

REPRODUCTIVE BULK IN CAPITAL-BREEDING LEPIDOPTERA

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ABSTRACT. Reproductive bulk is the weight of the individual egg load, also the mathematical product of individual fecundity \times mean egg weight. Somatic bulk is its complement. Interrelations among nonindependent maternal weight, reproductive bulk, somatic bulk, fecundity, egg weight and related variables were explored with eight sets of data; three original, and five previously published, all representing four capital-breeder species in three families. In traditional fecundity–maternal weight regressions, response and explanatory variables are not statistically independent because maternal weight includes reproductive bulk. Comparative regressions where nonindependent maternal weight was the explanatory variable yielded median coefficients of determination of 0.62 for fecundity and 0.76, or 0.14, for reproductive bulk among the data sets. When maternal weight was rendered independent by subtracting reproductive bulk, the median coefficient of determination for reproductive bulk plummeted from 0.76 to 0.12, which exposes the extent to which nonindependence inflates regression test statistics. Reproductive bulk nevertheless increased with both independent and nonindependent maternal weight. Nonindependence does not necessarily invalidate the practical use of traditional fecundity–maternal weight regression models. Reproductive bulk is potentially useful as a response variable in regression models of reproductive potential where trade-offs between fecundity and egg weight occur, and where independent maternal weight is otherwise desired as an explanatory variable.

Additional key words: fecundity, egg weight, reproductive potential, reproductive effort, *Malacosoma disstria*, *Dendrolimus pini*, *Chilo partellus*, *Choristoneura fumiferana*

'Capital-breeding' refers to Lepidoptera that depend for reproduction entirely or chiefly on metabolic resources assembled during the larval rather than the adult stage (Boggs 1992, Miller 1996, Tammaru and Haukioja 1996). The great majority of Lepidoptera are capital breeders, as are the great majority of outbreak Lepidoptera (Miller 1996, 2005; Tammaru and Haukioja 1996). Capital breeders that assemble resources entirely during larval growth are termed 'perfect', and those that assemble most resources during larval growth but some during posteclosion adult feeding are termed 'imperfect' (Miller 2005).

Because reproductive potential in capital breeders is solely or heavily dependent on larvae, initial maternal weight has long been considered an indicator of fecundity (Honek 1993, Miller 2005). Indeed, retrospective analysis of capital-breeder fecundity–maternal weight regressions confirms a consistent relation between fecundity and maternal weight (Miller 2005). Moreover, extrinsic factors such as temperature and diet quality during larval development influence fecundity indirectly through their influence on maternal weight. Although lineal maternal size variables, including forewing length and pupal diameter, are also predictive, weight has traditionally predominated.

Trade-offs between fecundity and egg weight for a given maternal weight also can alter fecundity–maternal weight regressions. Trade-offs may vary temporally, spatially, and among subgroups of a cohort. Trade-offs are probably adaptive, and two notable examples are the geographic trade-off clines in *Choristoneura fumiferana* (Clem.) (Tortricidae) and *Malacosoma disstria* (Hbn.)

(Lasiocampidae) (Harvey 1983, Parry *et al.* 2001). Trade-offs highlight the potential utility of reproductive bulk as a response variable in regression models of reproductive potential (Miller 2005).

Reproductive bulk, R , is the weight of the individual egg load, or some meaningful fraction of it such as laid eggs or realized fecundity (Miller 2005). R also is the mathematical product of fecundity, F , \times mean egg weight, E . Somatic bulk, or non R , is maternal weight less R , or $W - R$. The expressions non R and $W - R$ are interchangeable. Reproductive effort, RE , is the proportion of maternal weight consisting of egg load, or $R/(W + R)$. These definitions are approximations in that they do not account for energy used in maintenance and in the development of reproductive structures (Roff 1992).

Traditional fecundity–maternal weight regressions for capital breeders are usually formulated as

$$F = bW + a \quad (\text{Eq. 1})$$

where W is weight of first-day pupae or of adults at eclosion, b is the slope parameter, and a is the intercept or scaling parameter (Honek 1993, Miller 2005). Reproductive bulk–maternal weight regressions may be analogously formulated as

$$R = bW + a \quad (\text{Eq. 2})$$

W in Eqs. 1 and 2 almost always includes R such that $W = \text{non}R + R$. Thus R is represented on both sides of these equations, thereby creating statistical nonindependence between response and explanatory variables (Roff 1992, Honek 1993, Miller 2005). Nonindependence masks data variability, inflates regression test statistics, and exaggerates the strength of relations. If measures of R are available, statistical

independence can be attained with the formulation

$$R = b(W - R) + a \quad (\text{Eq. 3})$$

Probably because fecundity is so obviously important in reproduction, and has so often been regressed on nonindependent maternal weight, pure R in capital breeders has been little investigated.

The objectives of this report are (i) to illuminate reproductive bulk, R , by examining its interrelations with nonindependent maternal weight, $W + R$, or non $R + R$, independent maternal weight or somatic bulk, non R or $W - R$, reproductive effort, RE , fecundity, F , mean egg weight, E , and (ii) to assess the impact of nonindependence between explanatory and response variables on the reliability of regression models for estimating reproductive potential.

MATERIALS AND METHODS

I sought capital-breeder data sets where R , non R , F , and E were given or could reasonably be derived. Before analysis, all weights were standardized to fresh weights at adult eclosion expressed in milligrams. Dry weight in data sources was converted to fresh weight using the factor 3.3 (Honek 1993), and pupal fresh weight to adult fresh weight using the factor 0.54, the reciprocal of 1.85 for the opposite conversion (Miller 2005). Data sets were accepted if they included more than eight mothers and did not require more than two conversions to obtain fresh weights of any variable. Some sample sizes are slightly less than in sources because individual observations were not always complete enough for use in this study.

I compared test statistics derived from each data set for regressions of F relative to $W + R$ (Eq. 1), R relative to $W + R$ (Eq. 2), and R relative to $W - R$ or non R (Eq. 3). Most statistics were computed with SYSTAT (1992) software. Correlations refer to Pearson r -values, and coefficients of determination to r^2 . Mean RE s were based on individual mother RE s. Lack of statistical significance at the 0.05 level is indicated by 'ns'. More specific methodological information is given as the analysis of each data set is discussed below.

RESULTS

Eight data sets, marginally to eminently suitable, were found for four capital breeders in three families. Three sets are considered original because they were used only partially in previous publications. Three or more comparative regressions are presented for each data set as well as mean RE and the correlation between F and E . Regression test statistics where $W + R$ rather than $W - R$ is the explanatory variable should be interpreted cautiously because of inherent nonindependence.

No. 1. In this and the following two analyses, pupal weights, fecundities and reproductive bulk for *Malacosoma disstria* (Hbn.) (Lasiocampidae), a perfect capital breeder, were transcribed from enlarged photocopies of scatterplots in Fig. 2 of Parry *et al.* (2001). Regression slopes computed from transcribed values were compared with slopes given in the source, and F -tests showed that departures were small and nonsignificant. In each of these three data sets two conversions were necessary: fresh first-day female pupal weight to fresh maternal weight at eclosion, and dry reproductive bulk to fresh reproductive bulk. Louisiana results are presented first.

Regressions (all $n = 29$):

$$F = 0.98(W + R) + 23.4, r^2 = 0.81, P < 0.01.$$

$$R = 0.84(W + R) - 18.5, r^2 = 0.85, P < 0.01.$$

$$R = 0.05(W - R) + 181.0, r^2 = 0.00, \text{ns.}$$

$$\text{Mean } RE = 0.76. r_{FE} = 0.24, \text{ns.}$$

No. 2. Michigan *M. disstria*.

Regressions (all $n = 29$):

$$F = 0.77(W + R) + 37.4, r^2 = 0.77, P < 0.01.$$

$$R = 0.70(W + R) - 16.4, r^2 = 0.86, P < 0.01.$$

$$R = 0.76(W - R) + 85.7, r^2 = 0.17, P = 0.03.$$

$$\text{Mean } RE = 0.63. r_{FE} = 0.29, \text{ns.}$$

No. 3. Manitoba *M. disstria*.

Regressions (all $n = 24$):

$$F = 0.76(W + R) - 30.9, r^2 = 0.89, P < 0.01.$$

$$R = 0.64(W + R) - 38.8, r^2 = 0.90, P < 0.01$$

$$R = 1.04(W - R) - 2.06, r^2 = 0.40, P < 0.01.$$

$$\text{Mean } RE = 0.50. r_{FE} = 0.28, \text{ns.}$$

No. 4. The Minnesota *M. disstria* data analyzed below originated in simultaneous laboratory rearings of three subgroups of larvae from a cohort of eggs collected near International Falls on *Populus tremuloides* Michx. (Salicaceae). The subgroups were reared at constant temperatures of 20°, 25°, and 30°C on foliage of the source foodplant, and the data used here are subsamples. Experimental procedure is detailed further in Miller (2005). Two conversions were necessary: fresh first-day pupal weight to fresh maternal weight at eclosion, and dry egg weight to fresh egg weight.

Regressions (all $n = 24$):

$$F = 0.71(W + R) + 6.4, r^2 = 0.63, P < 0.01.$$

$$R = 0.56(W + R) - 23.7, r^2 = 0.68, P < 0.01.$$

$$R = 0.27(W - R) + 60.2, r^2 = 0.05, \text{ns.}$$

$$\text{Mean } RE = 0.44. r_{FE} = 0.45, P < 0.05.$$

No. 5. In the following analysis of data for *Dendrolimus pini* (L.) (Lasiocampidae), a perfect

capital breeder, Eckstein (1911) may have provided the earliest published evidence for relations among the variables of capital-breeder reproductive potential. These are the only data here in which individual maternal weight was reported both before oviposition (gravid condition) and after eggs were laid or removed from ovaries (spent condition). Neither transcription nor conversions were necessary, making this the most experimentally satisfactory data. In the third regression below, $W - R$ was computed indirectly as $W_{\text{gravid}} - (W_{\text{gravid}} - W_{\text{spent}})$, and in the fourth, directly as W_{spent} .

Regressions (n=55–58)

$$F = 0.10(W + R) + 33.8, r^2 = 0.60, P < 0.01.$$

$$R = 0.82(W + R) - 220.1, r^2 = 0.93, P < 0.01.$$

$$R = 1.20(W - R) + 491.6, r^2 = 0.16, P = 0.01.$$

$$R = 1.22(W_{\text{spent}}) + 477.7, r^2 = 0.17, P = 0.01.$$

$$\text{Mean RE} = 0.67. \text{ RE} = 0.000093(W + R) + 0.525, r = 0.59, P < 0.01. r_{F,E} = -0.12, \text{ ns.}$$

The third and fourth regressions above differ only negligibly.

No. 6. The source data treated below are from Berger (1989) who reared *Chilo partellus* (Swinhoe) (Crambidae), an imperfect capital breeder, on artificial diet. After adults eclosed and were weighed and individually mated, Berger recorded numbers and weights of eggs laid on the first three nights of oviposition during which 80% of eggs typically are deposited. It appears that mothers were provided with water for imbibing. The data were transcribed from enlarged photocopies of Berger's Figs. 3 and 4. No conversions were necessary.

Regressions (all n = 9):

$$F = 1.80(W + R) + 247.7, r^2 = 0.20, \text{ ns.}$$

$$R = 0.19(W + R) + 6.33, r^2 = 0.55, P < 0.01.$$

$$R = 0.18(W - R) + 12.1, r^2 = 0.35, \text{ ns.}$$

$$\text{Mean RE} = 0.25. r_{F,E} = -0.10, \text{ ns.}$$

No. 7. In the two following analyses, data sets for *Choristoneura fumiferana* (Clem.) (Tortricidae), an imperfect capital breeder, originated with pupae collected near Duluth, Minnesota, from severely infested *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss. (both Pinaceae). Eclosing adults were divided into two groups, individually paired, and the group discussed first provided with sponges soaked in sweetened water for imbibing. Numbers of eggs laid by mothers of both groups were recorded daily. Eggs were weighed at least twice, the first time on the first or second day of oviposition, and the second and sometimes third on the fourth day of oviposition or later. Forewing length of mothers was measured after they

expired. Experimental procedure is detailed further in Miller (1987). Two conversions, the first involving two steps, were necessary in both sets: forewing length, FL, to dry weight, DW, by the species-specific formula $DW = 0.0057[FL^{3.336}]$ ($r^2 = 0.97$, $df = 211$, $P < 0.01$), and from dry to fresh weights.

Regressions (all n = 33):

$$F = 2.47(W + R) + 91.9, r^2 = 0.31, P < 0.01.$$

$$R = 0.52(W + R) + 9.7, r^2 = 0.34, P < 0.01.$$

$$R = -0.15(W - R) + 45.9, r^2 = 0.09, \text{ ns.}$$

$$\text{Mean RE} = 0.68. r_{F,E} = -0.02, \text{ ns.}$$

No. 8. These *C. fumiferana* results are from the second group mentioned above, which was provided with unsweetened water for imbibing.

Regressions (all n = 26):

$$F = 0.83(W + R) + 97.8, r^2 = 0.06, \text{ ns.}$$

$$R = 0.21(W + R) + 12.4, r^2 = 0.08, \text{ ns.}$$

$$R = -0.18(W - R) + 30.6, r^2 = 0.09, \text{ ns.}$$

$$\text{Mean RE} = 0.44. r_{F,E} = 0.11, \text{ ns.}$$

DISCUSSION

Comparison of regressions where fecundity, F , and reproductive bulk, R , were response variables to nonindependent W , that is to $W + R$ or $\text{non}R + R$ (Eqs. 1 and 2), shows coefficients of determination to be higher for R than for F among the eight data sets. This result reveals less variability in R than in F relative to the explanatory variable. Median coefficients of determination were 0.76 for R and 0.62, or 0.14 less, for F , and their intraspecific differences ranged 0.01–0.35, with a median difference of 0.08. This result was expected because R integrates fecundity, F , and egg weight, E , and, unlike F alone, takes account of trade-offs between F and E .

By contrast, when independent maternal weight, $W - R$ or $\text{non}R$, was the explanatory variable (Eq. 3), the median coefficient of determination for reproductive bulk among the data sets was only 0.12. This plummeting of the coefficient reflects the extent to which nonindependence artificially elevates test statistics. The fact that coefficients of determination for Eqs. 1 and 2 are inflated is not surprising; what is surprising is the extent of inflation. Even if barely satisfactory data sets 7 and 8 for *Choristoneura fumiferana* are omitted, the median coefficient of determination for reproductive bulk does not change appreciably (nor does that for fecundity). It is also telling that the corresponding coefficient of determination in an eminently satisfactory data set—No. 5 for *Dendrolimus pini*—dropped from 0.93 to 0.16, and thus reflects the overall trend among the eight data sets. Low coefficients of determination where

response and explanatory variables were independent—all ≤ 0.40 —expose the true variability in nonindependent data. Clearly, nonindependence in traditional regressions using $W + R$ as the explanatory variable has led to gross overstatements of the strength of maternal weight in models of reproductive potential.

Slopes in regressions of reproductive bulk relative to independent maternal weight or somatic bulk ranged 0.05–1.2 and were positive if not significant in six of the eight data sets. Positive slopes confirm Honek's (1993) reasoning that larger-bodied mothers are necessary—probably sufficient—for greater R as well as greater F . In the two exceptions, Nos. 7 and 8 for *Choristoneura fumiferana*, negative slopes may be anomalous as suggested by some but not all previous work (Miller 2005), and may be due to conversion errors, although variability in the life system of this species should not be ruled out. Other data sets with slopes not statistically different from zero—Nos. 1, 4, and 6—likewise may be due to transcription and conversion error. As indirectly measured variables become smaller, errors of conversion are magnified. The slope values show that reproductive bulk changes disproportionately relative to independent and nonindependent maternal weight, just as found for fecundity (Miller 2005). Disproportionate change between these variables may have implications for rates of population buildup and decline.

As already mentioned, trade-offs between fecundity, F , and mean egg weight, E , may occur temporally or spatially, and are doubtless adaptive. An example of statistically significant increase in E accompanying increasing F is data set No. 4 for *Malacosoma disstria*. An example of decrease is evident in *Bupalus piniaria* (L.) (Geometridae), where egg diameter was a surrogate for E (Klomp 1966) (data omitted here). Klomp noted the counterintuitive situation where even though surrogate egg weight of individual mothers increased serially, it still decreased overall with increasing fecundity. An example of constant E with increasing F is data set No. 5 for *Dendrolimus pini*. A remarkable further example is *Bombyx mori* (Bombycidae) (Fig. 1), illustrated here because it may represent the most extensive data in existence concerning egg weight relative to fecundity in a capital breeder. Unfortunately, the corresponding maternal weights were unavailable.

Reproductive effort, RE , ranged from 0.20s–0.70s among the eight data sets. RE is expected to vary adaptively in different species and environments (Roff 1992). It appeared static in all but one data set—No. 5 for *Dendrolimus pini*—but RE is derived and its test statistics relative to other reproductive variables are also subject to inflation. In *Choristoneura fumiferana* data sets 7 and 8, mothers provided with sweetened water

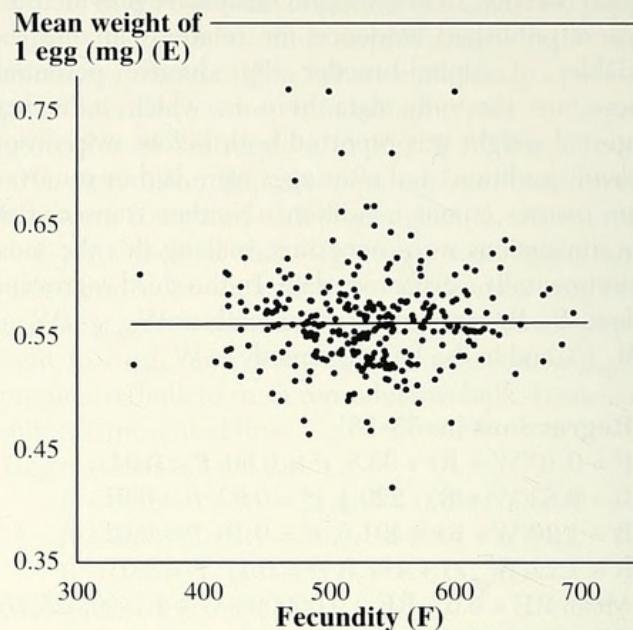


FIGURE 1. Relation of mean egg weight, E , to fecundity, F , in 293 races of *Bombyx mori*. Each point represents one or more females per race. The regression line is described by $E = 0.0000109 + 0.56F$, $r^2 \approx 0.00$, ns. Data were plotted from tables in Hiratsuka (1999).

had an RE of 0.68 compared with only 0.44 for those provided with unsweetened water; the 0.24 difference further demonstrates the enhancing role of adult nutrition in reproductive performance (Miller 1987, 1989).

Lack of independence between response and traditional explanatory variables does not necessarily invalidate practical use of fecundity-maternal weight regression models for estimating reproductive potential (Roff 1992). Maternal weight, whether independent or not, remains indicative of fecundity and reproductive bulk. In most basic research, however, response and explanatory variables should be statistically independent for reliable results. Further, all weights ideally should be measured directly and in dry form. The use of dry weights would warrant adoption of the stricter terminology of 'reproductive mass' and 'maternal mass'.

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