

**Birth weight and the rate of increase in the cowpea aphid *Aphis craccivora*  
(Homoptera: Aphididae)**

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**Aphids, fitness, parental investment, optimal birth weight**

**Abstract.** Consequences of birth weight for development, survival and fecundity were studied in the offspring of the alate morph *Aphis craccivora* (Koch), with the aim of testing the hypothesis that birth weight is near optimal. Aphids large at birth were found to mature sooner and achieve higher total reproduction than those born smaller.

A bootstrapping procedure was used to estimate the correlation between birth weight and two measures of fitness ( $r_m$ ): one calculated from unadjusted life-table data, the other from life tables adjusted to correct for the trade-off between offspring weight and offspring number. The unadjusted data yield a highly significant positive correlation – large neonates are fitter than small ones. The correlation estimated from the adjusted life table is no longer significant – mothers producing large offspring are no fitter than those producing small ones.

INTRODUCTION

Current theories on the evolution of parental investment are based on an assumed trade-off between the number of offspring and their fitness: a parent can produce either a few fit or many relatively unfit offspring (Smith & Fretwell, 1974). The fitness of an optimal level of parental investment (P.I.) (often measured as birth weight) is that which maximises fitness. The fitness of a semelparous organism can be estimated as the product  $F = p_s R_o$ , where  $R_o$  = fecundity and  $p_s$  = the offspring's chance of surviving to reproduce. In iteroparous organisms, however, fitness should be measured as  $r_m$  (Yodzis, 1982), defined by the Euler-Lotka equation:

$$1 = \sum l_x m_x \exp[-r_m x]$$

where  $l_x$  = survival to age  $x$ , and  $m_x$  = reproduction during age class  $x$  (Birch, 1948).

There are three main ways of testing the theory of parental investment:

1) Comparative studies – in general, a neonate's ability to withstand stress increases with its birth weight; there is thus a higher premium on being born large in harsh environments than in lush ones. It has been suggested that there are correlation between environmental stress and birth weight (Dixon, 1985).

2) Tests of quantitative predictions – accurate measurements of the form of the relations between birth weight and the components of fitness (e.g. development rate, the  $l_x$  and  $m_x$  schedules) can in principle be used to estimate the optimal birth weight. If only one component depends on birth weight the relation between birth weight and  $r_m$  can be determined fairly simply. If however, birth weight influences several components simultaneously the problem becomes much more complex. A second, practical, problem is that this approach

requires life-table data from a much wider range of birth weight than is normally available.

3) The correlational approach – here we propose a third means of testing birth weight theory. If a population's mean birth weight is below the optimum,  $r_m$  will be positively correlated with birth weight; if the mean is above the optimal birth weight, then the correlation will be negative. If birth weight is near-optimal, however, selection should be stabilising rather than directional, so there should be no correlation between birth weight and fitness; the benefits from increased offspring fitness should be exactly balanced by the cost in lost fecundity. Any correlation between birth weight and an  $r_m$  calculated from offspring life tables should disappear once this cost is taken into account.

Since the nutritional quality of the host of an aphid clone varies both spatially and temporally, so too will the selection on life-history characters. Aphid birth weight depends on both maternal adult weight and host quality (Dixon, 1985), so it is clearly flexible. The question is: does this flexibility reflect an adjustment of investment to yield a birth weight adapted to prevailing conditions? Or is it instead a side-effect of mechanisms that have evolved for other reasons? The fact that small or stressed mothers produce relatively small nymphs suggest the latter; to understand what mechanisms are we need to be able to recognise when neonates are too small, too large or the right size for the environment they are born into.

The likelihood that host quality changes with time produces two problems, one related to the approach to optimisation, the other to measurement of the components of fitness:

1) The evolutionarily stable strategy should be not a single optimal birth weight but an optimal sequence of birth weights, conditional on the temporal changes of host quality through the year. If an aphid's birth weight influences not only her longevity and age-specific fecundity but also the birth weight of her offspring, we are faced with a problem in dynamic optimisation. We show below that this is not the case for *A. craccivora*, so static optimisation suffices, but it may well be an important consideration in studies on other species or under other conditions.

2) We set out here to test whether neonate *A. craccivora* are too large, too small or the right size for the environment into which they are born. "The right size" means that the potential benefits of being born larger are exactly balanced by the reduction in the mother's fecundity. These benefits may include increased fecundity in aphids born large, but the fecundity of such an aphid depends in turn on the size of her own offspring. How, then, should we use life-table data to estimate the relation between birth weight and fitness ( $r_m$ )? We argue as follows: The benefits of being born large depend somehow on the effects of birth weight on the temporal patterns of acquisition and allocation of resources. The allocation schedule can be expressed as the age-specific pattern of reproductive output by weight, say  $\Sigma_x = B' \cdot m_x$ , where  $B'$  is the weight at birth of the offspring of the individuals whose production is being measured. If aphids born large [i.e. with high birth weights ( $B$ )] produce equally large offspring (high  $B'$ )  $r_m$  could be estimated directly from the observed  $l_x$  and  $m_x$  schedules, but they are not (see below); the cost of producing large offspring (reduced fecundity) should be incorporated by correcting the  $m_x$  values to give  $m'_x = m_x \cdot B/B'$ .

In other words, we measure the benefits of increased birth weight by correlating birth weight with  $r_m$  calculated from the observed  $l_x$  and  $m_x$  schedules; and correct for the cost of

increased birth weight by adjusting the  $m_x$  values – we generate  $r_m$  (adjusted) for hypothetical aphids with birth weights that remain constant from generation to generation.

In this paper we use the correlational approach to examine birth weight in the cowpea aphid, *Aphis craccivora*. We first examine the effects of birth weight on developmental rate, longevity and fecundity. We then use bootstrapping to estimate the correlations between birth weight and two  $r_m$  values: one calculated from offspring life tables, the other from life tables adjusted to correct for the trade-off between offspring weight and offspring number.

## MATERIAL AND METHODS

Aphids were taken from a clone of *A. craccivora* established from a single individual in 1988 and cultured since then on broad beans, *Vicia faba* var Coles Dwarf. The aphids were kept in a growth cabinet at  $20 \pm 2^\circ\text{C}$  with a photoperiod of L 12 : D 12 produced by six twenty-watt fluorescent globes and 1 incandescent globe. The broad bean plants were grown in a glass house for 4–5 weeks. Broad bean plants with 6–8 leaves and a height of 30–40 centimeters were used.

### Effects of birth weight on offspring fitness

Nymphs were collected at birth from alate adults, weighed and caged singly on broad bean. They were weighed again at adult moult, replaced in their cages and left to reproduce until they died. Their offspring were counted and removed daily; whenever possible, these were weighed within 1 hour of birth.

Fitness was calculated using iteration to find the intrinsic rate of natural increase,  $r_m$ .

## ANALYSIS

### Benefits of increasing birth weight

The aim here is to present and quantify the effect of an aphid's birth weight on her subsequent survival and reproduction. The total benefit of increased P.I. may depend on the effects of birth weight on several fitness components, and must thus be measured as the relation between birth weight and the  $r_m$  estimated from the unadjusted  $l_x$  and  $m_x$  schedules.

We separate the results into five life-tables, each containing the data from all aphids in a birth-weight class. Bootstrapping (Efron, 1982; Meyer et al., 1986) was used to estimate confidence intervals for  $r_m$  for each birth-weight class.

The benefits of increasing birth weight can be detected as the correlation between birth weight and  $r_m$ . This too was calculated by bootstrapping, as follows:

Each 200 bootstrap replicates of the correlation coefficient,  $r$ , was calculated from five pairs of data – bootstrap replicates of birth weight and  $r_m$  for each of the five birth-weight classes. To calculate mean birth weight and  $r_m$  values for, say, class 1 (the smallest 28 nymphs), 28 “nymphs” were chosen at random, with replacement, from among 28 real nymphs in the weight class. The mean birth weight was used as the bootstrap replicate of birth weight; their  $r_m$  was calculated by iteration, using the unadjusted life-table data on the 28 “nymphs”. This was repeated for the five birth-weight classes, so the bootstrap replicates of the correlation coefficient,  $r$ , was calculated from five generated points on the birth weight- $r_m$  plane.

### Do the costs equal or outweigh the benefits?

Here again we use bootstrapping to estimate  $r_m$  for each birth weight class, and the correlation between birth weight and  $r_m$ . Now, however, the  $r_m$  values were calculated from the life tables in which  $m_x$  was replaced with  $m_x' = m_x B/B'$ , where  $B$  = the birth weight of the randomly chosen aphids and  $B'$  = birth weight of their offspring.

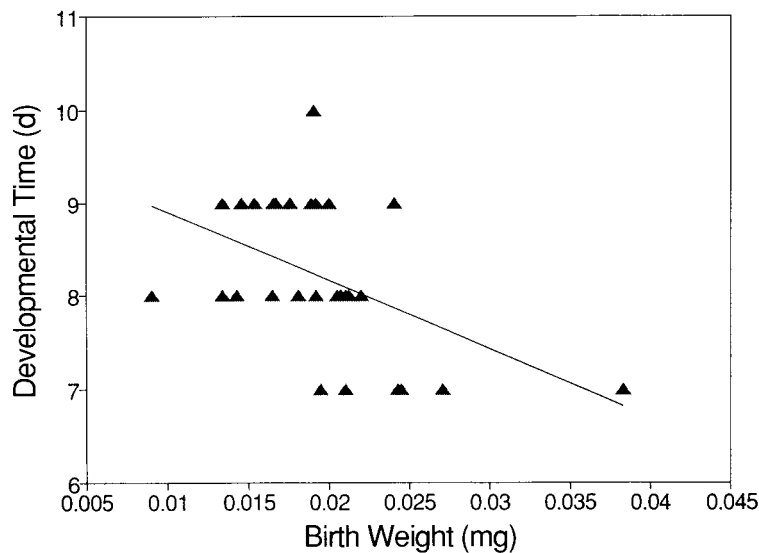


Fig. 1. The relationship between developmental time and birth weight found for the apterae morph *A. craccivora*. The regression equation is: developmental time =  $9.64 - 73.6 * (\text{birth weight})$ .

## RESULTS

### Consequences of birth weight

**MORTALITY.** Only 22.5% of the weighed neonates settled; the remainder died within 24 h. Survival did not depend on birth weight (2-sample t-test, survivors versus those that died:  $t = 1.11$ , 45 d.f.,  $p = 0.27$ ). We know of no reason for the high neonate mortality: subsequent experiments have found no significant effect of handling (this includes weighing and anaesthetising).

**DEVELOPMENTAL TIME.** Linear regression showed that developmental time ( $Dt$ ) decreased significantly with increasing birth weight:  $Dt = 9.64 - 73.6 B$ ;  $F_{1,28} = 8.17$ ,  $p = 0.008$ . Large neonates reach maturity earlier than smaller nymphs (Fig. 1).

**FECUNDITY.** Linear regression showed that birth weight significantly affected fecundity ( $F_{1,29} = 7.52$ ,  $p = 0.011$ ) (Fig. 2). However, birth weight had no significant effect on adult weight ( $F_{1,29} = 2.67$ ,  $p = 0.114$ ),  $\log(\text{longevity})$  ( $F_{1,29} = 0.51$ ,  $p = 0.480$ ), mean daily fecundity ( $F_{1,29} = 3.64$ ,  $p = 0.67$ ), RGR ( $F_{1,29} = 0.06$ ,  $p = 0.816$ ) or offspring birth weight ( $F_{1,29} = 1.98$ ,  $p = 0.165$ ).

### Birth weight and fitness

To examine the relation between birth weight and  $r_m$  the results were divided into five birth weight classes, 1, 2, 3, 4 and 5 (Table 1). From the original analysis it was established that aphids born bigger are more fecund. We also established that large nymphs reached maturity sooner than smaller ones. The life-tables showing percent mortality are

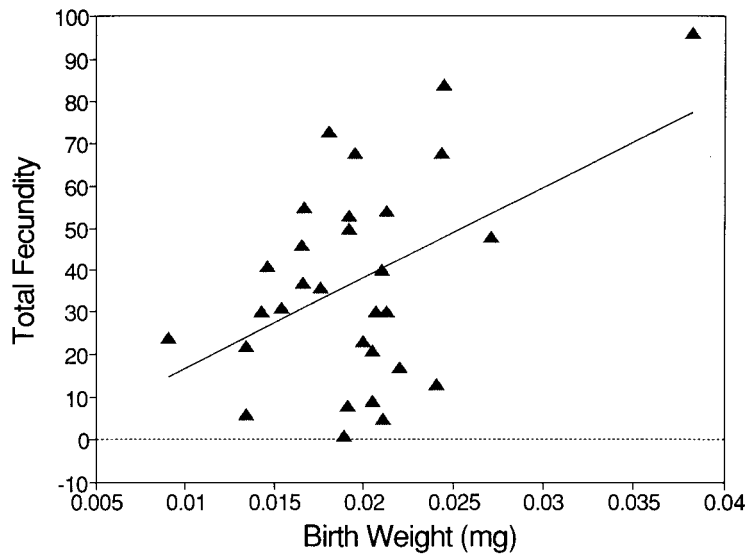


Fig. 2. The relationship between total fecundity and birth weight found for the apterae morph *A. craccivora*. The regression equation is: Total fecundity =  $-4.8 + 2149 \cdot (\text{birth weight})$ .

also presented in Table 1. Birth weight class 1 had the highest percentage mortality followed by birth weights 2, 3, 5 and 4.

TABLE 1. A summary of the birth weight classes used to estimate  $r_m$ : including mean birth weight for each class and percentage mortality for each size class.

Class	Class range	Mean weight (mg)	N	% mortality
1	0.0068–0.0143	0.0118	28	86.4
2	0.0144–0.0169	0.0158	31	83.0
3	0.0174–0.0194	0.0184	29	79.6
4	0.0195–0.0228	0.0209	31	69.4
5	0.0229–0.0383	0.0267	29	79.6

No data are available on the fraction of nymphs failing to settle in the field, although large discrepancies between observed and simulated populations suggested high nymphal mortality (Dixon & Wratten, 1971). Since it is unclear whether or not the high neonate mortality observed here was an artefact,  $r_m$  for each size class was estimated with and without this mortality (Table 2).

Fig. 3 shows the relation between unadjusted fitness ( $r_m$ ) and birth weight and Fig. 4 shows the adjusted fitnesses of aphids producing nymphs in the five birth-weight classes. Neonate mortality has no apparent effect on the forms of these relations, so for the remainder of this section we concentrate on the results of analysis of the full data set.

Fig. 5 shows the distributions of the bootstrap values of the correlation coefficients between  $r_m$  and birth weight, for both adjusted and unadjusted fitnesses.

Large nymphs are fitter than small ones (Fig. 3); unadjusted  $r_m$  is significantly correlated with birth weight: bootstrap  $r = 0.659$ , 96% of bootstrap values of  $r > 0$  (Fig. 5, open bars). The benefit to nymphs from being born large, however, is approximately balanced by the reduction in their mothers' fecundity; mothers producing a few large offspring are not significantly fitter than those producing more smaller nymphs (Fig. 4; Fig. 5, shaded bars; bootstrap estimate of  $r = 0.278$ , 70% of values  $> 0$ ).

EFFECTS OF MOTHER'S WEIGHT AND NYMPH'S POSITION IN THE PROGENY SEQUENCE ON BIRTH WEIGHT. Multiple regression showed that birth weight increased significantly with mother's teneral weight but was independent of position in the progeny sequence (Table 3).

TABLE 2. Calculated  $r_m$  for each size class for aphids with and without heavy initial nymphal mortality. Adjusted  $r_m$  assumes that the fitness of an aphid will be dependent on the size it is born and that it will produce offspring of that same size.

	Class 1	Class 2	Class 3	Class 4	Class 5
With heavy initial nymphal mortality included					
$r_m$ (unadjusted)	0.0723	0.1233	0.1274	0.1517	0.1736
$r_m$ (adjusted)	0.1036	0.1308	0.1310	0.1464	0.1442
With heavy initial nymphal mortality omitted					
$r_m$ (unadjusted)	0.2507	0.2694	0.2692	0.2530	0.3200
$r_m$ (adjusted)	0.2874	0.2757	0.2639	0.2395	0.2864

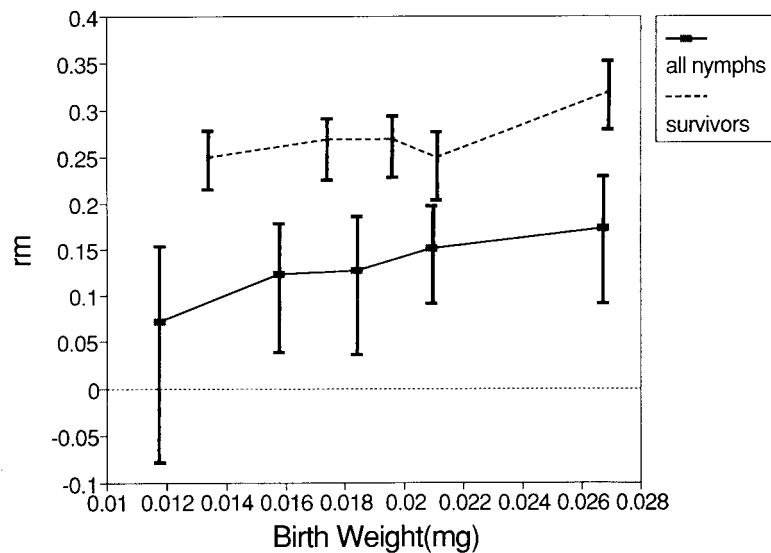


Fig. 3. Relationship between  $r_m$  (unadjusted) with heavy initial nymphal mortality included (all nymphs) and aphids with heavy initial nymphal mortality omitted (survivors), versus aphid size.

TABLE 3. Multiple regression of birth weight on mother's weight and nymph's position in the progeny sequence. Birth weight = 0.018 + 0.0093 (mother's weight) + 0.000035 (position in sequence).

Predictor	Slope	Std. Dev	t-ratio	p
constant	0.018	0.0013	13.80	< 0.001
mother's weight	0.0093	0.0041	2.26	0.028
position in sequence	0.000035	0.000029	12.1	0.232

R-sq = 20.0%

ANALYSIS OF VARIANCE

Source	DF	SS	MS	F	p
Regression	2	0.00017	0.000086	6.02	0.005
Error	48	0.00069	0.000014		
Total	50	0.00086			

DISCUSSION

Optimal P.I.: the nature of the trade-off

Theoretical studies of life history evolution almost always incorporate some form of trade-off between life history variables. One of the most fundamental trade-offs is that between the amount of resources invested per offspring (parental investment: P.I.) and the number of offspring produced (McGinley et al., 1987): a mother can produce either a few large or many small offspring. Increased P.I. may yield a wide range of benefits, including an increase in the offsprings' chances of survival and a reduction in their developmental

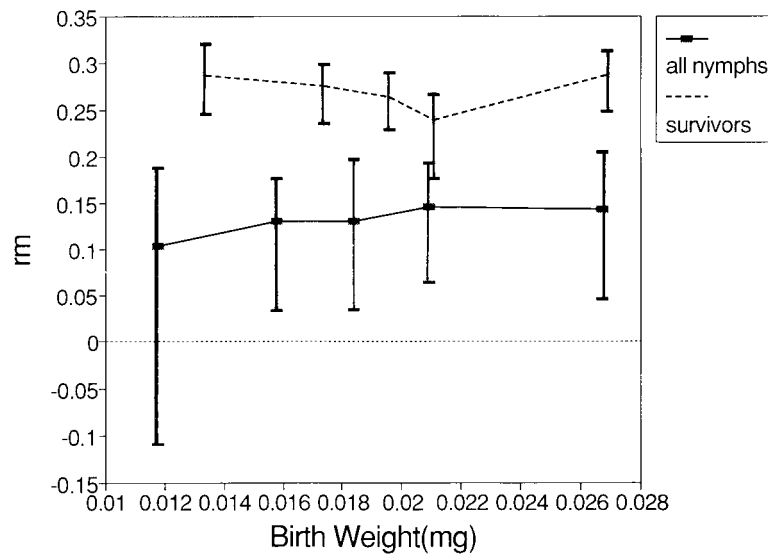


Fig. 4. Relationship between  $r_m$  (adjusted) with heavy initial nymphal mortality included (all nymphs) and with heavy initial nymphal mortality omitted (survivors), versus aphid size.

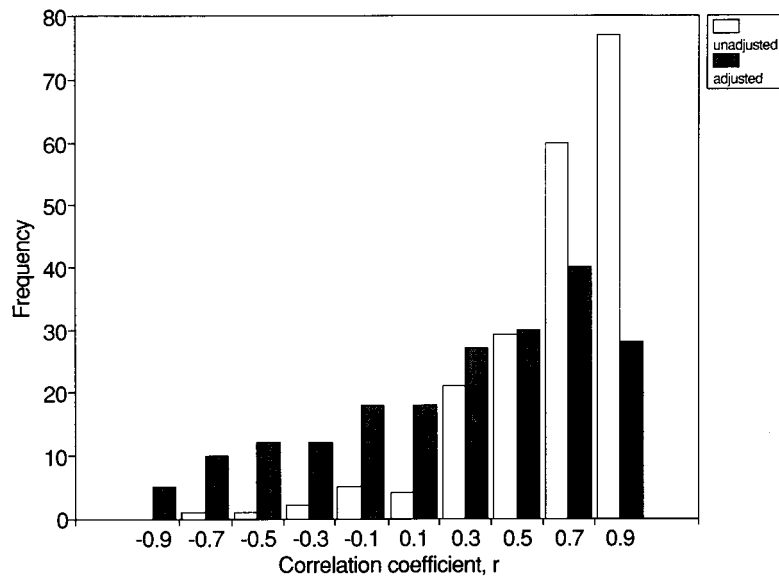


Fig. 5. Distributions of bootstrapping replicates of correlation coefficients between birth weight and  $r_m$  (unadjusted), and birth weight and  $r_m$  (adjusted).

time. For example, increased P.I. improves survivorship in birds (*Parus caeruleus*) (Nur, 1984), sea turtles (*Dermochelys coriacea*) (McGinley, 1989), and plants (Venable, 1992). Developmental time depends on P.I. in the frog *Bombina orientalis* (Kaplan, 1992) and increased P.I. increases growth rates in plants (Venable, 1992).

In the cowpea aphid an increase in P.I. results in a decrease in developmental time and an increase in fecundity. Large (and presumably expensive) nymphs reach adult moult faster than smaller nymphs, begin reproducing earlier and achieve greater life-time fecundity. Similar results have been found for *Rhopalosiphum padi* and *Aphis fabae* (Dixon, 1977, 1985).

#### Fitness

The cost of producing large fit offspring is a reduction in fecundity – the larger the offspring, the fewer can be produced from the resources available to the mother. Our analysis of the adjusted life-table data for *A. craccivora* shows that while fitness, measured as  $r_m$ , is correlated with birth weight the correlation is not significant. Clones that produced a few large offspring would not be significantly fitter than those producing more, smaller nymphs. This is the result expected if offspring are close to the optimal weight for the environment into which they are deposited.

This result cannot demonstrate that the mean birth weight is close to the optimal value – it relies on the absence of a significant correlation between fitness and P.I. – but it does show that the marginal cost of increasing P.I. is large enough approximately to balance the

marginal benefits in terms of offspring fitness. Work in progress is aimed at determining the power of this method to detect small deviations from the optimal birth weight.

#### Effects of mother's weight and the nymph's position in the progeny sequence

Current life-history theory predicts that birth weight should depend only upon the environment of the offspring. However, the results from this study refute this prediction. Large mothers produce large nymphs, which suggests that nymphal birth weight is not simply an adaptation to the nymph's environment.

No relationship was found between progeny sequence and offspring size of *A. craccivora* nymphs born to wingless mothers. These results are in agreement with Dixon & Wratten (1971) and Karczewska (1976): offspring born to wingless mothers tend not to change birth size with being born later in the sequence.

#### Vivipary and special constraints on birth weight in aphids

The results presented above suggest that within the range of birth weights observed for *A. craccivora* on broad bean the marginal benefits of an increase in P.I. are approximately balanced by the cost in terms of reduced fecundity, as would be expected if the mean birth weight were near optimal. This does not mean, however, that each aphid is roughly optimising the size of her offspring.

The model developed by Smith Fretwell (1974) predicts that the optimal birth weight is independent of the quantity of resources available for production of the clutch; it should depend only on the relation between the size and fitness of the offspring. Our results, however, and those of other authors (Dixon 1985), show that large mothers produce larger nymphs. This means either that large mothers' offspring are larger than they need be or that small mothers produce offspring smaller than the optimal size. The reasons for this are unclear, but may perhaps be related to the mechanisms of investment in offspring in aphids: Smith & Fretwell's (1974) model implicitly assumes that the production of a clutch involves the instantaneous division of a package of resources into many small or few large offspring. Aphids, however, begin investing in their offspring before they themselves are born; this, and the fact that achieved fecundity depends on the number of ovarioles in the ovaries (Ward, Dixon & Wellings, 1983) suggests that reproduction is sink-limited – that reproductive output depends not only on the rate at which the mother can acquire resources but also on the rate at which the embryos in her gonads can use them for growth and development. If so, a large aphid with a high consumption rate may benefit more by prolonging the gestation of her most mature embryos than by investing resources in additional ovulations that will yield offspring only after a long delay.

If sink-limitation is indeed an important factor in aphids' partitioning of resources among their offspring, then the adaptive significance of birth weight may depend not only on the birth weight-dependent fitness of nymphs but also on the nutritional status of the investing mother, in stark contrast to the predictions of existing models of parental investment.

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