>Choristoneura fumiferana</i> (Clem.)	NH	78	19	181	162	0.92, 0.11	-23.3	0.61	43	Lorimer & Bauer 1983
39.	"	MN	106	68	132	64	0.60, 0.38	60.7	0.06	45	"
40.	<i>Zeiraphera griseana</i> (Hbn.)	"	28	66	138	72	1.87, 0.29	-105.0	0.52	41	Benz 1974
41.	<i>Cydia pomonella</i> (L.) ^a	"	51	47	153	106	1.19, 0.11	-25.1	0.46	136	Deseö 1971
42.	<i>Parapediasia tetrella</i> (Zinck.) ^a	Crambidae	31	51	150	99	1.37, 0.21	-24.2	0.41	66	Marshall 1990
43.	<i>Eoreuma loftini</i> (Dyar)	"	42	36	164	128	0.87, 0.06	8.9	0.83	50	Spurgeon et al. 1995
44.	<i>Agrotis ipsilon</i> (Hufn.)	Noctuidae	259	46	154	108	1.58, 0.02	-58.4	0.98	30	Moawad & Nasr 1978-79
45.	<i>Utetheisa ornatrix</i> (L.)	Arctiidae	137	53	147	94	1.48, 0.13	-59.7	0.53	113	LaMunyon 1997
46.	<i>Pectinophora scutigera</i> (Holdaway)	Gelechiidae	22	73	127	54	0.88, 0.20	2.5	0.42	27	Vickers 1982
47.	<i>Yponomeuta evonymella</i> (L.) ^a	Yponomeutidae	29	48	152	104	0.64, 0.08	34.2	0.79	20	Leather & Mackenzie 1994
48.	<i>Cadra cautella</i> (Wlkr.) ^a	Pyralidae	12	36	176	140	1.17, 0.05	-44.2	0.90	56	Takahashi 1956
Imperfect-multiform											
49.	<i>Spodoptera exigua</i> (Hbn.)	Noctuidae	112	58	142	84	1.29, 0.12	-17.0	0.52	128	Tisdale & Sappington 2001
50.	<i>Diatraea saccharalis</i> (F.) ^f	Crambidae	154	38	162	124	0.99, 0.06	4.6	0.69	116	Bessin & Reagan 1990
51.	<i>Cadra cautella</i> ^a	Pyralidae	28	61	138	77	0.52, 0.18	20.1	0.10	77	Hagstrum & Tomblin 1975
52.	<i>Corcyra cephalonica</i> (Staint.) ^a	"	33	28	171	143	0.80, 0.12	-5.3	0.49	51	Russell et al. 1980
53.	<i>Choristoneura fumiferana</i>	Tortricidae	106	45	137	92	0.97, 0.15	1.24	0.50	42	Original

54. <i>Cnephasia jactatana</i> (Wlkr.)	"	41	76	124	48	1.53, 0.26	-61.1	0.48	41	Ochieng'-Odero 1990
55. <i>Epiphyas postvittana</i> (Wlkr.)	"	30	48	152	104	0.68, 0.18	3.89	0.19	60	Danthanarayana 1975
56. <i>E. postvittana</i> ^a	"	31	21	145	124	0.55, 0.13	35.5	0.19	78	"
57. <i>Lobesia botrana</i> (D. & S.) ^a	"	12	46	154	108	1.45, 0.09	-57.0	0.76	87	Torres-Vila et al. 1999
58. <i>Crociosema plebejana</i> Zell.	"	16	59	141	82	2.09, 0.09	-99.9	0.89	75	Hamilton & Zalucki 1991

^a Pupal wt. estimated as adult wt. x 1.85.

^b Based on numerical data in source.

^c Mont St. Hilaire.

^d Havelock.

^e State or province abbreviation.

^f Pooled data for johnsongrass, corn, and cane var. CP 61-37.

TABLE 2. Regressions relating fecundity, F_p , to pupal weight, W_p , in capital breeders based on transformed values for grouped specimens.

No.	Species	Family	No. groups	Group size	Equation		Source of data
					$(F_p = bW_p + a)$		
					b	a	
Perfect-uniform							
1.	<i>Antheraea mylitta</i> Drury ^a	Saturniidae	6	20	0.60	34.9	Badhera 1992
2.	<i>Samia cynthia ricini</i> Boisd. ^a	"	6	30	1.98	-96.0	Kotikal et al. 1989
3.	<i>Lymantria dispar</i> (L.) ^a	Lymantriidae	8	1-83	1.40	-47.8	Lozinsky 1961
4.	<i>Dendrolimus spectabilis</i> Butler ^a	Lasiocampidae	14	32-244	1.27	-24.0	Kokubo 1973
5.	<i>D. pini</i> (L.) ^a	"	5	2-19	1.35	-33.6	Rudelt 1935
Perfect-multiform							
6.	<i>Antheraea assama</i> Westw.	Saturniidae	40	10	1.70	-70.5	Barah & Sengupta 1991
7.	<i>Lymantria dispar</i> ^a	Lymantriidae	18	1-58	1.12	-14.4	Lewitt 1934
8.	<i>Dendrolimus punctatus</i> Wlkr., 1 st gen. ^a	Lasiocampidae	40	1-40	1.34	-36.9	Tsai et al. 1958
9.	<i>D. punctatus</i> , wintering gen. ^a	"	65	1-22	1.24	-25.1	"
10.	<i>Hyphantria cunea</i> (Drury)	Arctidae	24	≈30	1.35	-34.5	Morris & Fulton
Imperfect-multiform							
11.	<i>Trichoplusia ni</i> (Hbn.) ^a	Noctuidae	12	10	1.21	-16.2	Henneberry & Kishaba 1966
12.	<i>Diatraea saccharalis</i> (F.) ^a	Crambidae	8	≈29 - ≈90	2.06	-104.1	Van Dinter & Goosens 1970
13.	<i>Hofmannophila</i> <i>pseudopretella</i> (Staint.) ^a	Oecophoridae	21	1-27	1.17	-14.0	Woodroffe 1951

^a Based on numerical data in source.^b Pupal weight estimated as 1.85 x adult weight.

and egg size. Temporally, only one of three pairs of available *Malacosoma disstria* slopes differed significantly—0.58 and 0.72 for Louisiana between 1998 and 1999 ($F = 4.14$; $df = 1, 95$; $P = 0.045$) (transcribed data) (Parry et al. 2001).

Temperature effects. Nine multiform relations involved different larval rearing temperatures among cohort subgroups (Nos. 24, 25, 29–31, 34, 35, 53, and 58 in Table 1), and each relation is discussed below.

Relation 30. This previously unpublished *M. disstria* relation is discussed first because it typifies the effects of multiform rearing temperatures on fecundity-maternal pupal weight relations. The data derive from overwintered egg rings collected in April from quaking aspen, *Populus tremuloides* Michx. (Salicaceae), near International Falls, Minnesota. Larvae hatching from several egg rings were mixed and subdivided into three subgroups. The subgroups were laboratory-reared on source foliage through pupation, one subgroup each at arbitrary temperatures of 20, 25, 30° C in separate growth chambers fluorescent-illuminated on a 12:12 D:N schedule. Rearing containers were transparent, screen-topped 20-liter plastic garment boxes. Foliage was renewed every third day and its turgidity maintained by sealing stem bases in water bottles. Pupae were weighed within 24 hr after transformation and placed singly in 25-ml cream cups for eclosion. A subsample of newly eclosed female adults developing at each temperature was frozen for egg counting. Essentially all *M. disstria* eggs are mature at eclosion (OI = 1).

In the whole sample, mean weights of female pupae reared at 20, 25, and 30° were 326, 461, and 331 mg, and the 461 mg weight at 25° is inferred to be statistically the highest ($F = 65.6$; $df = 2, 109$; $P < 0.001$).

In the subsample, both fecundity and female pupal weight peaked at 25° C (Fig 1a), making their reaction norms across the rearing temperatures congruent. A fecundity-maternal pupal weight relation for each temperature was computed (Fig. 1b), but neither their slopes nor intercepts differed significantly (slope $F = 0.80$; $df = 2, 25$; $P = 0.46$, intercept $F = 0.85$; $df = 2, 25$; $P = 0.44$). The three cohort subgroups are pooled in the summary relation (Fig. 1c, Table 1).

Relation 24. Zwölfer (1933) reared *Lymantria monacha* at six arbitrary constant temperatures from 11–28° C. Both fecundity and female pupal weight peaked at ≈25°, making their reaction norms across the rearing temperatures congruent. Points in the source scatterplot were noncoded, which precluded deconstruction for further analysis.

Relation 25. Maksimovic (1958) reared *Lymantria dispar* at six arbitrary constant temperatures from 15.5–31.9° C. Both fecundity and female pupal weight peaked at ≈15.5°, making their reaction norms congruent. I divided these data into two temperature classes for further analysis, 15.5–24.5° and 27.6–31.9°. Mean female pupal weights were 1533 mg at the cooler temperatures and 1189 at the warmer, and the difference is highly significant (Student's $t = 3.6$; $df = 50$; $P < 0.001$) (tabulated data). Slopes and intercepts of fecundity-maternal weight relations for the two classes were 0.41 and -43.4, and 0.46 and -157.8, neither difference proving significant (slope $F = 0.20$; $df = 1, 48$; $P = 0.66$, intercept $F = 0.72$; $df = 1, 48$; $P = 0.40$) (tabulated data).

Relation 29. Mehmet (1935) reared *Malacosoma neustria* at four arbitrary constant temperatures from 18.5–31.5° C. The mean female pupal weight of 551 mg at 22.7° is inferred to be significantly greater than the

FIG. 1. Fecundity-maternal weight relations in cohorts of *Malacosoma disstria* reared at different constant temperatures. a. Reaction norms of female pupal weight and fecundity to rearing temperatures. Weights based on 21-56 individuals; fecundities based on 4-14 individuals. b. Scatterplot and regressions of fecundity vs. female pupal weight for each rearing temperature. Equations: at 20° C, $F = 0.44W - 19.5$, $r^2 = 0.86$; at 25°, $F = 0.54W - 81.7$, $r^2 = 0.94$; at 30°, $F = 0.56W - 57.3$, $r^2 = 0.90$. c. Scatterplot and summary relation of fecundity vs. female pupal weight after transformation to percentages of pooled midrange values. Equation is $F_p = 1.35W_p - 18.3$, $r^2 = 0.81$.

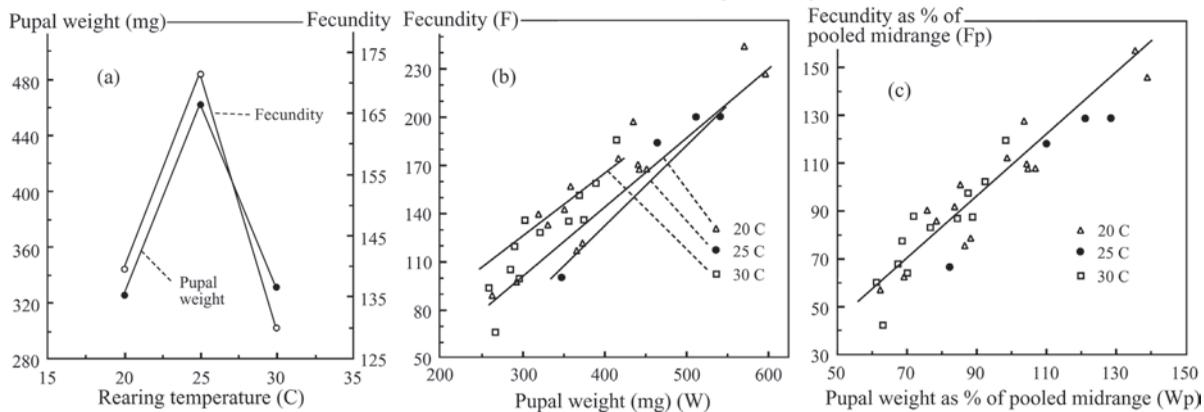
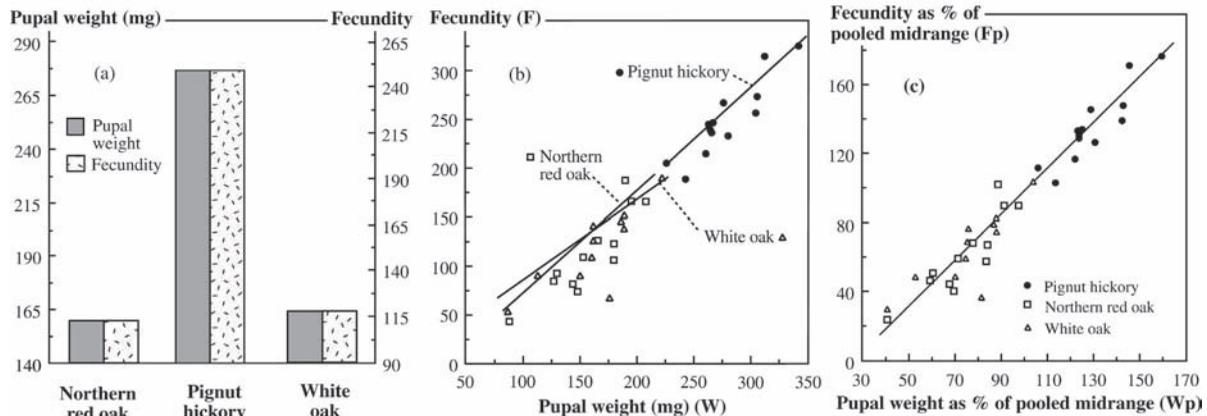


FIG. 2. Fecundity-maternal weight relations in cohorts of *Ennomos subsignarius* reared on different foodplants in the laboratory. a. Pupal weights and fecundities by foodplant. b. Scatterplot of preceding data, with regression statistics as follows: pignut hickory, $F = 1.14 W - 67.1$, $r^2 = 0.81$; northern red oak, $F = 1.11 W - 63.8$, $r^2 = 0.79$; white oak, $F = 0.88 W - 24.9$, $r^2 = 0.66$. c. Scatterplot and summary relation of fecundity vs. pupal weight after transformation to percentages of pooled midrange values. Equation is $F_p = 1.31 W_p - 34.7$, $r^2 = 0.92$. Data transcribed from Drooz (1965).



467, 485, and 406 mg at 18.5, 25.4, and 31.5° ($F = 11.55$; $df = 3, 90$; $P < 0.001$) (transcribed data). Both fecundity and female pupal weight peaked at 22.7°, making their reaction norms congruent. Points on the pertinent source scatterplot were not temperature-coded, which precluded deconstruction.

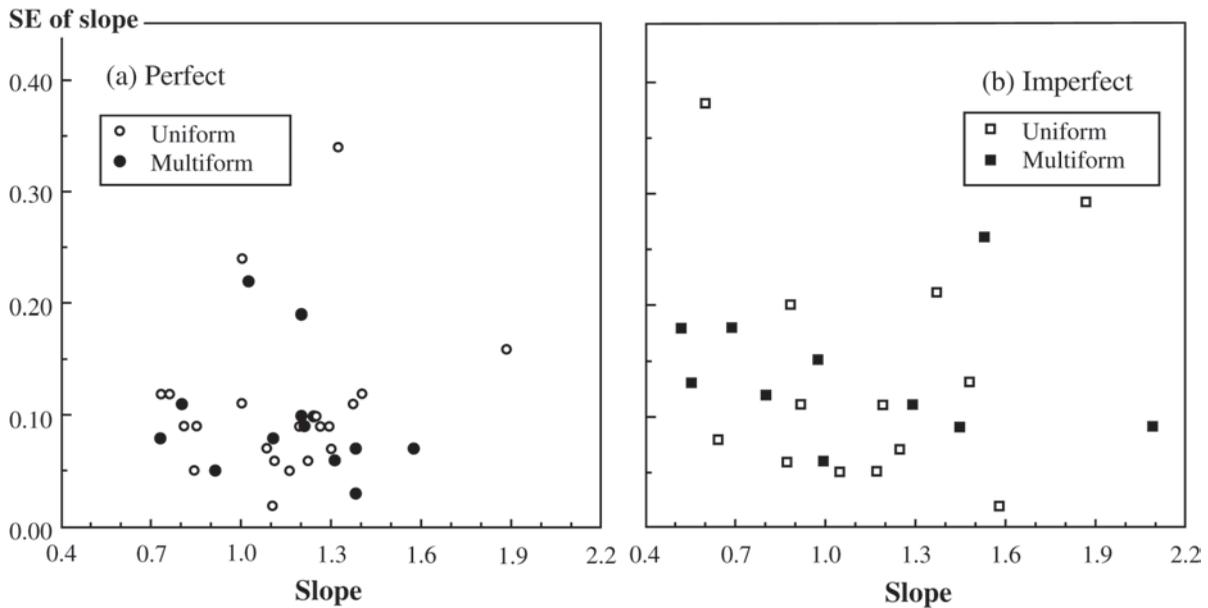
Relation 31. Calvo and Molina (2005) reared *Streblote panda* at four arbitrary constant temperatures from 19–28° C on two foodplants. Congruency of fecundity and maternal weight to the temperatures and foodplants is indeterminate, and the noncoded scatterplot precluded deconstruction.

Relation 34. Kamata and Igarashi (1995) reared *Quadricalcarifera punctatella* at arbitrary constant temperatures from 10–25° C. At the lower temperatures, most larvae had four stadia, and at higher ones, most had five. The authors also field-collected pupae for comparison with the laboratory rearings. Points on their scatterplot of fecundity vs. adult female weight were coded as four-stadium, five-stadium, and field-collected, which permitted deconstruction for analysis and comparison of cohort subgroup regressions. After adult-to-pupal weight conversion, female pupae averaged 390, 520, and 741 mg for the four-stadium (cooler), five-stadium (warmer), and field-collected, all of which are inferred to differ significantly from one another ($F = 391.8$; $df = 2, 74$; $P < 0.001$) (transcribed data). In the three subgroup fecundity-maternal weight relations, slopes and intercepts were 0.72 and -108.4, 0.64 and -74.8, and 0.64 and -48.3. The slopes did not differ significantly ($F = 0.82$; $df = 2, 71$; $P = 0.44$), nor did the intercepts ($F = 0.88$; $df = 2, 71$; $P = 0.42$) (transcribed data). Congruency of fecundity and maternal weight is indeterminate.

Relation 35. Mizuta et al. (1969) reared Japanese and Chinese varieties of *Bombyx mori*, and resulting points on their scatterplot of fecundity vs. female pupal weight were coded as spring or summer and assumed to represent individual specimens. No rearing temperatures were given, but temperatures in spring were likely cooler than those in summer. Mean spring and summer female pupal weights were 1451 and 1133 mg, and the difference, 318 mg, is highly significant (Student's $t = 10.5$; $df = 144$; $P < 0.001$) (transcribed data). Corresponding fecundity-maternal weight slopes and intercepts are 0.30 and 70.8, and 0.45 and -128.3. The slopes do not strictly differ ($F = 3.0$; $df = 1, 142$; $P = 0.085$), nor do the intercepts ($F = 3.79$; $df = 1, 142$; $P = 0.053$). Occurrence of a fecundity-egg size tradeoff could not be ascertained, but given the many varieties of *B. mori* involved here and known generally (Hiratsuka 1999), tradeoffs would not be surprising. Congruency of fecundity and maternal weight is indeterminate.

Relation 53. This previously unpublished *Choristoneura fumiferana* relation is drawn from a two-part experiment. The first part used the whole sample, which focused on the response of female pupal weight to different rearing temperatures. The second part used a subsample of the whole in which fecundity as well as female pupal weight was measured. Certain comparisons in both groups are abbreviated because some data were unfortunately lost as detailed further on. Foliage harboring overwintered second instars within 3 m of the ground was collected in early May from *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss (both Pinaceae) near Cloquet, Minn. The second instars were light-extracted (Miller 1958) and placed at densities of 1 and 3 per cup in 25 ml

FIG. 3. Funnel diagrams showing standard errors of slopes, SE_{b_i} , relative to the corresponding slopes, b_i . a. Perfect group. b. Imperfect group.



plastic cups with artificial diet. Cups with each density were divided into three subgroups and reared as outlined by Grisdale (1970) in three growth chambers programmed for different temperatures. The first chamber simulated the natural seasonal march of daily mean day-night temperatures based on long-term averages at a weather station ≈ 20 km from the collection site, and presumably approximated the temperature regime to which the insect was acclimated. Chamber temperatures were increased 1°C every 4–6 days during May and June until adult eclosion. At the start, day-night temperatures were 10° and 3° , and at the end, 26 and 12°C . The second and third chambers housed cups at each density, with one chamber programmed 5° cooler than presumed acclimation and the other 5° warmer, their temperatures being increased incrementally as in the first chamber. All chambers were fluorescent-illuminated on a 16:8 D:N schedule. In early June, four weeks after the first collection, fifth instars were collected at the site, placed singly in cups with artificial diet, and added to the experiment for exposure to the rearing temperatures only during the late larval stage, from the latter part of stadium 5 through final stadium 6. All pupae were weighed and sexed within 24 hr after transformation. The subsample for computing fecundity-maternal weight regressions consisted of female-male pupal pairs placed one each with a 6 cm long sprig of foodplant in 0.5 liter cardboard ice cream containers in which they eclosed, mated, and oviposited. The OI of this species is ≈ 0.4 (Outram

1971, Miller 1987), but no liquids were provided to adults during posteclosion ovigenesis. Laid eggs were counted daily, and unlaid chorionated eggs were added to the daily counts after females died, with chorionation evaluated by ovarian staining with methylene blue (Miller 1987). As in the whole sample, a subsample subgroup developed under each of three temperature regimes, under long and short exposures to temperature regimes, and at two rearing densities.

In the whole sample, mean weights of long-exposure female pupae at single and triple densities across all temperatures were 100.0 and 101.7 mg, indicating no real difference due to density. Long-exposure single-density female pupal weights at presumed acclimation, at 5° cooler, and at 5° warmer, were 103.8, 106.9, and 85.8 mg, and the 18.0 mg lesser weight at warmer than presumed acclimation is highly significant (Student's $t = 3.75$; $df = 196$; $P < 0.001$). Long-exposure triple-density weights were 99.4, 111.9, and 93.6 mg, and the 12.5 mg greater weight at cooler than presumed acclimation is significant (Student's $t = 2.90$; $df = 248$; $P = 0.006$). Short-exposure single-density female pupal weights were 111.3, 110.8, and 104.7 mg, and the 6.6 mg lesser weight at 5° warmer than presumed acclimation is significant (Student's $t = 2.24$; $df = 293$; $P < 0.038$). The foregoing reliance on t -tests rather than more comprehensive F -tests was necessitated by loss of some data before analysis was completed. In the fecundity-maternal pupal weight subsample with densities and exposure lengths pooled, mean fecundities and mean

female pupal weights at presumed acclimation and 5° warmer were 167.2 and 106.6, and 112.6 and 88.5, indicating congruent reaction norms to rearing temperatures in the surviving data, data from 5° cooler than acclimation having been lost. These subgroup pupal weights mirrored those of the whole sample, but the associated fecundities were depressed compared with published experiments in which females received imbibing liquids (Miller 1987, 1989). Slopes and intercepts of pooled subsample data at presumed acclimation and 5° warmer were 1.26 and 23.2, and 1.91 and -56.3, but although seemingly disparate, neither slopes nor intercepts differed significantly (slope $F = 0.046$; $df = 1, 38$; $P = 0.83$, intercept $F = 0.12$; $df = 1, 38$; $P = 0.75$).

Relation 58. Hamilton and Zalucki (1991) reared *Crociosema plebejana* at a number of arbitrary constant temperatures from 14–31° C. Fecundity and female adult weight were congruent. Their scatterplot of fecundity vs. female adult weight is temperature-coded for seven rearing temperatures, which enabled deconstruction for analysis of constituent regressions. I computed two fecundity-maternal weight regressions, one for 14–21° C, and the other for 25–31°. Their slopes and intercepts were 51.8 and -237.6, and 47.9 and -195.0, and neither the slopes nor intercepts differed significantly (slope $F = 0.64$; $df = 1, 71$; $P = 0.42$, intercept $F = 0.99$; $df = 1, 71$; $P = 0.32$) (transcribed data). In addition, the authors showed statistically that fecundity depended on female weight independently of temperature.

Diet effects. Twelve multiform relations involved cohort subgroups that received different larval diets (Nos. 26, 28, 32, 33, 50, 52, 54–56, 67) or different adult diets (Nos. 49, 51). Subgroup larvae were reared separately on different foodplants or on diets differing otherwise in quality or quantity. In the adult group, different imbibing liquids were provided, or withheld, during posteclosion ovogenesis. Each relation is discussed below.

Relation 32 for *Ennomos subsignarius* is discussed first because it typifies the effect different larval diets have on fecundity-maternal weight relations. Drooz (1965) reared this species on pignut hickory, *Carya glabra* (Mill.) Sweet (Juglandaceae), northern red oak, *Quercus rubra* L., and white oak, *Q. alba* L. (Fagaceae). He found that fecundity and female pupal weight were significantly higher on pignut hickory than on the oaks (transcribed surrogate values here in Fig. 2a). Fecundity and female pupal weight across foodplants were congruent. In a subsample, Drooz computed regressions of fecundity vs. female pupal weight by

individual and pooled foodplants (transcribed surrogate values in Fig. 2b). I confirmed that differences among slopes and intercepts of these regressions do not differ significantly (slope $F = 0.63$; $df = 2, 30$; $P = 0.54$, intercept $F = 0.51$; $df = 2, 30$; $P = 0.50$) (transcribed data). The three subgroups are pooled in the summary relation (Fig. 2c, Table 1).

Relation 26. Cambini and Magnoler (1997) reared cohort subgroups of *Lymantria dispar* on juvenile foliage alone and mixed juvenile-mature foliage of cork oak, *Quercus suber* L., and holm oak, *Q. ilex* L. They showed that female pupae were significantly heavier on cork than on holm oak, and on juvenile than on mixed juvenile-mature foliage. Six-stadium females predominated on cork oak, and 7-stadium females predominated on holm oak. The authors also showed that neither slopes nor intercepts of fecundity-maternal pupal weight relations among the subgroups differed significantly by foodplant. Fecundity and female pupal weight were consistently congruent.

Relation 28. Van der Linde and Voûte (1967) reared *Euproctis chrysorrhoea* on English oak, *Quercus robur* L., and buckthorn, *Rhamnus sp.* (Rhamnaceae), and their scatterplot of fecundity vs. pupal weight was foodplant-coded, which permitted deconstruction. Mean weights of female pupae were 186 mg on English oak and 268 on buckthorn, and the difference, 82 mg, is highly significant (Student's $t = 6.66$; $df = 54$; $P < 0.001$) (transcribed data). Corresponding slopes and intercepts were 1.78 and -112.4, and 1.63 and -62.1, but neither slopes nor intercepts differed significantly (slope $F = 0.31$; $df = 1, 52$; $P = 0.58$, intercept $F = 0.61$; $df = 1, 52$; $P = 0.44$). Congruency of fecundity and female pupal weight is indeterminate.

Relation 33. Gruys (1970) reared *Bupalus piniaria* at different densities including 1 larva/container, considered uncrowded, and 2–5 larvae/container, considered crowded. He presented uncrowded and crowded fecundity-maternal weight scatterplots separately. Mean weights of uncrowded and crowded female pupae were 184 and 152 mg, and the difference, 32 mg, is highly significant (Student's $t = 15.1$; $df = 311$; $P < 0.001$) (transcribed data). Gruys speculated that increased bodily contact in the crowded group adversely affected nutrition. He found that both slopes and intercepts of fecundity-maternal pupal weight regressions differed significantly between the two groups. He also found that crowding significantly reduced mean egg weight, which indicates a fecundity-egg size tradeoff between the two densities. Fecundity and female pupal weight proved congruent. Because density varies naturally, uncrowded and crowded

subgroups are pooled in the summary relation.

Relation 49. Tisdale and Sappington (2001) fed three groups of mated female adult *Spodoptera exigua* different liquid diets—10% honey in water, 10% sucrose in water, and plain water. They showed that fecundity of females on both carbohydrate diets significantly exceeded that of females on plain water. Their diet-specific scatterplots of fecundity vs. female pupal weight allowed deconstruction. I confirmed that pupal weights among treatment groups were statistically equal at the start ($F = 0.51$; $df = 2, 126$; $P = 0.60$) (transcribed data). Slopes and intercepts for the honey, sucrose, and plain water diets were 13.3 and 12.8, 12.4 and 43.6, and 16.5 and 1.78. The slopes did not differ significantly ($F = 1.00$; $df = 2, 122$; $P = 0.37$), nor did the intercepts ($F = 2.03$; $df = 2, 122$; $P = 0.14$) (transcribed data). It should be mentioned that *S. exigua* might be borderline between capital and income breeding.

Relation 50. Bessin and Reagan (1990) field-collected pupae of *Diatraea saccharalis* from two varieties of sugarcane, *Saccharum* spp.; corn, *Zea mays* L.; and johnsongrass, *Sorghum halapense* (L.) Persoon (all Gramineae). They showed that weights of female pupae differed significantly by foodplant but that differences among slopes and intercepts of the corresponding fecundity-size regressions did not differ significantly. Congruency of fecundity and pupal weight is indeterminate.

Relation 51. Hagstrum and Tomblin (1975) provided drinking water to mated female adults of one group of stock-culture *Cadra cautella* and withheld it from a second group. They presented scatterplots of fecundity vs. female weight separately for drinkers and nondrinkers. I confirmed that weights of the two groups were statistically equal at the start (Student's $t = 1.83$; $df = 75$; $P = 0.07$) (transcribed data). The authors found that drinkers laid significantly more eggs than nondrinkers, and that the corresponding fecundity-maternal weight regressions also differed significantly. Drinkers and nondrinkers are pooled in the summary relation because extent of drinking probably varies in environments where this species occurs.

Relation 52. Russell et al. (1980) reared two strains of *Corcyra cephalonica* on grain of millet, *Panicum* sp., and sorghum, *Sorghum* sp. (both Gramineae), which had been adjusted to differing moisture levels from 5–13%. Rearings were separate by strain, foodplant, and level of grain moisture. Mean weight of adult females of both strains ranged from 9.8–21.3 mg between the lowest and highest levels of grain moisture. No statistical tests were reported, but most of the weight differences are probably real. The scatterplot of fecundity vs. adult female weight was not treatment-

coded so could not be deconstructed. Congruency of fecundity and maternal size is indeterminate.

Relation 54. Final instars of *Cnephasia jactatana* were subjected to different levels of starvation to create differences in amount of food ingested (Ochieng'-Odero 1990). The author's scatterplot of fecundity vs. weight of female pupae was not treatment-coded, which precluded deconstruction. Congruency of fecundity and maternal weight is indeterminate.

Relations 55, 56. Danthanarayana (1975) reared *Epiphyas postvittana* on four foodplants—curled dock, *Rumex crispus* L. (Polygonaceae); plantain, *Plantago lanceolata* L. (Plantaginaceae); capeweed, *Arctotheca calendula* L. (Asteraceae); and apple, *Malus sylvestris* (L.) Mill. (Rosaceae). His scatterplots of fecundity vs. female weight were based on separate samples for pupae and adults. Neither scatterplot was diet-coded, which precluded deconstruction, and congruency of fecundity and maternal weight is indeterminate.

Relation 57. Torres-Vila et al. (1999) reared cohort subgroups of *Lobesia botrana* on *Vitis* sp. (Vitaceae), one on inflorescences, a second on unripe fruit, and a third on ripe fruit. These groups simulated three *L. botrana* generations associated with the annual march of foodplant phenology. The authors found that both maternal weight and associated fecundity differed significantly by subgroup. The diet-coded scatterplot allowed deconstruction, and slopes and intercepts for inflorescences, unripe fruit, and ripe fruit were 11.3 and 0.0, 15.5 and -15.5, and 23.8 and -35.1 (transcribed data). The slopes, although seemingly disparate, do not differ significantly ($F = 1.63$; $df = 2, 81$; $P = 0.20$), nor do the intercepts ($F = 0.34$; $df = 2, 81$; $P = 0.71$) (transcribed data). Fecundity and maternal weight proved congruent. The three generations are pooled in the summary relation.

Grouped-specimen relations

The 13 fecundity-maternal pupal weight relations based on grouped specimens number 10 of the perfect kind and 3 of the imperfect, 5 uniform, and 8 multiform. Perfect-uniform and perfect-multiform categories number five each and imperfect-uniform and imperfect-multiform categories number zero and three (Table 2). Grouping damps variation and equally weights groups of differing sample sizes, which biases regression statistics. Presentation of statistics for fecundity-maternal weight relations is therefore limited to slopes and intercepts of summary relations (Table 2) and to cohort subgroup relations, these statistics being useful despite aggregation bias.

Meta-analysis. Slopes of the summary relations vary from 0.60 to 2.06 (Table 2), with mean and SE 1.37 ± 0.10 . This mean is significantly higher than the

1.13 for individual-specimen relations (Student's t [one-tailed test] = 2.30; df = 69; P = 0.04). Slopes of the perfect-uniform category range 0.60–1.98, averaging 1.32; those of the perfect-multiform, 1.12–1.70, averaging 1.35; and those of the imperfect-multiform, 1.17–2.06, averaging 1.48.

Temperature effects. One relation involved different rearing temperatures, as discussed below.

Relation 13. In one experiment, Woodroffe (1951) apparently reared *Hofmannophila pseudospretella* at two temperatures and relative humidities: 25°C–70%, 10°C–70%, and 25°C–20%, but whether larvae were reared or ovipositing adults held under these conditions is not entirely clear. Although Woodroffe reported significant differences in fecundity among some female adult weight classes, I found no differences among adult female weights overall, which averaged 26, 22, and 24 mg (F = 0.31; df = 2, 18; P = 0.74) (tabulated data). I tested differences among the three corresponding fecundity-maternal pupal weight regressions whose slopes and intercepts were 12.8 and -7.4; 10.1 and -0.53; and 10.6 and -24.4, and the slopes did not differ significantly (F = 2.54; df = 2, 15; P = 0.89), nor did the intercepts (F = 0.12; df = 2, 15; P = 0.11) (tabulated data). The three presumed rearings are pooled in the summary relation. In a second rearing experiment mentioned only cursorily, fecundity and female adult weight across three temperature-humidity combinations slightly different than above proved congruent.

Diet effects. Diet was involved in seven relations (Nos. 6–12 in Table 2), each of which is discussed below.

Relation 6. Barah and Sengupta (1991) reared *Antheraea assama* on four foodplants and reported significant differences in female pupal weight by foodplant. Slopes and intercepts of fecundity-maternal pupal weight relations were 84.0 and -334.3 on *Litsaea* sp. No. 1, 47.3 and -95.2 on *Machilus bombycina* King ex Hook, 47.7 and -96.6 on *Litsaea* sp. No. 2, and 33.6 and -23.9 on *Cinnamomum* sp. (all Lauraceae), and the differences were highly significant (slope F = 7.52; df = 3, 32; P < 0.001) (transcribed data). Whether suspected tradeoffs between fecundity and egg size existed by foodplant could not be ascertained. Fecundity and maternal weight were congruent. The foodplants occur together in nature, and data from the four are pooled in the summary relation.

Relation 7. Lewitt (1934) field-collected *Lymantria dispar* pupae from a large area and segregated them into three groups by foodplant damage levels ranging ≈5–100%. Lewitt reported that pupal weight decreased with increasing foodplant damage and attributed this to decreasing food availability. Fecundity and female pupal weight across damage levels were congruent. The data

could not be deconstructed for detailed analysis.

Relations 8 and 9. Tsai et al. (1958) field-collected *Dendrolimus punctatus* pupae of the first and wintering generations from *Pinus* (Pinaceae) and segregated them by three levels of needle damage. Where 50, 80 and 100% of needles were damaged, mean weights of first-generation female pupae were 1210, 940, and 840 mg. Where <50, 50, 80, and 100% of needles were damaged, mean weights of wintering-generation female pupae were 1230, 1680, 1470, and 1490 mg. Although not tested, some differences among the pupal weights of both generations are probably real. Fecundity-maternal weight regressions did not differ among damage levels in either the first generation (slope F = 1.46; df = 2, 34; P = 0.25) or the wintering generation (slope F = 0.03; df = 3, 52; P = 0.99) (tabulated data). However, relations did differ significantly between generations (slope F = 135.2; df = 1, 96; P < 0.001) (tabulated data). Whether suspected tradeoffs between fecundity and egg size occurred could not be ascertained. Fecundity and maternal weight were exactly congruent in the first generation, and approximately so in the wintering generation. A summary relation is tabulated for each generation.

Relation 10. Morris and Fulton (1970) reared *Hyphantria cunea* in different years on different but unspecified diets. Their scatterplot of fecundity vs. female pupal weight was not treatment-coded, which precluded deconstruction for detailed analysis. Congruence of fecundity and maternal weight is indeterminate.

Relation 11. Henneberry and Kishaba (1966) reared 12 groups of *Trichoplusia ni* at 4 densities each with 3 different amounts of artificial diet. Female pupal weights declined significantly with increasing density and decreasing amount of food. Fecundity and maternal weight reaction norms across densities and amounts of food were congruent. The overall relation could not be usefully deconstructed for further analysis.

Relation 12. Van Dinther and Goossens (1970) reared *Diatraea saccharalis* on stalks of rice, *Oryza sativa* L., and corn, *Zea mays* L. (both Gramineae), and on differing amounts of various artificial diets. Magnitudes of reported means, standard deviations, and numbers of test individuals suggest significant differences among female pupal weights. Fecundity and maternal weight were approximately congruent. It was not possible to meaningfully deconstruct the summary fecundity-maternal pupal weight regression for further analysis.

DISCUSSION AND CONCLUSIONS

Exhaustive search yielded 56 more relations, 27 more species, and 8 more families of capital breeders than in

Honek (1993).

Meta-analysis

Few differences in fecundity-maternal pupal weight relations emerged at the metadata level. Individual-specimen slope means for perfect, imperfect, uniform, and multiform categories of summary relations did not differ statistically. The mean slope of 1.37 for the 13 grouped-specimen relations proved significantly higher than the 1.13 for the 58 individual-specimen relations. Also, the mean slope of 1.22 for Honek's (1993) 15 capital breeders exceeded that for the individual-specimen relations, but not significantly. Aggregation bias probably artificially elevated grouped-specimen mean slopes, including Honek's, who divided each data set into 3–8 grouped-specimen values. That the 1.13 slope mean statistically exceeds 1.00 may indicate that fecundity is increased or decreased disproportionately by change in maternal weight. This would indirectly intensify the influence on fecundity by an extrinsic factor like rearing temperature.

Fully deployed meta-analysis seeks to find a single best estimate of an effect or parameter (Gates 2002), but meta-analysis here is not meant to go beyond minimizing bias in selecting data sets and enabling group and subgroup comparisons. Despite evident similarity of slopes among capital breeders, one fecundity-maternal weight relation does not apply to all. Tradeoffs between fecundity and egg size sometimes occur. Also, capital breeders are taxonomically and ecologically diverse, as demonstrated by 15 families represented in this survey. Funnel diagrams of SE_b plotted on b for imperfect and perfect groups exhibit much scatter, especially in the imperfect group (Fig. 3a, b), which often can indicate low study precision (Gates 2002). However, adult nutrition potential—present in the imperfect group but absent in the perfect—probably increases variation in fecundity, thereby increasing scatter, and adults of the imperfect group usually had access to fluids. Studies of individual imbibing are few, but in one, *Choristoneura fumiferana* females imbibed erratically, which undoubtedly increased variation in fecundity (Miller 1989).

Individual-specimen midrange pupal weights averaging 63 mg for the imperfect group and 1401 mg for the perfect confirm casual observations that perfect capital breeders are typically larger-bodied than imperfect ones.

Extrinsic effects

Extrinsic effects on fecundity-maternal pupal weight relations were reflected predominantly in pupal weight and fecundity. In all nine individual-specimen summary relations involving different rearing temperatures (Nos. 24, 25, 29–31, 34, 35, 53 and 58 in Table 1), female

pupal weight formed steeple-shaped reaction norms across the temperatures, which fecundity closely tracked, as in Fig. 1a. Of the six where cohort subgroups could be compared (Nos. 25, 30, 34, 35, 53, and 58), slopes may have been affected in only one (No. 35 for *Bombyx mori*). Hamilton and Zalucki (1991) showed statistically that in *Crocidosema plebejana* (Relation No. 58) fecundity was controlled directly by maternal weight and only indirectly by rearing temperature. In all four individual-specimen summary relations concerning different larval diets where cohort subgroups could be compared (Nos. 26, 32, 33, and 57 in Table 1), female pupal weight and fecundity peaked on the same diet, and only one (No. 33 for *Bupalus piniaria*) exhibited an effect on slope. That maternal weight directly determines fecundity can be inferred from all of the individual-specimen relations.

In the grouped-specimen multiform relations, larval diet was most often the focus, and different diets affected female pupal weight the same as in individual-specimen relations. Although fecundity and maternal weight were congruent in grouped-specimen relations, slopes sometimes differed between cohort subgroups, signaling fecundity-egg size tradeoffs. Different adult diets altered posteclosion ovigenesis in two imperfect capital breeders (Relations 49 and 51 in Table 1), but adult studies were too few to permit broad generalizations.

In a study of maternal weight and fecundity in *Choristoneura fumiferana* developing on normal, fourth- and fifth-year severely infested foliage—a sequence of declining diet quality—Miller (1957) found that the slopes did not differ significantly, but that the intercepts and maternal sizes declined in parallel with the declining diet-quality sequence. In a study whose surprising results need confirmation, Carisey and Bauce (2002) found that maternal size in *C. fumiferana* did not differ among cohort subgroups reared on three artificial diets simulating midcrown, lower crown, and old foliage of *Abies balsamea*, whereas fecundity and egg size declined in parallel with this sequence of declining diet quality.

In several capital-breeder studies not heretofore mentioned, mean fecundity also peaked jointly with mean female pupal weight across rearing temperatures, providing additional examples of congruency. These involved *Galleria mellonella* (L.), *Achroia grisella* (F.) (both Pyralidae), *Bupalus piniaria* (Oldiges 1959), and *Lobesia botrana* (Torres-Vila 1996). Also, in a supplement to Relations 55 and 56 for *Epiphyas postvittana* (Table 1), Danthanarayana et al. (1995) reared *E. postvittana* on four foodplants, including three used in the earlier study, plus an artificial diet, at

six constant temperatures from 10.3–32° C. A 6-temperature \times 5-diet matrix totaling 30 female pupal weights and fecundities resulted. Maternal weight and fecundity peaked exactly together at five of the six temperatures, and did so approximately at the sixth, and exactly together on three of the five diets, and approximately so on the remaining two. The authors showed that most peak fecundities and maternal weights significantly exceeded nonpeak counterparts.

Rearing temperatures in most of the assembled temperature-focused studies were selected arbitrarily, but those for *Choristoneura fumiferana* (Relation 53 in Table 1) were selected purposefully to compare pupal weights and fecundities at warmer and cooler regimes with those at simulated natural temperatures. The natural regime was presumed to represent the regime of acclimation. Pupal weights and fecundities slumped at 5° warmer but peaked at or near 5° cooler. This occurred in both the short- and long-exposure experiments, which suggests that rapidly accelerating weight increase in the late fifth and sixth stadia (Eidt and Cameron 1972) made short exposure virtually equal to long exposure. Thus, brief anomalous warm weather might result in lighter, less fecund females, and brief anomalous cool weather in heavier, more fecund females. More often than not, cooler temperatures produced heavier, more fecund females even though temperatures were selected arbitrarily. Because of its population dynamics interest, this phenomenon should be sought in other capital breeders.

Deconstructing some fecundity-maternal pupal weight relations to obtain cohort subgroup regressions for comparison created smaller samples with fewer degrees of freedom, which may have led to false negatives in some tests of slope differences. Possible examples are *Choristoneura fumiferana*, *Lobesia botrana* (Relations 53 and 57 in Table 1), and *Hofmannophila pseudospretella* (Relation 13 in Table 2). However, these few cases do not seriously challenge the conclusion that extrinsic alteration of slopes occurs infrequently.

Leather (1988) cautioned against interpreting fecundity-size relations simplistically. His point that potential fecundity does not necessarily translate to field fecundity is unarguable. However, Leather's critique envisaged Lepidoptera as a whole without distinguishing between the divergent life systems of capital and income breeders. Also, he did not realize that extrinsic alteration of maternal size does not necessarily alter underlying fecundity-size relations. With the tally of more than 25 exactly congruent maternal pupal weights and fecundities emerging in this survey, and with no clear counter examples, the direct

dependence of fecundity on maternal weight probably warrants the axiomatic status it has been accorded for capital-breeding Lepidoptera. Moreover, extrinsic influences like rearing temperature and larval diet affect the dependence through maternal weight and thus only indirectly.

When slopes differed either spatially or among cohort subgroups, as they did in 10 cases, egg size, where reported, also differed, indicating tradeoffs with fecundity. Spatial examples include *Choristoneura fumiferana* (Harvey 1983) and *Malacosoma disstria* (Parry et al. 2001). A cohort subgroup example is that of *Bupalus piniaria* (Gruys 1970). Although not precisely understood, such tradeoffs are probably adaptive. They raise the possibility not only of their wider occurrence among capital breeders but that reproductive bulk, R —the mathematical product of fecundity \times mean weight of one egg (Roff 1992)—might constitute a reproductive response as useful as fecundity. The expression $R = b(W - R) + a$ removes R from W on the right-hand side of the equation so that maternal weight alone remains. This equation would be suitable where fully independent response and explanatory variables are desirable.

ACKNOWLEDGMENTS

I thank J. L. Stanis for researching *Choristoneura fumiferana* (Relation 53 in Table 1); R. D. Moon for analytical guidance, stimulating discussions, and useful comments on the manuscript; also M. A. Roberts and an unnamed reader for useful manuscript reviews; J. M. Muggli for laboratory assistance; and J. L. Moe for computer support. For translations, I thank K. Nishida and D. A. Andow (Japanese), S. S. Slocum (Russian and Ukrainian), and L. L. Niu (Chinese). I dedicate this paper to A. T. Drooz, friend, sometime colleague, and contributor to fecundity-maternal weight research (Relation 32 in Table 1) (Drooz 1965).

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Received for publication 23 December 2004, revised and accepted 18 May 2005