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**"Optimal life history model for multicellular organisms
 with aphids as a model group"**

P. KINDLMANN
 Czechoslovak Academy of Sciences
 South Bohemian Biological Research Centre
 Department of Mathematics
 370 05 Ceske Budejovice
 Czechoslovakia

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**Optimal life history model for multicellular organisms
 with aphids as a model group: 1. The r_m/RGR ratio**

P. Kindlmann (1), A.F.G. Dixon (2) and L.J. Gross (3)

- (1) Department of Biomathematics, Biological Research Centre,
 Czechoslovak Academy of Sciences, Branišovská 31,
 370 05 České Budějovice, Czechoslovakia.
- (2) School of Biological Sciences, University of East Anglia,
 Norwich, NR4 7TJ, U.K.
- (3) Department of Mathematics, University of Tennessee,
 121 Ayres Hall, Knoxville, TN 37996, U.S.A.

Page Heading: Optimal life history

Abstract: A model incorporating the optimal partitioning of energy gained from assimilation between soma and gonads, the optimal time of maturation and constraints on the gonadal growth rate and the size of the soma at birth, predicted that the upper limit to the ratio of the population to individual relative growth rate, r_m/RGR , in multicellular organisms is 0.86. Empirical data for parthenogenetic aphids, which have overcome the constraint on their rate of increase imposed by developmental time by telescoping generations, shows that they achieve this ratio.

Keywords: aphids, life history, optimization, rate of increase

Introduction

Individual and population growth rates are usually not compared. However, intuitively it seems likely that a population that consists of fast growing individuals will grow fast, as the individuals will mature early and/or reach a larger size and thus a higher fecundity relative to a population of slow growing individuals. If population (r_m) and individual relative growth rates (RGR) are correlated then it should be possible to predict the population dynamics from a knowledge of how fast individuals grow.

In many animals and plants the population growth rate is considerably smaller than the individual growth rate. Organisms such as mammals and birds.

devote considerable time and energy to parental care, learning, hunting and other activities, which increase their competitive ability. These may not directly contribute to an increase in r_m . The highest possible r_m/RGR ratio could be reached by protozoa under ideal conditions. In the absence of mortality caused by predators or other factors these potentially immortal organisms, when reproducing by division, could achieve a ratio close to 1. In reality, $r_m/RGR < 1$ for the simple reason that there is a loss of soma at the inevitable death of each member of the population. It is interesting to ask what is the upper limit for this ratio for mortal organisms?

To determine this limit we assume the major constraint to be energy, optimize the way a mortal organism allocates the energy gained from assimilation to its vegetative and reproductive organs (soma and gonads, respectively) and also optimize the time of maturation. That is, r_m is maximized subject to energetic constraints. This gives the optimum r_m/RGR ratio, for which r_m is maximal. If evolution tends to maximize r_m rather than r_m/RGR or RGR, this r_m/RGR ratio will also be the upper limit we are looking for.

A commonly used approach in energy partitioning models is that pioneered by Cohen (1971), King & Roughgarden (1982), Ziolkowski & Kozlowski (1983) and others. Recently a model of optimum energy partitioning was developed, which is derived from the previous ones, but includes a constraint on the gonadal growth rate (Kindlmann & Dixon, 1989).

A group that could reach the upper bound of the r_m/RGR ratio are insect herbivores, especially aphids. The latter have morphs that do not spend time or energy in parental care, hunting or developing costly organs for moving or protection against predators. In most generations they do not use energy to produce males but reproduce parthenogenetically! Therefore, the only constraint on their potential r_m/RGR ratio seems to be survival and somatic growth. However, when using aphids as a model group, a constraint on their gonadal growth rate should be introduced, the existence of which is suggested by their simultaneous commitment to growth and reproduction and the telescoping of generations (Kindlmann & Dixon, 1989). This constraint was incorporated in order to develop an empirically testable model.

The optimum partitioning of energy during development

The size of soma at time t is denoted by $s = s(t)$, the size of gonads at time t by $g = g(t)$ and the developmental time by D . The usual assumption in most models of this type is that assimilation, E_{ass} , by the soma of size s is a power function of s : $E_{ass}(s) = as^\alpha$, where intraspecifically $\alpha = 2/3$ (the surface/volume ratio, c.f. Schmidt - Nielsen, 1984). In a previous model (Kindlmann & Dixon, 1989) the respiration costs,

$E_{resp}(s,g)$, of a body of size $s+g$ (soma + gonads) was assumed to be a power function of $s+g$: $E_{resp}(s,g) = b(s+g)^\beta$. This does not significantly affect the outcome as the respiration costs are negligible with respect to assimilation. Therefore, for the sake of simplicity, it is assumed that the net energy production ($E_{prod} = E_{ass} - E_{resp}$) is a power function of s : $E_{prod}(s) = as^\alpha$.

Given initial sizes of soma and gonads, $s_0 = s(0)$, $g_0 = g(0)$ and adult sizes of soma and gonads, $s_A = s(D)$, $g_A = g(D)$ and a constraint on the gonadal growth rate, R (see Kindlmann & Dixon, 1989), the optimum strategy for minimizing the developmental time, D , (and thus maximizing r_m) is to maintain the gonadal growth rate at a maximum throughout development and devote the rest of energy to the growth of soma (Kindlmann & Dixon, 1989). Mathematically, if biomass is measured in units of energy needed to build it:

$$s' = as^\alpha - Rg, \quad s(0) = s_0, \quad \text{Equation 1a}$$

$$g' = Rg, \quad g(0) = g_0, \quad \text{Equation 1b}$$

where $' = d/dt$.

Necessarily, s' becomes zero at a finite time D , which is the best time for maturation (Kindlmann & Dixon, 1989), i.e. when

$$as^\alpha_A = Rg_A \quad \text{Equation 2}$$

After that the organism should devote all the energy gained from assimilation to reproduction. Thus reproductive investment per unit time will be equal to $as^\alpha_A = Rg_A$.

In this model, which reveals the best strategy for energy allocation during nymphal development when there is a constraint on the gonadal growth rate, adult size is uniquely determined by the initial conditions s_0, g_0 and by the parameters a, α and R . The parameter $\alpha = 2/3$ in most models and the parameters a and R are species specific physiological constraints. This leaves the question of what determines s_0 and g_0 , which is central to the problem of maximizing r_m .

Calculation of fitness

A good measure of fitness is thought to be r_m . In looking for the optimum shape of the fecundity function, we have followed the arguments of Lewontin (1965). Firstly, r_m increases, if the peak of reproduction comes forward in time (Lewontin, 1965; Yodzis, 1989 and others). Thus the optimum shape of the fecundity function for maximizing r_m is triangular with the maximum at the onset of reproduction. Secondly, r_m increases, as the developmental time, D , decreases (Lewontin, 1965). Finally, Lewontin (1965) argues that r_m increases, as the length of the reproductive period, T , gets longer, although this is the least important factor in the maximization of r_m (see also Yodzis, 1989).

There is no general theory for predicting the optimal length of the reproductive period. Such an optimization would require a good knowledge of the mechanisms governing senescence, which we do not have at present (Calow, 1978). Therefore, we restricted our analysis by making a simplifying assumption, which was derived from what we know about the situation in nature. There is good empirical evidence that within a taxa T/D is constant (Charnov & Berrigan, 1990). In most organisms that attain an extremely high r_m , like aphids, mites etc., T is close to D (Bonnemaison, 1951; Frazer, 1972 etc.). Theoretical support for the constancy of T/D is put forward by Charnov (1990). As stated above, the value of T only makes a small contribution to r_m , and, moreover, it has been shown (Lewontin, 1965) that an increase in T may not result in an increase in r_m , providing all the other values remain constant. Thus fecundity late in life contributes little to r_m and the assumption of $T = D$ is both acceptable in the sense of Lewontin (1965) and Charnov (1990), and close to what is observed in nature.

In view of this/ it does not seem unreasonable to accept the widely used estimator of r_m suggested by Wyatt and White (1977):

$$r_m = .738 \ln M_d/D, \quad \text{Equation 3}$$

as a good measure of fitness.

Here M_d is the initial fecundity, i.e. the fecundity over a period equal in length to the developmental time, D . The reason for using equation 3 may be explained as follows:

Equation 3 resembles the widely used (May, 1976; Calow, 1978; Pianka, 1988 etc.) approximation of r_m :

$$r_m = \ln (F)/T_g, \quad \text{Equation 4}$$

which gives a good estimate of r_m provided it is close to zero or if the coefficient of variation of the generation time is not too large (May, 1976). However, the shape of the fecundity function is also important (May, 1976). Moreover, if one is interested only in estimating r_m over a short period of time, the initial age distribution is also important (Meats, 1972; Calow, 1978; Charlesworth, 1980; Pianka, 1988). Finally, equation 4 gives an exact estimate of r_m over one generation, which is the case for organisms with non-overlapping generations and those which optimize their r_m over short periods of time, e.g., those living in rapidly changing environments. Thus overall, equation 4 would appear to be appropriate. Equation 3 follows from equation 4 and implicitly assumes that the developmental time is equal to the length of the reproductive period. Moreover, that the constant should be close to .738

follows from the assumption that the fecundity function is triangular and that the length of the reproductive period is equal to the developmental time, i.e., in this case the generation time becomes equal to $D + D/3 = 4D/3$ (May, 1976), and the corresponding constant in equation 3 would be .75. As the empirical data was calculated using equation 3, the constant .738 was used throughout so that the results are compatible. The consequences for our results of using the constant .738 will be discussed later. In addition, the expression $DRg_A / (s_0 + g_0)$ used for estimating the initial fecundity, defines the balance in terms of energy between the input from soma and the output in the form of number of offspring produced during the reproductive period.

Thus our estimate of r_m becomes:

$$r_m = .738 \ln [DRg_A / (s_0 + g_0)]/D. \quad \text{Equation 5}$$

Consequences of optimizing birth size

In order to calculate the optimum g_0 , which maximizes r_m in equation 5, equation 1 was simulated using the fourth-order Runge-Kutta-Fehlberg method. Since, as described below, the trajectories in s - g space are the same for fixed s_0 , g_0 and a/R , a maximization was carried out for a/R varying from 1 to 20 in steps of 1 unit, s_0 varying from 5 to 100 in steps of 5 units, and with R fixed at 0.5. The maximization was carried out using Brent's method of inverse parabolic interpolation (Brent, 1973) on a SUN Microsystems 3/110. Due to the relative flatness of the r_m vs. g_0 relation (Fig. 1), the maximization was carried out several times with alternative bounding intervals. The effectiveness of the maximization scheme was checked by comparing its predicted optimum with that of a brute-force method, which involved calculating the maximum r_m directly from the r_m vs. g_0 relation (Fig. 1).

The optimization of g_0 with respect to r_m has consequences for other characteristics of the organism, such as the r_m/RGR ratio, where the individual growth rate, RGR , is defined as

$$RGR = \{\ln[(s_A + g_A) / (s_0 + g_0)]\}/D. \quad \text{Equation 6}$$

Division of equation 1a by 1b shows that for the same a/R exactly the same trajectories are obtained and thus the same s_A and g_A values, which also gives the same r_m/RGR ratio (from equation 5 and 6 where DR in equation 5 can be replaced by $\ln(g_A/g_0)$). Therefore, it is only necessary to determine the r_m/RGR ratio predicted by equations 5 and 6 for optimal g_0 for different combinations of a/R and s_0 , as in Fig. 2.

This figure shows a plateau of r_m/RGR ratios of around 0.86 for a broad range of values of a/R and s_0 . This ratio only declines when the a/R values are very low, i.e., when assimilation is very low compared with the gonadal growth rate, R (e.g., $r_m/RGR = .80$ when $a/R = 1$). Also, as expected, the r_m/RGR ratio approaches 1 when s_0 is very small and a/R is large, (e.g., $r_m/RGR = .90$ when $a/R = 20$ and $s_0 = 10$). The predicted best g_0 then becomes at least 10 times larger than s_0 . Such creatures would consist almost exclusively of gonads even at birth, which is not biologically realistic. In all other cases the r_m/RGR ratio was very close to .86 (the plateau), which is much more clearly shown in Fig. 3.

Comparison with empirical data

The model predicts $r_m/RGR = .86$, which exactly corresponds to the empirical data for six aphid species reared under a wide range of conditions (Dixon, 1987, Fig. 3). Although the range of values of a/R and s_0 used in the simulations are thought to be realistic, nevertheless good estimates of these values for our model group, aphids, would greatly strengthen our argument. Unfortunately, an exact measurement of a/R is not possible in such small organisms. However, we can obtain an estimate.

For some species we have adult somatic and gonadal sizes, which indicate that g_A/s_A is close to 1, s_A ranges from more than 10 to about 1000 micrograms (Dixon, 1990), s_0 is usually smaller than 100 micrograms and, of course $s' = 0$ for adults. Other measurements (Brough et al, 1990, Newton & Dixon, 1990, unpublished results) indicate that R is close to $0.5 \mu g/\mu g/day$. From equation 2 we can get an estimate of a/R :

$$a/R = s^{1-\alpha} \cdot g_A/s_A \quad \text{Equation 7}$$

Therefore, a/R ranges from more than 1 to less than 10, if weight is measured in micrograms. For one species, *Megoura viciae*, we have an indirect measure of $a/R = 5$ (Kindlmann & Dixon, 1989), which falls within the above mentioned range.

The r_m and RGR values are plotted against each other in Fig. 3. This figure shows the correspondence between our model's predictions and empirical data even more strikingly.

Discussion

The conventional wisdom is that r_m scales on body weight with a negative exponent (Fenchel, 1974; Blueweiss et al, 1978; Reiss, 1989) and so does relative growth rate (Calder, 1984). That is, generally populations that consist of small fast growing individuals will grow fast. However, except for aphids, (Leather & Dixon, 1984;

Dixon, 1985, 1987, 1990) no attention has been given to determining the relationship between individual and population growth rates, possibly because body size is seen as all important in determining an insect's pattern of distribution and abundance (Gaston & Lawton, 1988). There are no grounds for expecting the weak association between r_m and body size observed between taxa (Heron, 1972) to apply at the level of a taxum where phylogenetic constraints are all important in determining the overall bionomic strategy (Dixon, 1990).

In those unicellular organisms that reproduce by division, all tissue is potentially immortal, and they are capable of achieving an r_m/RGR ratio close to 1. Multicellular organisms have a body made up of a soma, the assimilatory and mortal part, and gonads, the reproductive and potentially immortal part. Investment in soma results in an r_m/RGR ratio of less than 1. For realistic values of assimilation, gonadal growth and size of the soma at birth, our model which optimizes the allocation of energy to soma and gonads and the time of maturation, predicts that the r_m/RGR ratio for aphids will be in the region of 0.8, which conforms with empirical data. Our choice of the constant in equation 5 affects the outcome. We used the value .738; if .75 were used instead, then the ratio for both the empirical data and the simulations would be .87. Small changes in the value of α do not significantly bias the outcome. Moreover, the intraspecific value of α is close to $2/3$ (Reiss, 1989; Schmidt - Nielsen, 1984). That is, the cost for aphids of having a soma, is a reduction of 0.2 in their potential r_m/RGR ratio.

Size in aphids is closely associated with the nature of the plant tissues on which they feed, with the largest feeding on trunks and branches of trees and the smallest on leaves of trees and herbaceous plants (Dixon, 1985, 1990). Their relative growth rate is positively associated with food quality and temperature (Dixon, 1987), which are unlikely to be correlated with the plant tissue on which a particular aphid feeds. Hence the lack of a correlation between r_m and body size in aphids. Thus in aphids the selection pressures that have determined their rate of increase and size are likely to have been different.

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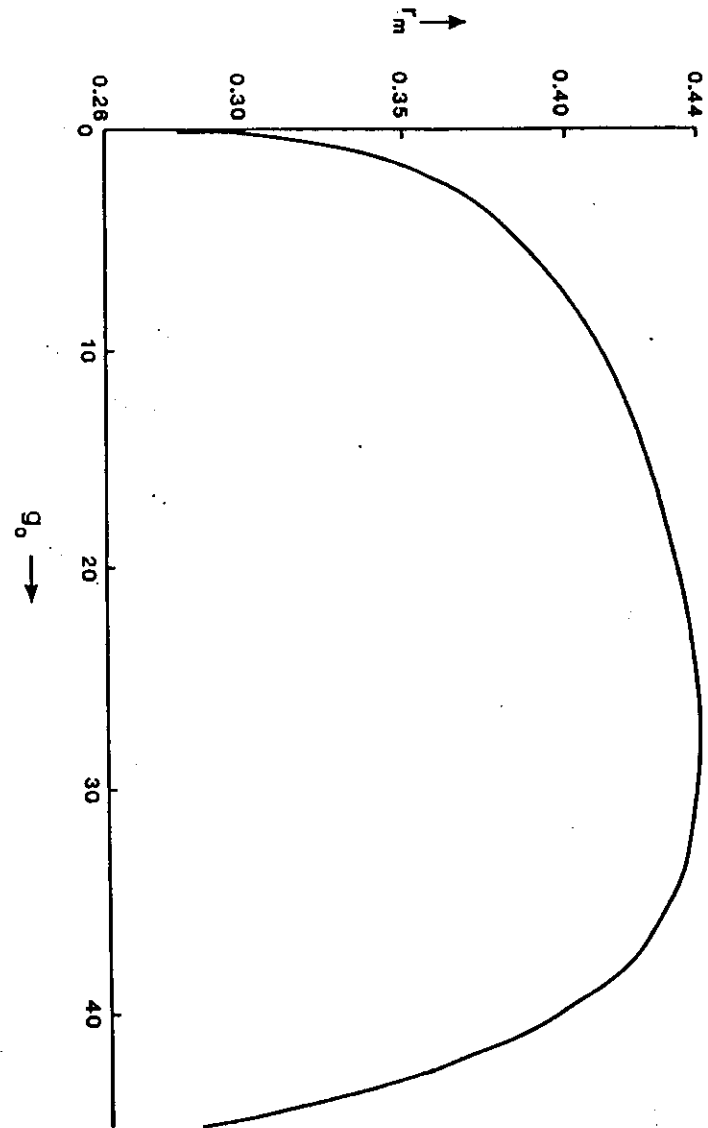
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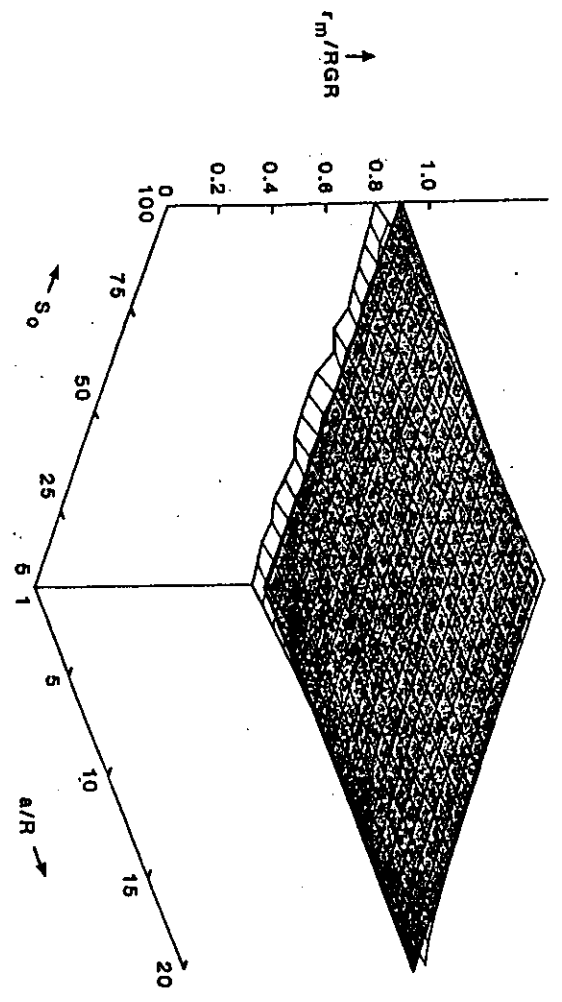
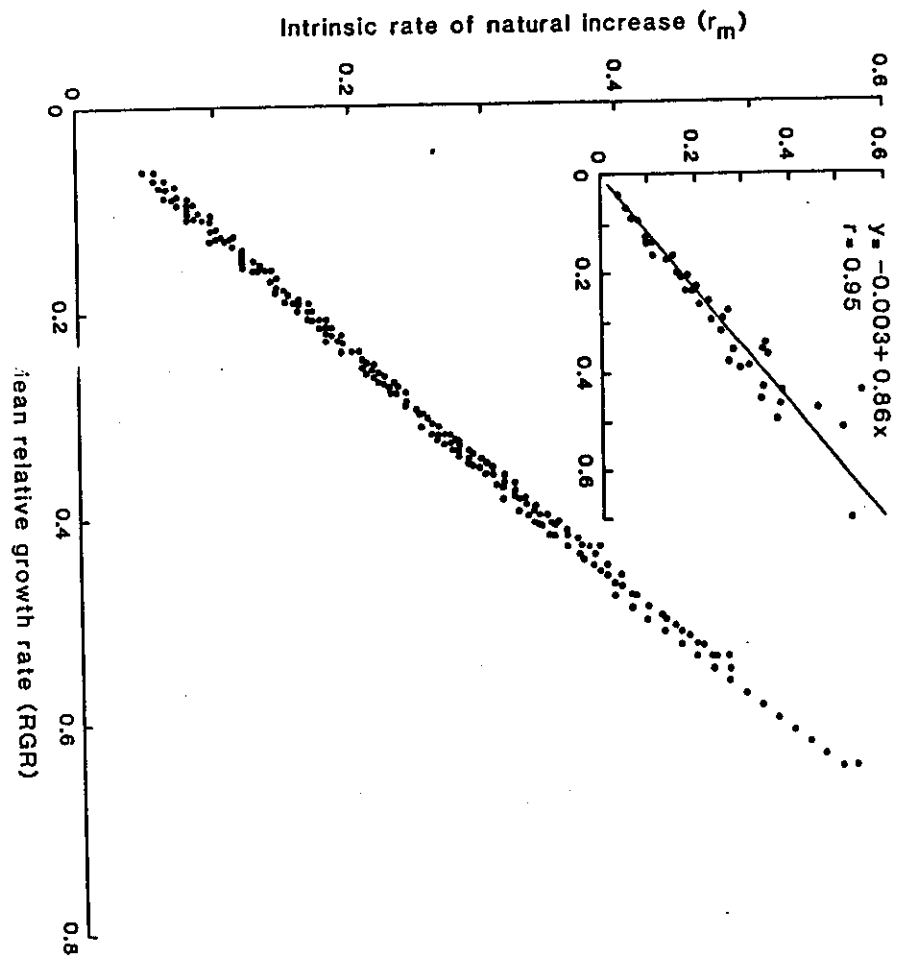
Figure Legends

Fig. 1. An example of the dependence of the intrinsic rate of increase, r_m on weight of gonads at birth, g_0 , predicted by equation 1 and 5 when $R = 0.5$, $a = 5$, $s_0 = 20$, $\alpha = 2/3$.

Fig. 2. The ratio r_m/RGR as a function of parameters a/R and s_0 . The values of the dependent variable are close to 0.86 for a wide range of realistic parameter values. (Shading represents a plateau of 0.86)

Fig. 3. The relation between r_m and RGR predicted for a/R ranging from 1 to 10, an s_0 ranging from 5 to 100 and an R of between 0.4 and 0.6. Circles are simulation results and the relationship has a slope of 0.86. The inset figure shows empirical data for 6 aphid species reared under a range of environmental





Intra- and interspecific relationships of reproductive investment to body weight in aphids

P. Kindlmann (1), A.F.G. Dixon (2) and C.N. Brough(3)

(1) Department of Biomathematics, Biological Research Centre, Czechoslovak Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czechoslovakia.

(2) School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, U.K.

(3) Department of Environmental Biology, University of Manchester, Williamson Building, Oxford Road, Manchester, M13 9PL, U.K.

Running heading: Reproductive investment in aphids

Abstract: Recently, Reiss (1985) proposed an allometric model to account for why large species invest relatively less in their offspring, which he subsequently extended to intraspecific relationships (1987), i.e., large animals should invest relatively less in their offspring even within a species. The data on aphids do not conform to this hypothesis, although Reiss used aphids among other groups for verification of his model's predictions. Here we propose an explanation for this discrepancy based on a model, which incorporates the optimal partitioning of energy, gained from assimilation (a), between soma and gonads, the optimal time of maturation and constraints on the gonadal growth rate (R) and the size of soma at birth (s_0). The optimum investment in reproduction depends upon size of soma at birth (s_0), a and R . The values of a and R depend upon environmental conditions, while s_0 tends to be species-specific. When s_0 varies and a and R change at the same rate, the exponent on weight is less than one. When s_0 is fixed, and a and R vary differentially the exponent on weight is larger than one.

Keywords: aphids, reproductive investment

Introduction

Both interspecifically and intraspecifically larger females generally invest proportionally less in their offspring than smaller ones. Reiss (1985, 1987) proposed a hypothesis to account for this phenomenon. Allometric equations are used to define the energy intake, $E_{in} = k_2 W^b$ and the energy requirements of free-living adult females, $E_{req} = k_1 W^a$. The difference, $E_{in} - E_{req}$, is used for growth and reproduction. As both exponents a and b are less than 1, it is concluded that the energy females devote to reproduction should scale relative to their weight, W , as $W^{0.5}$ to $W^{0.8}$, intraspecifically (Reiss, 1987) and as $W^{0.52}$ to $W^{0.95}$ interspecifically (Reiss, 1985). However, for a species that reproduces several times over a wide range of body weights the exponent may be greater than 1 (Reiss, 1989) but this does not apply to aphids, which vary little in weight during the reproductive phase of their lives (c.f. Reiss, 1989, p.33).

For verification, Reiss (1987) uses a large data set for aphids published by Llewellyn & Brown (1985). This data set indicates that the reduced major moments relating total embryo number to adult weight ranged from .51 to .69. However, this ignores the substantial variability in offspring size in aphids both within and between species. Generally, larger species and larger individuals of a species produce larger offspring with the exponent of the dependence between investment in individual offspring and body size being approximately 0.5 (Dixon, 1985; Gruber & Dixon, 1988). If this is taken into consideration it increases the exponent of the relationships between reproductive investment and body size to one or greater.

Why doesn't the aphid data conform with Reiss' predictions? He uses allometric equations for his E_{in} and E_{req} and assumes that the parameters k_1 and k_2 are constant. This may be true for higher taxa, but not for aphids. For an explanation of the aphid case a model was developed, which has already explained the importance of telescoping of generations and the simultaneous commitment to growth and reproduction, and even predicts the ratio of population to individual growth rate very exactly (Kindlmann & Dixon, 1989; Kindlmann, Dixon & Gross, submitted). Below an outline of this model is presented and its predictions concerning the ratio of the size of soma to gonads in adult aphids considered.

Material and Methods

A clone of *Megoura viciae* Buckton was maintained on *Vicia faba* (var Aquadulce) L. in a glasshouse at approximately 20°C and a 16 h photoperiod. The apterous virginoparae used in the experiments were maintained in growth cabinets at 20 ± 0.5°C. Aphids were killed by rapid freezing prior to dissection. Aluminium foil strips were cleaned in chloroform/methanol and weighed, and adult aphids of known weight were dissected on them by tearing back the cuticle from the anterior segments on the ventral surface of the abdomen to expose the gonads. The gonads were removed and cleaned by repeated flooding with distilled water before transfer to another foil strip. The two samples, gonads and soma, were then dried to constant weight at 38°C.

Results and Discussion

Relationships between reproductive investment and body weight for aphids.

Intraspecifically, the data in the literature indicate that aphids actually produce a biomass of offspring per unit time that scales relative to their weight with an exponent ranging from 0.9 to 1.6 (Table 1). The dry weight of the gonads of reproductively mature apterous virginoparae of *M. viciae* scales relative to their total dry weight with an exponent of 1.2, which is significantly greater than 1 ($t = 68.3$, $P < 0.001$) (Fig. 1).

Parthenogenetic aphids allocate energy to the development of reproductive organs throughout their larval life and the biomass of offspring produced per unit time is proportional to adult gonadal size (Kindlmann & Dixon, 1989; Kindlmann, Dixon & Gross, submitted). Therefore an alternative and equally good measure of reproductive investment in aphids is gonadal size. Comparison of the relative size of the gonads in apterous individuals of seven species of a wide range of weights indicate that a constant proportion of the body tends to be made up of gonads (Dixon, 1990). This corresponds to the exponent in Reiss' relation being equal to 1.

The model

The size of soma at time t is denoted by $s = s(t)$, the size of the gonads at time t by $g = g(t)$ and the developmental time by D . A usual assumption in most models of growth is that the assimilation, E_{ass} , of soma of size s is a power function of s : $E_{ass}(s) = as^\alpha$, where $\alpha = 2/3$ (the surface/volume ratio).

It is assumed that net energy production ($E_{prod} = E_{ass} - E_{resp}$) is a power function of s : $E_{prod}(s) = as^\alpha$. Given the initial sizes of soma and gonads at birth, $s_0 = s(0)$, $g_0 = g(0)$ and adult sizes of soma and gonads, $s_A = s(D)$, $g_A = g(D)$ and a constraint on the gonadal growth rate, R , the optimum strategy for minimizing the developmental time, D , (and thus maximizing r_m) is to maintain the gonadal growth rate at a maximum throughout development and devote the rest of energy to the growth of soma (Kindlmann & Dixon, 1989). Mathematically, if biomass is measured in units of energy needed to build it:

$$s' = as^\alpha - Rg, \quad s(0) = s_0 \quad (1a)$$

$$g' = Rg, \quad g(0) = g_0 \quad (1b)$$

Necessarily, s' becomes 0 at a finite time D , which is the best time for maturation (Kindlmann & Dixon, 1989) when

$$as_A^\alpha = Rg_A \quad (2)$$

the organism should devote all the energy gained from assimilation to reproduction. Thus unit time fecundity will be equal to $as_A^\alpha = Rg_A$. We shall use $\alpha = 2/3$, as many other models do, and as a measure of fitness the expression

$$r_m = -738 \ln M_d/D, \quad (3)$$

where D is the developmental time and M_d is the initial fecundity (fecundity during the period D). The appropriateness of this equation is explained in Kindlmann, et al. (submitted). The optimum size of soma for maximizing r_m is constrained by physiology, as we have shown previously (Kindlmann et al., submitted). Thus, we only need to optimize g_0 with respect to r_m , provided a , R and s_0 are given. In order to calculate the optimum g_0 , which maximizes r_m , the model described by equation (1) was simulated using a fourth-order Runge-Kutta-Fehlberg method. Since the trajectories in s - g space are the same for fixed s_0 , g_0 and a/R , a maximization was carried out for a/R varying from 1 to 20 in steps of 1 unit, and s_0 varying from 5 to 100 in steps of 5 units, with R fixed at 0.5. The maximization was carried out using Brent's method of inverse parabolic interpolation (Brent, 1973) on a SUN Microsystems 3/110.

Comparison of the model's predictions and empirical results

The model's predictions concerning the relationship between g_A and adult weight (W_A) are summarized in Fig. 2. There is no clear relationship between g_A and W_A , which depends on the s_0 and a/R values. A detailed survey shows that for fixed a/R and varying s_0 the exponent in the relationship $g_A = a \cdot W_A^\alpha$ is smaller than one (Fig. 2B), while for fixed s_0 and varying a/R the value of g_A depends linearly on W_A with the elevation of the regression line being negative. If one fitted a power function to the simulation results in the latter case, it would result in the exponent being larger than one, but the fit would be worse. In general, however, if any of these fitting methods is used, both yield the same result: the ratio of g_A/W_A increases, whenever W_A increases (Fig. 2A).

The optimum ratio of soma to gonads in adult aphids (s_A/g_A) for maximizing the intrinsic rate of increase depends on the optimum size of the soma at birth (s_0) and the a/R value. The optimal size of the soma at birth is likely to be related to the nature of the habitat an aphid exploits, e.g., aphids that feed on the trunks and branches of trees have to be larger at birth in order to feed whereas those species that feed on leaves where the phloem elements are close to the surface can be small at birth (Dixon, 1985, 1987a). Thus we would expect more variation in s_0 between species. The ratio a/R is likely to be markedly affected by food quality. The effect of food quality on growth within species is well documented (Dixon, 1987b) but because of the difficulties presented by the way aphids feed, no interspecific comparisons are available.

Intraspecifically well fed aphids have a shorter development time, are larger and produce a greater biomass of offspring per unit time than do poorly fed aphids (Dixon, 1987b and the data presented). Therefore, it is not surprising that intraspecifically large individuals invest proportionally more in offspring than do poorly fed ones, i.e., the exponent relative to weight is greater than 1. In terms of our model, s_0 is relatively constant, as irrespective of adult size, they are exploiting the same habitat. However, the food quality they experience is likely to affect the a/R ratio. A relatively constant s_0 and variable a/R results in an exponent greater than 1, which is in agreement with the empirical data.

Between species s_0 , as stated above, varies, and a/R is also likely to vary. This results in a 'cloud' of g_A and W_A values, in which the ratio g_A/W_A is relatively constant and the exponent in the relationship $g_A = a \cdot W_A^\alpha$ is close to one (Fig. 2). This is supported by the empirical data on aphids. Indeed, it appears that within several groups of insects, butterflies,

flies and ladybird beetles, the g_A/W_A is relatively constant (Gilbert, 1989; Stewart et al. 1991; Wickman & Karlsson, 1989).

Although Reiss' allometric model does not appear to apply to aphids, it has been used to explain the partitioning of energy between growth and reproduction observed in other organisms (Reiss, 1989). This raises the question of whether aphids are a special case, a consequence of parthenogenesis and telescoping of generations. That other groups of insects, at least, show similar interspecific relationships to aphids argues against them being a special case. It will be interesting to see whether an understanding of the relationship between individual and population growth rates (r_m/RGR) that has proved such a successful explanatory tool for aphids (Kindlmann et al. 1991) will help unravel the bionomic strategies of other groups of insects.

Acknowledgments

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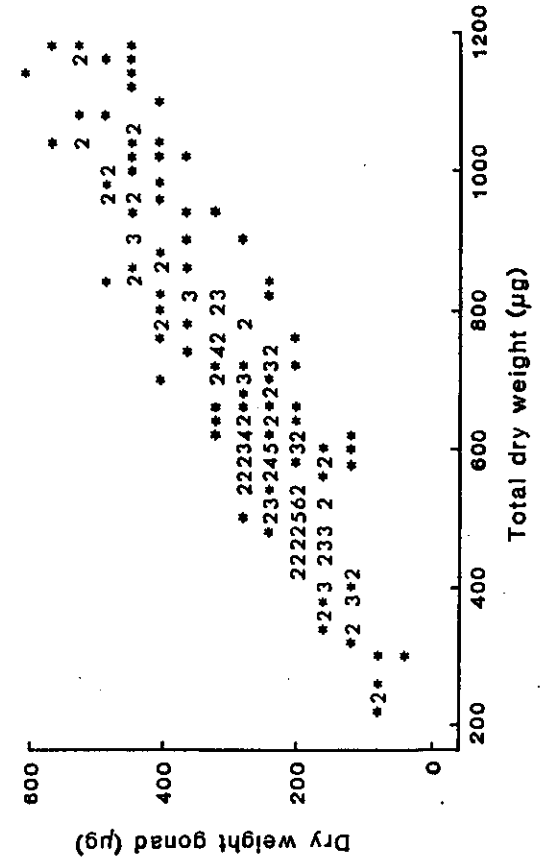
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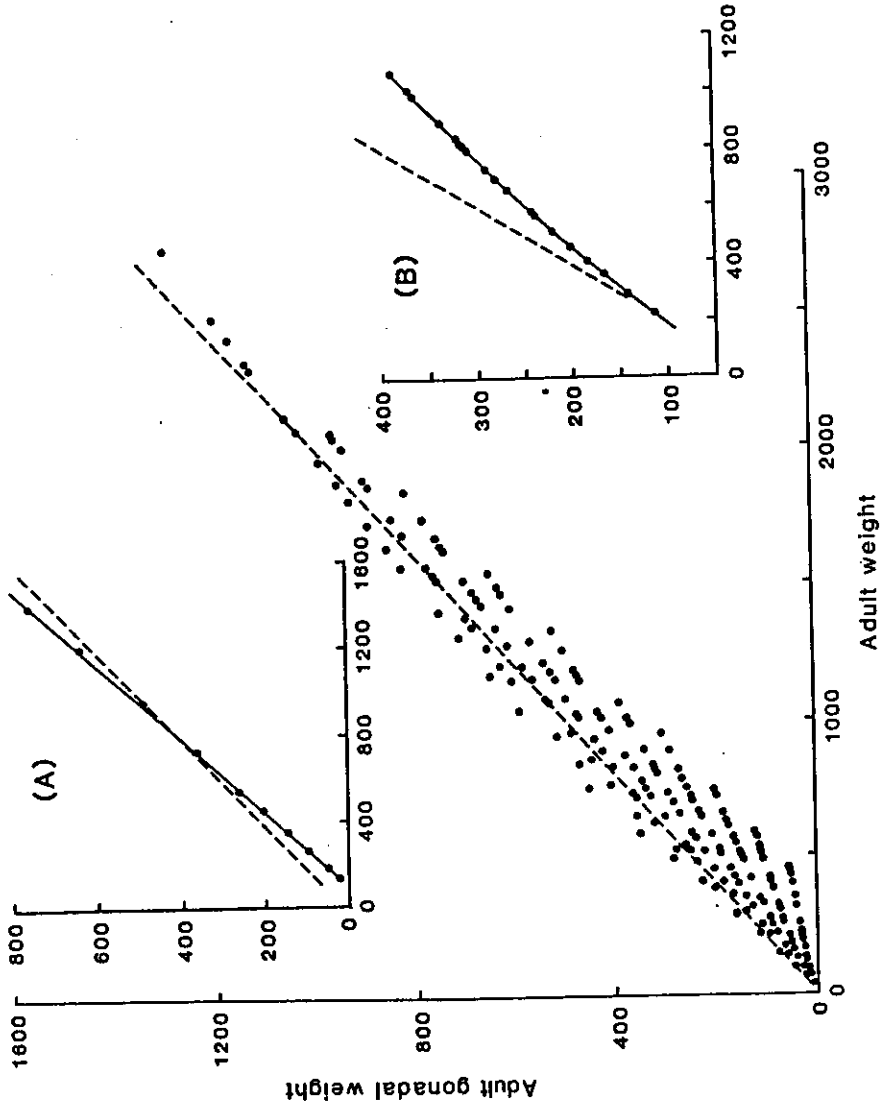
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Figure Legends

Figure 1. The relation between the dry weight of the gonads and total dry weight at the onset of reproduction for apterous virginoparae of Megoura viciae

Figure 2. The relation between adult gonadal and total weights predicted by model (1). The dashed line represents situations in which the gonads make up half the adult dry weight. A is the relationship between gonadal weight and adult weight when s_0 is fixed and a/R varies; the proportion made up of gonads increases with increasing adult weight, $g_A = 0.57 W_A - 55.7$. B is the relationship when s_0 varies and a/R is fixed; the proportion made up of gonads decreases with increasing adult weight; $g_A = 1.71 W_A^{0.78}$





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Table 1 Intraspecific dependence of female reproductive effort on body weight measured in terms of number of offspring produced/unit time, individual weight of offspring and biomass of offspring produced per unit time.

| | Offspring | | Source |
|---------------------------------------|--------------------------|--------------------------|-------------------------------------|
| | No/unit time weight | Biomass/unit time | |
| <i>Drepanosiphum dixoni</i> HRL | Macropterae | - 1.94 W ^{1.03} | Dixon, 1972 |
| | Brachypterae | - 1.33 W ^{0.85} | |
| <i>D. plananoidis</i> (Schr.) | - 2.97 W ^{1.28} | 1.07 W ^{0.24} | Dixon, 1970 |
| <i>Eucallipterus liliac</i> (L.) | - 3.4 W ^{1.4} | 0.84 W ^{0.1} | Barlow & Dixon, 1980 |
| | 0.08 W ^{0.44} | 0.03 W ^{0.5} | Thornback 1983; Gruber & Dixon 1988 |
| <i>Metopolophium dirhodum</i> (Walk.) | 0.08 W ^{0.44} | 0.03 W ^{0.5} | Thornback 1983; Gruber & Dixon 1988 |
| measured over | | | |
| <i>Aphis fabae</i> Scop. | -0.86 W ^{0.8} | 0.52 W ^{0.4} | 0.34 W ^{1.16} |
| Apterous Exules | -0.27 W ^{0.7} | 0.52 W ^{0.4} | 0.25 W ^{1.04} |
| 15 days | 0.26 W ^{0.5} | 0.5 W ^{0.4} | 0.78 W ^{0.9} |

Switch from μg to mg changes the coefficient but not the exponent

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