

Dyar's Rule and the Investment Principle: optimal moulting strategies if feeding rate is size-dependent and growth is discontinuous

JOHN M. C. HUTCHINSON^{1,2*}, JOHN M. McNAMARA²,
ALASDAIR I. HOUSTON^{2,3} AND FRITZ VOLLRATH^{3,4}

¹ *School of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, UK*

² *School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*

³ *Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

⁴ *Department of Zoology, Universitetsparken B135, DK 800 Aarhus C, Denmark*

CONTENTS

	PAGE
1. Introduction	114
2. Earlier work	115
3. The growth equation and further assumptions of the model	116
(a) Efficiency of moulting	117
(b) Accumulation of reserves	117
(c) Restrictions of the power-law growth equation	118
4. Optimal growth ratios and durations of successive instars	119
(a) Results when $\alpha = 1$	119
(b) Results when $\alpha < 1$	119
(c) Results when $\alpha > 1$	120
(d) How much does optimizing growth ratio and instar duration matter?	120
5. Testing predictions about change of growth ratio with successive instars	121
(a) Tests on populations of identifiable individuals	121
(b) Tests on data pooled over a population	122
6. Explanations for non-monotonicity in growth ratios and instar durations	123
(a) Other growth equations	123
(b) Size-dependent mortality	124
7. Predicting the effect of environmental manipulations when growth is discontinuous	124
(a) Loci of maximum size attainable within a growth period	125
(b) Fitness functions	125
(c) Other shaped loci and fitness functions	127
(d) Norms of reaction with other moulting strategies	128
(e) Comparison with continuous growth	128
8. Optimizing number of instars	129
(a) The effect of environmental parameters	129
(b) Predictions of growth ratios; the effect of α and ϵ	130
(c) Tests of the influence of ϵ on growth ratio	130
(d) Dyar's Rule explained?	131
(e) Robustness	132
9. Conclusions	132
References	133
Appendix 1	134
Appendix 2	
(a) Optimal change in growth ratio	135
(b) Optimal change in instar duration	135
Appendix 3	
(a) Estimation of α and κ	136
(b) Testing for other forms of the dependence of u_{i+1} on u_i	136
Appendix 4	137

* Address for correspondence: School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK.
majmch@ssa.bristol.ac.uk

SUMMARY

We consider animals whose feeding rate depends on the size of structures that grow only by moulting (e.g. spiders' legs). Our Investment Principle predicts optimum size increases at each moult; under simplifying assumptions these are a function of the scaling of feeding rate with size, the efficiency of moulting and the optimum size increase at the preceding moult. We show how to test this quantitatively, and make the qualitative prediction that size increases and instar durations change monotonically through development. Thus, this version of the model does not predict that proportional size increases necessarily remain constant, which is the pattern described by Dyar's Rule. A literature survey shows that in nature size increases tend to decline and instar durations to increase, but exceptions to monotonicity occur frequently – we consider how relaxing certain assumptions of the model could explain this. Having specified various functions relating fitness to adult size and time of emergence, we calculate (using dynamic programming) the effect of manipulating food availability, time of hatching and size of the initial (or some intermediate) instar. The associated norms of reaction depend on the fitness function and differ from those when growth follows Dyar's Rule or is continuous. We go on to consider optimization of the number of instars. The Investment Principle then predicts upper and lower limits to observed size increases and explains why increases usually change little or decline through development. This is thus a new adaptive explanation for Dyar's Rule and for the most common deviation from the Rule.

... the widths of the head of a larva in its successive stages follow a regular geometrical progression.

(Dyar 1890)

It is reasonable to assume therefore that molting in soft-bodied insects is a device that allows them to increase the size of their mouthparts and optimize their rate of feeding.

(Nijhout 1981)

1. INTRODUCTION

Arthropods and some other organisms grow discontinuously even if they are feeding more or less continuously. For instance, a locust while feeding accumulates reserves in its expandable abdomen, and so the size of this storage organ and its overall mass increase between moults; but the dimensions of the rigid pronotum and legs increase only at a moult (Clarke 1957). Crucially for the argument in this paper, many of the parts of the body involved in acquiring food cannot stretch and therefore grow discontinuously. Even in maggots and caterpillars, which can swell considerably before moulting, the sclerotized jaws grow only at the moult.

Besides mouthparts, other inextensible structures may also affect feeding rate. Longer legs can increase the area searched per unit time, and can reach farther and subdue larger prey in raptorial arthropods such as spiders, or can filter more water in filter-feeding species. Longer antennae and larger eyes allow the animal to detect food at larger distances, and increased separation of such paired sensory organs can increase the success of prey capture through improved distance estimation. However, it is not always true that the size of inextensible parts of the body limits the rate of accumulation of reserves. For instance Reynolds (1990) has evidence that mass increase in caterpillars in culture is limited not by the size of the rigid jaws but by the area of the gut, and this can increase continuously between moults. But we suspect that in many arthropods feeding rate indeed is constrained by the size of structures that grow discontinuously, and this paper restricts its scope to cases where this assumption is justified.

The size of these structures that determine feeding rate depends on how much they grew at the last moult, which we suppose depends on how much reserves were accumulated before that moult, which in turn depends on feeding rate. This reciprocal influence of size on feeding rate and feeding rate on size leads to a dilemma that is the focus of this paper. Suppose for simplicity that an arthropod hatches, accumulates reserves, moults once (converting these reserves into a size increase), accumulates reserves again at this larger size

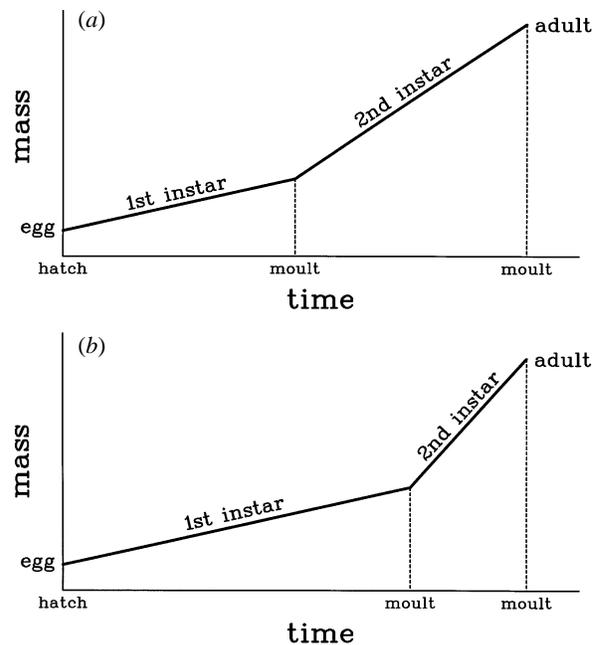


Figure 1. Schematic representation of two growth strategies in a hypothetical arthropod that moults twice before reaching adulthood at a fixed time. Although mass accumulates continuously through feeding, size increases only at the moult, as a result of which subsequent accumulation of mass is faster (graph has steeper slope). The longer spent in the first instar, the more reserves have been accumulated by the first moult and thus the larger the second instar (but the less time available to feed at that larger size). Without specifying more details it is unclear whether moulting early or late is the best strategy.

(and thus at a faster rate than before), and then metamorphoses when winter arrives (figure 1). Reserves accumulated by the time of metamorphosis determine future reproductive success. By moulting later it would have longer to increase its reserves before moulting, so that the size of the second instar would be larger, and thus its increased rate of food acquisition in the second instar would be greater. But by moulting earlier it would increase in size earlier and thus its increased rate of food acquisition in the second instar would continue for longer. To summarize, it may moult late to increase feeding rate more, or moult early to increase its feeding rate for longer. This conflict results in there being an optimal compromise in the duration of each instar which will maximize size or reserves at the end of the growing season.

For convenience we need a shorthand to refer to the argument outlined above. An analogy can be made with the owner of a small factory or shop who is accumulating the profits in the bank. At some time it will be best to sell the factory and use the sum realized together with reserves in the bank to invest in new, larger premises, which will produce profits at a higher rate. Hence we name our explanation the Investment Principle.

This paper investigates theoretically the optimal moulting decisions that follow from the Investment Principle. If these correspond to observed moulting patterns, we can claim to have an ultimate explanation for arthropod moulting decisions. We will first make and test predictions about how instar durations and size increases at each moult should change as an animal grows. We then calculate how changes in environmental conditions affect the optimal instar durations and size increases (given various alternative assumptions about how adult size and time of the final moult determine fitness). Finally we consider what is the optimal number of moults if each moult has some cost in terms of increased mortality or loss of mass (as ecdysed skin, etc.), and show how optimizing the number of moults can generate Dyar's Law.

We find optima in the simpler cases using analytic solutions, but for more complex and specific cases we rely on numerical solutions using dynamic programming. Appendix 1 explains the principles. All computer programs used in the project are available from J.M.C.H.

It turns out that moulting decisions of real arthropods do not always correspond closely with the simplified versions of our model. Nevertheless, we explore these simple special cases thoroughly before incorporating real-life complications such as size-dependent mortality. Only by comparing the output of complex and simple models can we identify which features of complex models are sufficient to explain particular aspects of the patterns generated or observed. Similarly only having first explained optimal behaviour in simple models can we understand intuitively why, when and how optimal behaviour differs in more complex situations. Complex models involve many extra parameters and these have not all been measured in one species, so detailed predictions about specific cases are not yet possible. The alternative

approach is to perform a laborious sensitivity analysis by varying each of these parameters. The results are easier to investigate and summarize if interpreted as elaborations of the results from our simpler models, where it is possible to derive analytically the precise form of the interrelationships.

We hope that this paper will make empiricists aware what parameters need to be measured in order to use more complex models to test the Investment Principle more rigorously.

2. EARLIER WORK

We define 'growth ratio' as the size of one instar divided by the size of the preceding instar, where size is measured by a linear dimension. These growth ratios were a hot topic in entomology during the first half of this century. Most well known is Dyar's Rule (Dyar 1890), which asserts that the growth ratio does not vary between moults. Dyar, and many others after him, used the rule to detect whether instars had been overlooked in field collections (reviews in Gaines & Campbell 1935; Daly 1985). Prizibram & Megušar (1912) made the further claim that the ratio was 1.26; numerous other authors reported similar or contrasting ratios in their favourite arthropods. Later work found that the constant ratio may differ between different parts of an animal (most thoroughly Brown & Davies 1972) and that the ratio was not after all so constant between successive moults (e.g. Gaines & Campbell 1935). Experiments have examined the effect on growth ratios and the number of instars of changes in the environment, such as in crowding, food availability or temperature (e.g. Sehnal 1966; Wigglesworth 1971; Daly 1985), or of variation in size of the initial or an intermediate instar (e.g. Tanaka 1981; Ebert 1994). Also in a few species we have some idea of the physiological mechanisms that regulate when to moult (reviewed by Sehnal 1985) and of how the increase in size of the exoskeleton is achieved (Bennet-Clark 1971; Freeman 1990). However, little of this vast accumulation of data was used to test any hypotheses to explain particular moulting strategies.

This section discusses the explanations that have been published. The first is that there are physiological limits to growth. In particular, when arthropods moult the new exoskeleton is preformed inside the old exoskeleton; growth ratio is thus limited by the extensibility of the new cuticle. Bennet-Clark (1971) argues that extensibility is not fixed by some mechanical property of chitin, but by how much the epicuticle is folded. It is unclear what are the limits to epicuticle folding, and very high growth ratios can be achieved by some species (e.g. Cole (1980) cites examples of rigid head structures with growth ratios > 2.0. Wing area can expand by a factor of 20; Bennet-Clark 1971). Even if physiological constraints do limit growth ratios in some species, the variation observed between conspecifics reared in the same or different conditions, between instars of the same species and between closely related taxa, suggests that the ratio is usually unconstrained. Physiological constraints may be more important when considering how

individuals respond to, say, an exceptional superabundance of food, but our model is concerned with predicting optimal growth ratios, so we assume that evolution has had the opportunity to shift the physiological limits.

Other physiological constraints would arise if certain simple developmental rules determine when the moult occurs. For instance Przibram & Megušar (1912) interpreted a 1.26 growth ratio as following from a single cell division of all cells in the body, so that volume doubled between moults. Bodenheimer (1933) explained higher ratios as following from two or three full divisions per moult, leading to ratios of 1.59 and 2.0, respectively. If instead the area of epidermis limits expansion, a doubling of the number of epidermal cells leads to a growth ratio of 1.41. Although ratios close to these are found in particular species, within these species there is much inter-individual variation (Ludwig 1934) and histograms of growth-ratio variation between species show a broad spread rather than sharp peaks (Cole 1980; Rice 1968). If other species achieve these different ratios, these simple developmental rules seem an implausible explanation even in species with growth ratios close to 1.26 or 1.59.

In some bugs experiments have indicated that moulting is triggered by a stretch receptor detecting a critical food intake into the abdomen (Nijhout 1979). In other species, Jones *et al.* (1981) suggested that the mechanism controlling the timing of moult is some comparison between the relative sizes of extensible and inextensible structures; this might also be mechanical. Whatever the mechanism, it is tempting to suggest that isometry is simpler to engineer, resulting in constant growth ratios. But again an objection is that evolution has managed to program changes in growth ratio in many species.

One adaptive explanation for the constancy of growth increments is that the size increase has been selected to avoid competition between instars (Enders 1976). This is an extension of Hutchinson's (1959) suggestion that species of the same guild should differ in size by at least 28% so as to avoid competition. Typically, instars do differ by at least this amount. However the empirical evidence for Hutchinsonian ratios between species of a guild is now contested (e.g. MacNally 1988), and if this pattern does occur there are explanations other than competition (Eadie *et al.* 1987). Furthermore, Hutchinson's original model was too simplistic in predicting a regular spacing. For instance, one might expect competition between individuals of different sizes to be asymmetric, which can result in niche overlap changing with size (Rummel & Roughgarden 1985). Avoidance of competition between instars of a single species would need to be modelled as a dynamic game, and would often also have to incorporate sib competition and competition from other species. What we can suppose is that if some instar sizes are advantageous for other reasons (e.g. they maximize the growth rate), they should tend to be more heavily occupied even at the expense of the heavier competition (although this competition, by making those sizes less attractive, may broaden the size ranges occupied).

Enders (1976) suggested two further influences on growth ratios, both concerning the consequences of carrying around the reserves that will later convert into a size increase. He argued that more active species and those with a rapid escape response suffer from carrying around reserves, and so should grow proportionately less each instar; comparisons between spider families supported this hypothesis. Conversely, reserves can have a beneficial side-effect, to stave off starvation if food gets scarce. Both these costs and benefits should scale with size, which could be a reason for growth ratios to change with successive moults.

A different, but only partial, explanation for changes in growth ratio is due to Klingenberg & Zimmermann (1992). As an animal grows its optimal proportions change (for instance because surface-to-volume ratio changes). Any consequent allometry means that growth ratios must differ between different structures. Thus, a consistent decline in the growth ratio of head structures was explained by their negative allometry with respect to the legs and body. Growth ratios of the latter were constant.

For completeness we mention also a paper by Hutchinson & Tongring (1984). They argued that, for a given arithmetic mean of the growth ratio, size at final time will be maximized by having all the growth ratios constant. This is true, but different strategies with the same arithmetic mean growth ratio result in growth to adulthood taking different times. If time to reach adulthood is unimportant, it is unclear what biologically constrains the arithmetic mean growth ratio. In our model, time to reach adulthood is important: reproductive value decreases with the time taken and this restricts what growth ratios are achievable. Hutchinson & Tongring (1984) have nothing to say about this situation. We find that achieving the maximum size within a particular time usually does require growth ratios to differ between instars.

Most of these earlier explanations are not incompatible with each other, nor with our own Investment Principle; what real animals do may be a complex interaction of several factors. But our strategy is to model only the Investment Principle, so as to isolate its consequences. As it happens, when we allow the number of instars to be optimized, the Investment Principle not only gives rise to another explanation for a pattern close to Dyar's Rule, but also explains the most common pattern of divergence from the Rule.

3. THE GROWTH EQUATION AND FURTHER ASSUMPTIONS OF THE MODEL

We use the symbols introduced in this section throughout the rest of the text. See table 1 for a summary.

Throughout, our measure of the overall size of the i th instar (x_i) is proportional to the cube of the linear dimensions of the inextensible structures (i.e. proportional to volume, weight or calorific value, but excluding reserves accumulated during that instar). However, traditionally, size increase at a moult has been expressed as a linear dimension of the new instar

Table 1. Summary of symbols used frequently in the text

i	Number of the instar. The instar hatching from the egg has $i = 0$. For the adult $i = N$.
N	Number of juvenile instars (excluding the egg and adult stages) = number of moults.
x_i	Size of the i th instar, where size is measured as volume, mass or calorific content of the body excluding the reserves accumulated in that instar. Length of inextensible structures will be proportional to $x_i^{\frac{1}{3}}$.
x_0	Size of the initial instar after hatching from the egg.
x_N	Size of the adult.
u_i	x_{i+1}/x_i . It is the cube of the growth ratio of the moult at the end of the i th instar.
\hat{u}	The value of u that our model predicts does not change each moult (see figure 2).
d_i	Duration of the i th instar (more strictly, the time spent feeding in that instar).
t_i	Calendar time at the beginning of the i th instar.
t_0	Calendar time of hatching from the egg.
t_N	Calendar time at which the adult appears.
ϵ	Efficiency of moulting: the proportion of the mass of the old instar excluding accumulated reserves that can be reincorporated into the next instar.
f	A constant determining the availability of food.
α	Scaling with size of the rate of reserve accumulation.
$F(x, t)$	Fitness of an animal that becomes adult at size x and time t .
β	Scaling with size of the rate of offspring production.
θ	Instantaneous mortality rate when immature.
ρ	Instantaneous mortality rate when adult.

divided by the same dimension of the old. Such ratios of linear dimensions are easier to gauge intuitively than ratios of volumes. Accordingly the growth ratios that we present are based on linear dimensions and are written as $u_i^{\frac{1}{3}}$, where $u_i = x_{i+1}/x_i$.

We term the growth equation the equation that specifies size of the next instar (x_{i+1}) as a function of size of the previous instar (x_i) and the duration of that instar (d_i). In particular we consider the following example, which we call the power-law growth equation:

$$x_{i+1} = \epsilon x_i + f(x_i/x_R)^\alpha d_i,$$

where ϵ and f are constants. x_R is some reference size and is present to ensure that the equation is dimensionally correct. Henceforth we take x_R to be equal to 1 in whatever units of size are used and thus we abbreviate the equation to

$$x_{i+1} = \epsilon x_i + f x_i^\alpha d_i. \quad (1)$$

The two sections that follow explain the biological significance of the two terms on the right-hand side and then we consider to what extent this growth equation is only an approximation.

(a) Efficiency of moulting

The parameter ϵ determines the efficiency of the moulting process. More precisely it is the fraction of the volume of the old instar that can be remodelled into the new instar were the animal not to accumulate any reserves between moults. Thus if $\epsilon = 1$ no material is wasted, and $x_{i+1} = x_i$ if $d_i = 0$. But at least the volume of the ecdysed exoskeleton is lost, so we take typical values of ϵ to lie between 0.2 and 0.9. The assumption is that a constant proportion of volume (or mass) is lost in the moult, whereas the loss might scale as a proportion of surface area ($x_i^{\frac{2}{3}}$), or as some other function of x ; this would affect the quantitative

predictions that we make later. However, we now present empirical evidence that the loss is at least sometimes isometric.

One of us has published elsewhere details of an experiment that enables calculation of ϵ (Vollrath 1983). Fifty-nine individuals of the large tropical spider *Nephila clavipes* were followed in the laboratory throughout their growth. We suppose that the difference between the mass at the beginning of an instar and the mass of the ecdysed skin at the following moult is the amount of material present before reserve accumulation that has been reprocessed. In animals given a poor diet the mass of ecdysed skin scaled as the 1.04 power of mass at the beginning of the instar, whereas in better fed animals the power was 0.83 (the former coefficient is not significantly different from 1, the latter differs from 1 at $P < 0.001$). With a poor diet a mean of 0.77 of the mass at the beginning of the instar was reprocessed (s.d. = 0.13); with a rich diet the proportion was about 0.5 for the early instars, increasing to about 0.8 at larger sizes.

Other data from the literature suggest that approximate isometry of ϵ is the usual pattern. Unfortunately, although the cost of the moult has often been measured (e.g. Lynch 1989), usually mass loss at the moult is given only as a proportion of total mass after or before that moult, rather than just after the preceding moult (which is how we define ϵ). Clarke's (1957) data on the decline in mass of a locust directly after the moult imply a mean value of ϵ of 0.82 (s.d. = 0.05) and no relationship with size. Przibram & Megušar's (1912) data on a mantid indicate a proportionately lighter skin, with the mean value of ϵ around 0.97, again independent of size. However, all these figures probably overestimate ϵ because ecdysed skins are likely to be energetically more expensive mass-for-mass than whole bodies, because the latter contain more water. (Typically dry weights of whole bodies of insects are 0.2–0.4 of wet weights, whereas the proportion is about 0.5 for the exoskeleton in insect wings; personal observation.) On the other hand,

higher efficiencies are possible if the old exoskeleton is eaten.

(b) *Accumulation of reserves*

The expression $fx_i^\alpha d_i$ models the increase in mass of the next instar caused by the accumulation of reserves with the time spent in the instar (d_i). We manipulate environmental food availability in our model by altering the constant f . x_i^α makes the accumulation of reserves dependent on some power α of size.

α is roughly equivalent to the Van der Drift constant (which describes how ingestion, rather than assimilation, scales with size). In arthropods this typically lies around 0.67 (see Peters (1983) and Reiss (1989) for reviews; values ranged from 0.63 to 0.89 in the six intraspecific studies on arthropods cited by Reiss). Thus the empirical evidence is that assimilation rate scales with size with an exponent less than 1. However, we also make predictions for α greater than 1. Direct empirical measurements of α are from rather few types of arthropod maintained in the laboratory where food is freely available. The theoretical arguments that follow suggest that a wider range of values for α should apply in the wild.

α may be considered as the sum of two components, α_1 and α_2 : α_1 describes how food-gathering ability scales with size given a constant concentration of food, and α_2 describes how the concentration of food of a suitable size scales. We expect α_1 to depend on the mode of feeding. For a wolf spider waiting for prey to enter its patch of forest floor, reach may determine feeding rate, in which case $\alpha_1 = 0.33$. $\alpha_1 = 1$ might apply for an animal in which the volume of its oral cavity determined how much food it could gulp. Values of α_1 higher than 1 could arise if interference competition gave an extra advantage to larger individuals. As an example of how the mode of feeding does affect α , Lampert (1977) found in *Daphnia* that α increased from 0.67 to 1.0 if the prey species were large or difficult to handle.

α will also depend on the availability of food suitable for the different sizes. For a caterpillar eating leaves on a tree, food seems freely available regardless of the herbivore's size ($\alpha_2 = 0$), but for arthropods hunting or filter-feeding discrete prey items the size range of suitable prey changes as the arthropod grows. Suppose that the concentration of food of the right size range is proportional to the total biomass within this range. Griffiths's (1992) review of several studies found a roughly linear decline of size-class abundances with size, implying constancy of biomass (within a proportional size range) with size. This pattern is also usual for suspended particles in water (e.g. Sheldon *et al.* 1972). Constancy of biomass with size could mean that $\alpha_2 = 0$, but if smaller items are not dropped from the diet as the animal grows (e.g. for spiders using webs; Vollrath, personal observation in *Nephila*), the biomass available to a predator will increase linearly with size, so that $\alpha_2 = 1$, and thus α will be greater than 1. In contrast, Stork & Blackburn (1993) found in tropical forest that biomass within a size category increased linearly with size (which could mean $\alpha_2 = 1$,

or that $\alpha_2 = 2$ if smaller items are not dropped from the diet as the animal grows).

Besides α_1 and α_2 , other factors affecting α include allometry in parts of the body that determine feeding rate, and any tendency for time spent foraging to change with size, perhaps because some sizes must hide more from predators.

There is no guarantee that in real life these size-dependent effects will be well-described by a single power-law relationship. Our analytic solutions below do depend on a power-law relationship, but the numerical solutions by computer work with any function of x_i .

(c) *Restrictions of the power-law growth equation*

There is no term in the power-law growth equation to describe the loss of reserves through metabolism. Potentially this is a serious inaccuracy as typically between 20% and 50% of assimilated energy is lost through metabolism (Calow 1977; Schroeder 1981). However, metabolic rate on average scales roughly with mass^{0.75} (Reiss 1989), so that often the scaling exponent will be very close to that for energy intake ($\alpha \sim 0.67$). Reserve loss can then be incorporated into equation (1) merely by lowering the value of the constant f . Note also that a considerable proportion of metabolic costs is the chemical reactions that convert assimilated food to tissue (Schroeder 1981); this component of metabolism must scale as α (whatever its value), so only the other proportion of metabolic costs may scale with a different exponent.

In subsequent sections particular attention should therefore be paid to our predictions for the case $\alpha = 0.67$, as this is both the case commonly observed and the case where metabolic costs are likely to least affect the simple power-law relationship. For comparison we do include predictions for other values of α , when it is more likely that we should have replaced fx_i^α in equation (1) by a more complex function of x_i incorporating metabolic costs. Unfortunately we could not then have derived analytic solutions. We do check numerically how sensitive some of our predictions are to incorporating a metabolic cost scaling differently to intake rate.

The accumulation of reserves in our model is deterministic. As there is, therefore, no risk of starvation, the animal has no need to keep some reserves until after the moult; all reserves are converted into a size increase. Equation (1) will not fit unless any reserves carried over increase isometrically with body size of the new instar. In specific cases a stochastic model may be necessary to understand properly how size increase and reserves are traded off depending on the animal's estimate of future feeding success.

We do not allow feeding rate (f) to be a function of time of year. Obviously this is usually an unrealistic simplification. We also do not allow feeding rate or the efficiency of the moult (ϵ) to depend on the instar, which may be unrealistic when different instars show allometric changes in shape or habitat shifts (independent of any size effects). Nutritional requirements may have complex dependencies on instar (e.g.

Simpson & Simpson 1990) that we have not allowed for in our analysis. As discussed above, we ignore any direct effect of current reserves on the further accumulation of reserves.

In our model moulting can occur at any time of day. Jones *et al.* (1981) show how for physiological reasons moulting in a lepidopteran caterpillar occurs only at a particular time of day. This phenomenon may be widespread, as arthropods are vulnerable when moulting both to predation and to dehydration; it must often pay to coincide moulting with relatively safe or humid times of day. If the time of day that moulting occurs is absolutely constrained it is straightforward to simplify our numerical technique to find on which day moulting is optimal (see Appendix 1). Our analytical solutions will then be only approximations. The optimal policy under this constraint is potentially rather unstable, as a small change in ecological parameters may lead to spending an extra 24 hours feeding in an early instar, which will have knock-on effects on how long to spend in all subsequent instars.

Moulting in our model is instantaneous, whereas in reality it uses up time that might alternatively be spent feeding. When we allow the total number of moults to be optimized, the effect of a time penalty on moulting is then obviously to decrease the optimum number.

During growth the animal may be subject to mortality. Our simplest model copes only with mortality that is unchanged by any moulting decision, for instance if animals die at a constant rate. We never consider mortality to be a function of energy reserves or of instar. However, we do sometimes allow mortality to vary as a function of size (in spiders, for instance, both a decline in the rate of mortality with size and independence have been reported; Tanaka 1992). One of the most dangerous times for many arthropods is the moult; we thus sometimes allow an extra source of mortality each time the animal moults.

Another assumption is that no reproduction occurs until the final moult, which is true for insects and spiders, but untrue for those crustaceans that exhibit indeterminate growth (in their case the model still applies for those moults before reproduction starts). We discuss later the factors that affect reproductive success after the final moult.

In a later section we suppose that not only the durations of each instar, but also the number of moults are optimized according to the Investment Principle; a pattern of growth close to Dyar's Rule is then predicted. However, the next four sections do not assume that the number of moults optimizes growth; these results apply generally whether the number of moults is optimized or not.

4. OPTIMAL GROWTH RATIOS AND DURATIONS OF SUCCESSIVE INSTARS

In this section our optimization criterion is that adult size is maximized given that a specified time is available for growth. This is equivalent to minimizing the time taken to reach a specified size. (These criteria are not appropriate if mortality during growth depends on size.)

Given the power-law growth equation (equation (1)) we have managed to express how much an animal should grow in one instar as a simple function of how much it was optimal to grow in the previous instar. Appendix 2 gives the derivation and here we merely explain the results.

Let u_i be the cube of the optimal growth ratio at the moult following the i th instar ($u_i = x_{i+1}/x_i$). The relationship between the optimal value of one growth ratio and the optimal value of the preceding growth ratio is that $u_{i+1} = g(u_i)$ where g is the function defined as

$$g(u) = \epsilon + (u^\alpha - \epsilon)/\alpha. \quad (2)$$

The relationship between u_{i+1} and u_i is thus independent of the food available (f), the size of the first instar (x_0), the total number of instars (N), and the time and size at which it is optimal for the animal to switch from growth to reproduction (t_N and x_N). But although these parameters do not affect the relationship between successive growth ratios, they do affect the actual growth ratios themselves. For instance, increasing f will typically lead to the animal maturing at a larger final size; therefore all u_i 's will have increased. Nevertheless, given u_i , ϵ and α , u_{i+1} will be the same regardless of the other parameters; this enables us to make very general predictions about how growth ratios will change as an individual grows.

Similarly we can also make general statements about how durations in each instar change as an individual grows, since under the optimal policy

$$d_{i+1}/d_i = (1/\alpha)(u_i - \epsilon u_i^{1-\alpha})/(u_i - \epsilon).$$

How u_i and d_i change with i depends on whether α is equal, less than, or greater than 1.

(a) Results when $\alpha = 1$

In this case Dyar's Rule holds true: growth ratios are the same at all moults ($u_0 = u_1 = \dots = u_{N-1}$). Also the duration of each instar is constant ($d_0 = d_1 = \dots = d_{N-1}$).

(b) Results when $\alpha < 1$

Remember that the empirical data suggest that this is the normal situation. How u_i changes with each moult is shown in figure 2a. Given a value of u_i on the horizontal axis one can use the curve $u_{i+1} = g(u_i)$ to read off the value of u_{i+1} on the vertical axis. The straight line $u_{i+1} = u_i$ is also drawn so that the value of u_{i+1} can be readily relocated on the horizontal axis (so as to calculate by the same process the value of u_{i+2}). In figure 2a the only changes of parameters for the two sequences of u_i 's are in the food availability (f). It will be seen that, depending on f , u_i 's may either increase or decrease through development, but always converge towards the same value. As f is increased, typically it is optimal to mature at a larger size (see later), so all u_i 's must be larger. Consequently for small f growth ratios are small and increase through development whereas for large f they are large and decrease.

It is a general result when $\alpha < 1$ that u_i 's will

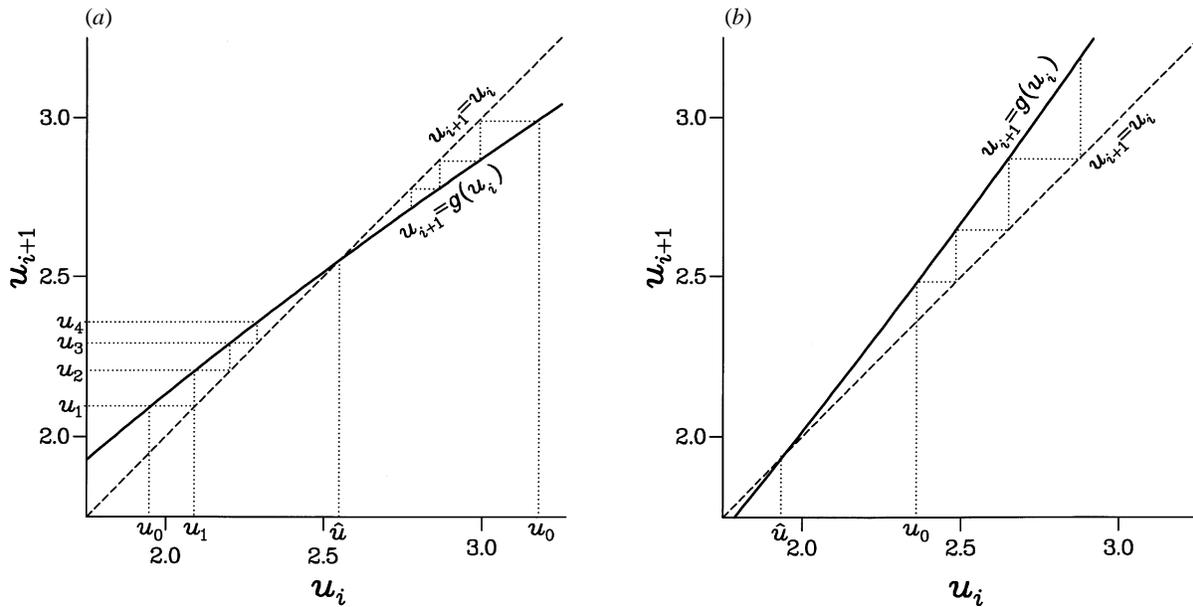


Figure 2. The line $u_{i+1} = g(u_i)$ shows how the growth ratio at one moult ($u_{i+1}^{\frac{1}{\alpha}}$) relates to the growth ratio at the preceding moult ($u_i^{\frac{1}{\alpha}}$), if both are optimal. To find the next growth ratio, the value of u_{i+1} is relocated on the horizontal axis by means of the line $u_{i+1} = u_i$. (a) applies to the power-law growth equation when $\alpha = \frac{2}{3}$ and $\epsilon = 0.5$; two sequences of u_i are indicated with dotted lines (the reading off of successive growth ratios is shown in more detail for the left-hand example). For both sequences 25 days are available for growth, $x_0 = 1$ g and five moults are used, but for that on the left-hand side $f = 0.6$ g/day, whilst for that on the right $f = 1.1$ g/day. It is apparent that all sequences of growth ratios converge towards $\hat{u}^{\frac{1}{\alpha}}$. In (b), $\alpha = \frac{4}{3}$ and $\epsilon = 0.5$, and for the single trajectory shown $f = 0.25$ g/day, again with 25 days available, $x_0 = 1$ g and five moults used; growth ratios diverge from $\hat{u}^{\frac{1}{\alpha}}$ for all $u_i \neq \hat{u}$.

Table 2. Values of $\hat{u}^{\frac{1}{\alpha}}$, for different combinations of growth parameters

(\hat{u} is the root of equation (2) and is the value of u which will not change from instar to instar under the optimal policy. \hat{u} does not exist for $\alpha = 1$ because in that instance any value of u can be the same for all instars.)

α	ϵ								
	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	
1.33	1.303	1.286	1.268	1.247	1.224	1.197	1.164	1.120	
1.00	—	—	—	—	—	—	—	—	
0.67	1.453	1.426	1.398	1.366	1.331	1.290	1.240	1.173	
0.33	1.661	1.622	1.579	1.532	1.479	1.419	1.346	1.248	

converge to a particular value with successive instars. This particular value, which we call \hat{u} , depends only on α and ϵ (it is the root of the equation $u = g(u)$). Exceptionally, $u_0 = u_1 = \dots = u_{N-1} = \hat{u}$ (Dyar's Rule obeyed), but otherwise either all u_i s are greater than \hat{u} and decrease each moult, or all u_i s are less than \hat{u} and increase. Table 2 shows the values of \hat{u} for different combinations of α and ϵ . The values typically lie within the range of growth ratios observed in the wild (Rice 1968; Cole 1980), so we expect both increases and decreases in growth ratio to occur.

Whether or not $u_i < \hat{u}$, instar durations should increase with successive instars.

(c) Results when $\alpha > 1$

Figure 2b shows this situation, in which u_i s now diverge from \hat{u} . If any u_i is greater than \hat{u} , u_i increases

each moult; if any u_i is less than \hat{u} , u_i decreases. Durations of successive instars now always decrease.

(d) How much does optimizing growth ratio and instar duration matter?

Here we investigate numerically the effects on fitness of following Dyar's Rule when this policy is not optimal. To do this we considered a range of values of α (0.33–1.33) and of ϵ (0.2–0.9) but in all cases we adjusted f (food availability) so that the animal took 25 days to achieve a linear size increase of a factor of 5 using five moults. These arbitrary, but not unrealistic, combinations of parameters produced some sequences of u_i that decreased with successive moults and some that increased, and some of the changes in u_i were appreciable. This is shown in table 3 along with the range in instar durations. We then altered the policy so that growth ratios were constant and examined both the size attainable if the same time was available (25 days) and the time necessary for the same size increase to be achieved ($\times 5$). These suboptimal size increases and times to reach maturity are given in table 3 as a percentage change from those attainable using the optimal policy. We similarly evaluated another sub-optimal strategy, that of spending equal times in each instar.

The most striking result is that equalizing instar durations is in all cases far worse a policy than equalizing growth ratios. Dyar's Rule is most costly when $\alpha > 1$, but this pattern might change if we chose a different overall growth increase, number of instars or time available.

Not surprisingly, the Dyar's Rule policy reduces

Table 3. Performance of suboptimal policies

(For each different combination of growth parameters (α and ϵ), $u_0^{\frac{1}{4}} \dots u_3^{\frac{1}{4}}$ and $d_0 \dots d_4$ are the ranges of growth ratios and instar durations under the optimal strategy. The number of moults is fixed at five (this is why one growth ratio is less than 1). Food is adjusted so that it takes 25 days to increase in linear dimensions by a factor of 5. The last four columns quantify the performance of two suboptimal strategies by the percentage change in adult size if 25 days are still available ($\Delta x_5 \%$), and by the percentage change in time necessary to reach the same size as the optimal strategy reached in 25 days ($\Delta t_5 \%$).

α	ϵ	optimal strategy		u_i s equal		d_i s equal	
		$u_0^{\frac{1}{4}} \dots u_3^{\frac{1}{4}}$	$d_0 \dots d_4$	$\Delta x_5 \%$	$\Delta t_5 \%$	$\Delta x_5 \%$	$\Delta t_5 \%$
0.33	0.8	1.429 ... 1.353	1.09 ... 11.81	-0.09	0.07	-15.74	12.96
0.33	0.5	1.138 ... 1.516	0.44 ... 14.59	-2.32	1.56	-37.46	38.12
0.33	0.2	0.923 ... 1.644	0.24 ... 16.07	-8.27	5.58	-55.19	71.81
0.67	0.8	1.460 ... 1.321	3.02 ... 7.43	-1.11	0.52	-6.06	2.93
0.67	0.5	1.389 ... 1.373	2.44 ... 8.48	-0.01	0.01	-14.67	6.97
0.67	0.2	1.322 ... 1.422	2.07 ... 9.22	-0.52	0.21	-24.96	12.11
1.33	0.8	1.305 ... 1.478	6.80 ... 3.44	-7.83	1.61	-10.62	2.13
1.33	0.5	1.325 ... 1.452	7.45 ... 3.03	-4.68	0.75	-24.08	4.19
1.33	0.2	1.345 ... 1.427	7.94 ... 2.74	-2.18	0.27	-41.04	6.53

fitness little when the optimal policy entails little change in growth ratio anyway. A 1% reduction in final volume as a consequence of using Dyar's Rule seems not untypical, which could easily translate into a similar reduction in fitness. If there were another strong selective pressure for Dyar's Rule to be followed we could not expect the Investment Principle to resist it, but otherwise this 1% reduction in fitness would mean that observed moulting strategies evolve away from Dyar's Rule.

Equally importantly, the constant-duration results demonstrate that the Investment Principle can put up a stronger selective pressure against certain other moulting patterns. These could include those favoured by the other adaptive explanations reviewed earlier.

5. TESTING PREDICTIONS ABOUT CHANGE OF GROWTH RATIO WITH SUCCESSIVE INSTARS

The essential thesis of this paper is that growth ratios optimize the conflicting advantages, when feeding rate is size-dependent, of moulting early or of moulting to a larger size (the Investment Principle). To test this general prediction would require establishing experimentally the growth equation, and also how mortality varies with size; optimal solutions could then be calculated and compared with observed growth ratios. Unfortunately the necessary parameters have not been measured; we hope this paper will inform empiricists that they are important parameters worth measuring. In the absence of direct measurements of the growth equation, we restrict ourselves to testing the predictions that rely on the additional assumptions that mortality is size-independent and that the growth equation is a simple power-law relationship of the form of equation (1) (α and ϵ constant; f can vary between individuals but not between instars). Real relationships will never be that simple, but it is worth asking whether these equations are a good enough characterization to produce predictions that resemble reality.

(a) Tests on populations of identifiable individuals

In Appendix 3 we develop a statistical test of whether the size increases in successive moults are compatible with our predictions. The test can best be explained by considering a plot of the cube of the observed growth ratio for one moult against the cube of the growth ratio for the preceding moult (u_{i+1} versus u_i). Through this scatter of points we then fit a curve that relates u_{i+1} and u_i according to the relation given in equation (2). The shape of the curve is determined by the values of α and ϵ ; these are estimated from the data so that the curve is the best least-squares fit. Our prediction is that single values of α and ϵ (i.e. a single curve) fit the scatter of points not significantly worse than if two or more such lines are fitted. For instance, one might try fitting separate lines for each instar, or for each sex, or for different diets. Whether such variation in α and ϵ significantly increases the fit can be tested by the usual F -test procedure familiar from analysis of variance.

As an example we show data gathered from 30 female spiders (*Nephila clavipes*) reared in the laboratory (see Vollrath 1983). Note that according to our hypothesis there should be no problem combining the data from individuals that differed in the number of instars they passed through, either because some matured at an earlier instar or because some were killed off early. The single line through the whole dataset corresponds to a value of $\alpha = 0.52$ and of $\epsilon = 0.68$ (figure 3). These seem plausible values, and the value of ϵ is similar to the values that we estimated earlier directly (from the weight of the ecdysed skin). However, the fit improves significantly by allowing α and ϵ to differ between individuals reared on rich and poor diets. Generally our interpretation of such non-agreement would not be that α and ϵ do necessarily differ between these categories, but that the assumptions of the model may be not met in some more fundamental way. In this case we know that ϵ really does differ between diets, but also that with a rich diet the assumption of ϵ being independent of size is

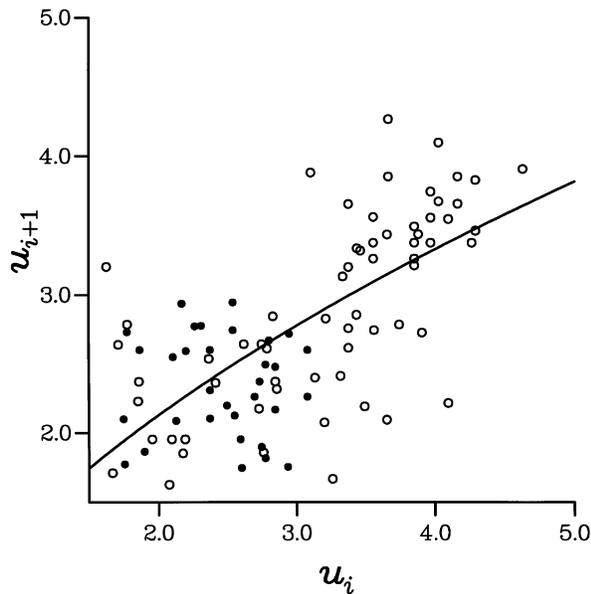


Figure 3. Growth ratio³ for one moult plotted against that for the preceding moult. Data are from 12 female *Nephila clavipes* fed a poor diet (closed circles) and 18 females fed a rich diet (open circles). The line is of the form given in equation (2) with the parameters α and ϵ chosen to optimize the fit.

violated. Once differences in diet are allowed for, no further significant improvement in fit is possible by allowing different values of α and ϵ for each instar. This agrees with our model, but the fitted values of α and ϵ for the poor diet are not realistic.

Another dataset from the literature (Przibram & Megušar 1912) agrees less well with our model: the plot of u_{i+1} versus u_i indicates a negative relationship, which the model never predicts. However, a negative relationship could arise from measurement error in the size data (too high a value for x_{i+1} will inflate u_i and deflate u_{i+1}), or if individuals sometimes hold reserves over at one moult to use in the succeeding moult. This negative relationship also occurs in *Galleria*, where Sehna (1985) explained it as a consequence of moulting being possible at only one time of day.

(b) Tests on data pooled over a population

A more qualitative prediction from equation (2), which can be tested against a wider range of species using published data, is that changes in growth ratios in successive moults should be monotonic (i.e. u_i should never increase then decrease with i , or vice versa). We predict monotonicity also in the durations of successive instars.

To avoid our selection of studies being biased, we used the same dataset as Cole (1980) when he calculated growth ratios averaged over all instars, but we discarded data on many of the species. Table 4 gives our rules for excluding data, and we discuss here the general problems with such datasets.

Unfortunately most papers give only the mean and standard error of the size in each instar, not of the growth ratio (individual growth ratios are unobtainable when animals are field-sampled or have to be killed to be measured). Consequently we have to

Table 4. Consistency of direction of change in growth ratio and instar duration

(If there are good data on N consecutive moults, the number of possible comparisons between consecutive moults is $n = N - 1$. Thus k , the number of consecutive instars for which an increase in growth ratio or instar duration is observed, must lie in the range $0 \leq k \leq n$. The tables show the numbers of species with k increases out of a possible n . Growth ratios increased in 39 out of 112 comparisons, and there was a significant lack of species in which increases exceeded decreases ($P = 0.014$). Instar durations increased in 66 out of 95 comparisons, and there was a significant excess of species in which increases exceeded decreases ($P = 0.002$).

Data are based on studies listed in Cole (1980). We excluded data in which generally less than 10 specimens were measured in each instar, in which the dimensions of more than the first two instars were reported to less than 3 significant figures, and in which durations were reported to less than 2 significant figures. Only one species per genus was included, and one sex, morph or diet (where these were separated) per species; the one included was chosen because of a more adequate sample size, larger dimensions or smaller durations, but bearing in mind also any data given on standard errors. Where data on more than one dimension were available we used that of the largest structure that was unlikely to stretch between moults. If the sex or morphs were split only at a late instar, comparisons that would be affected (see text) were not made. Otherwise all instars were considered, except the last when this had not been measured or when a metamorphosis had occurred. Ties scored as a half in each adjacent category.)

(a) Number of species with k increases in growth ratio

n	k					
	0	1	2	3	4	5
5	0	1	0	0	0	0
4	2	5	2	1	0	
3	4	11	3	0		
2	1	2	2			
1	0	3				

(b) Number of species with k increases in instar duration

n	k					
	0	1	2	3	4	5
5	0	0	0	0	1	1
4	0	1	7.5	4.5	4	
3	0	1	1.5	0.5		
2	0	2	2			
1	0	1				

estimate the mean growth ratio as the ratio of the mean of consecutive sizes; the standard error of the growth ratio is impossible to calculate, so parametric statistics are not applicable. (Even when growth ratios are calculated for each individual, it is theoretically possible for growth ratios to increase with successive moults in every individual and yet for the mean growth ratio not to show a monotonic increase; but this is likely to be a much more minor problem.) The accuracy of the growth ratios is often more seriously affected by sizes being given to an insufficient number

of significant figures and this is the commonest reason for excluding datasets from our analysis. Another problem when using data pooled over a population is that usually the sexes can be identified in only the last few instars. Frequently it is apparent that the smaller sex is exhibiting smaller growth ratios, but when comparing mean size of an instar that can be sexed with size in an instar that cannot, the growth ratio of the smaller sex is artificially deflated (because mean size of the earlier instar is inflated by the inclusion of the larger sex). This artificially low figure may interrupt an otherwise monotonic trend. The same problem occurs when species are polymorphic in whether the adult is winged or in the number of instars taken to mature.

If readers with their own data wish to test trends with more rigorous statistics, we draw attention to the use by Klingenberg & Zimmerman (1992) of geometric means and confidence intervals calculated by bootstrap techniques. Solow & Faber (1995) give a procedure based on likelihood ratios for testing whether two instars differ in size by a particular ratio. Also relevant are procedures used to test the constancy of Hutchinsonian size ratios between species in a guild (e.g. MacNally 1988).

Table 4 presents the result of our survey. Decreases in growth ratio and increases in instar duration predominate. The former has been realized before (e.g. Gaines & Campbell 1935), but the more consistent lengthening of instar duration, although commented on in particular contexts (e.g. in *Daphnia*; Lynch 1989), seems not to have been recognized previously as a general phenomenon. Indeed authors still cite Richards's (1949) claim that instar durations are normally equal and that it is slight deviations from this pattern that give rise to deviations from Dyar's Rule (Richards's misconception derives from plotting straight lines through points that obviously fit a curve; his data, too, show instar durations increasing!). A frequent exception to the general lengthening of durations is that the first instar lasts longer than the second (in 13 of 25 species duration decreases from the first to second instar; only 3 of 25 species show more decreases than increases in subsequent instars; $P = 0.005$ if the comparison had been *a priori*). In some cases the long first instar may be because these larvae do not feed for the first day or two after hatching (e.g. Peet 1979). The fact that growth ratios decrease whilst instar durations increase implies that the scaling coefficient α is usually less than 1. This follows regardless of whether the Investment Principle is determining instar durations and growth ratios.

Our expectation was that the distributions in table 4 should be U-shaped, with most species showing monotonic decreases or monotonic increases. In fact the tendency for growth ratios to decline and durations to increase means that one half of the U is missing. With the half that is left it is impossible to distinguish between two possibilities: that increases and decreases show no pattern and occur at random, although one is more common than the other; or that a monotonic change is usually what is underlying the data, but that special circumstances, noise and measurement error

mean that there are frequent exceptions to this rule. Measurement error is particularly disruptive of monotonic trends. For instance, an apparent increase in instar duration followed by a decrease could be an artefact caused by an overestimation of the duration of the intermediate instar.

Nevertheless we conclude that real exceptions to a monotonic change in both growth ratio and instar duration are probably not uncommon. This disagreement with our predictions may be because the Investment Principle is not important and is swamped by other considerations. However, in the next section we consider how dropping the simplifying assumptions in our model can generate non-monotonic patterns without changing the basic principle of our explanation. It is also only fair to point out that most other conceivable explanations for growth ratios and instar durations would probably also tend to predict that they change monotonically if at all, so it would also be necessary to elaborate these explanations to accommodate the facts.

6. EXPLANATIONS FOR NON-MONOTONICITY IN GROWTH RATIOS AND INSTAR DURATIONS

Two quite likely explanations are available to explain non-monotonic patterns without contradicting the essential principles of our model: the power-law relationship of equation (1) may be an inadequate fit over the full size range, or mortality may depend strongly on size. We now consider the kinds of growth trajectories that can result when these complications are incorporated (for these cases we found the optima numerically; see Appendix 1).

(a) Other growth equations

So far we have assumed that metabolic rate scales with size with an exponent similar to the scaling of energy assimilation. Now we assume that metabolic rate is proportional to $x^{0.75}$, but that assimilation rate is proportional to either $x^{0.628}$ or $x^{0.872}$. These exponents were chosen so that over a fivefold change in linear dimensions metabolism either increases from 25% of energy assimilated to 45%, or decreases from 45% to 25%. Observed values for the proportion of assimilated energy used by metabolism typically range from 20% to 50% between different species (Calow 1977; Schroeder 1981), so our 20% changes within a single individual seem quite extreme. To investigate the consequences of these growth equations we put ϵ equal to both 0.3 and 0.8, varied $x_0^{\frac{1}{3}}$ by a factor of two and varied the time taken to mature.

With these growth equations it was still true (as when $\alpha < 1$ in equation (1)) that when the animal spends a long time maturing to a large size, growth ratios consistently decrease with each moult, and that when it matures earlier to a smaller size, growth ratios consistently increase with each moult. However, in intermediate cases, where before growth ratios were constant, there now is a non-monotonic change in

growth ratio with each moult. Nevertheless in these non-monotonic cases the changes in growth ratio are sufficiently small that empirical data would still suggest constancy of the growth ratio. With the particular scaling exponents described, instar duration always showed a consistent increase with each moult, although this monotonicity is not inevitable if the scaling exponents are closer to 1.

We also investigated growth equations in which the intake rate was the sum of two different powers of size, and others in which the scaling exponent of intake rate changed gradually from one value to another over a range of sizes. Still it was true that monotonicity in growth ratio and instar duration was the norm, but that exceptions to both could occur even with quite smooth-looking functions. Usually any non-monotonicity was not strong enough to be likely to be detected empirically. We do not understand exactly why some growth equations give rise to non-monotonicity, so we cannot say how common such equations are in nature. In nature there might often be critical sizes above which a common prey species suddenly becomes available; in such cases all sorts of patterns of growth ratios and instar durations could be optimal.

A non-monotonic change of growth ratio with successive instars implies that u_{i+1} plotted against u_i (as in figure 2) should not now lie along a single line. However, for the models described above where relative metabolic costs increase or decrease with size, the scatter about a line is so small that empirically it would be swamped by measurement error.

(b) *Size-dependent mortality*

For simplicity we will restrict attention here to mortality that becomes less likely as the animal grows, which is probably the case in most arthropods (survivorship curve of Slobodkin type IV). The effects of this pattern of mortality are counter-intuitive. Suppose for the moment that mortality only strikes when the animal is feeding, rather than when it is moulting. We expected that animals should tend to rush through the early sizes when they were most vulnerable, so that initial instar durations and growth ratios would be reduced relative to later instars. This is sometimes the case, but the opposite may also occur. Animals may do best to endure the initial instars for longer so that in later instars they are larger and thus partially escape from mortality. Which strategy is better depends on the parameters of the growth equation (e.g. higher efficiency of moulting makes them spend longer in later instars) and on how mortality scales with size (the more concave-down the relationship, the longer they spend in early instars). Combining mortality that steadily decreases with size with a power-law growth equation that would otherwise give a monotonic change in duration and growth ratio, can readily produce non-monotonic changes in instar duration and growth ratio.

We have also modelled the situation when only mortality at the moult decreases with the size of the new instar. Our expectation here was that animals

would prolong the initial instars to avoid moulting to small-sized instars. Our computations confirm this. Again non-monotonic changes in instar duration and growth ratio are optimal in some cases.

7. PREDICTING THE EFFECT OF ENVIRONMENTAL MANIPULATIONS WHEN GROWTH IS DISCONTINUOUS

An obvious way to test our model further is to predict how changes to the parameters of the growth equation will change the timing and size increase of each moult. In particular many experiments have manipulated food quality, which correspond to a change in f (sometimes manipulations of crowding and temperature might be modelled as a change in f too). In non-experimental situations the variation in f may be unmeasured, but we might believe, for instance, that spiders with webs in different places will be subject to different abundances of food. In this case we can still predict the sort of variation in life history that should occur if f varies; e.g. will those spiders taking longer to moult, moult at a larger or smaller size? Such relations are termed norms of reaction. We emphasize here again that our model concerns a non-stochastic environment: the assumption is that the animal can instantaneously estimate the food availability in its local environment and can count on that availability not changing.

We also consider how the animal should respond if it hatches late in the season (an increase in t_0) or hatches from a larger egg (an increase in x_0). Similarly, if a manipulation or environmental stochasticity delays a moult or causes one instar to be smaller than usual, we may still predict the subsequent optimal policy by renumbering the subsequent instars from 0 and setting t_0 and x_0 as observed at the start of the chosen instar. We do not consider alterations to α and ϵ because these are intrinsic properties of a species that would seem difficult to manipulate (although scope exists for interspecific comparisons). Predation levels may be readily manipulated in the laboratory, but it is usually uncertain whether the animal can sense such an environmental change and thus we cannot expect its policy to change; however, comparisons between populations subject to different predation levels would be possible.

Altering f , x_0 and t_0 dictates what size is attainable if the final moult occurs at a particular time. What time is actually chosen will depend on how the time and size at which the animal matures affect survival up to that time and the reproductive success of the adult. We thus have to specify a fitness function $F(x_N, t_N)$ where x_N and t_N refer to the size and calendar time at the emergence from the final moult. We discuss various plausible fitness functions presently. Different populations of a species will often differ in their fitness functions, so this is another comparison that might be made to test our model's predictions.

The sections following deal with predictions of optimal x_N and t_N , and may appear to ignore growth ratios and instar durations, which are the focus of the

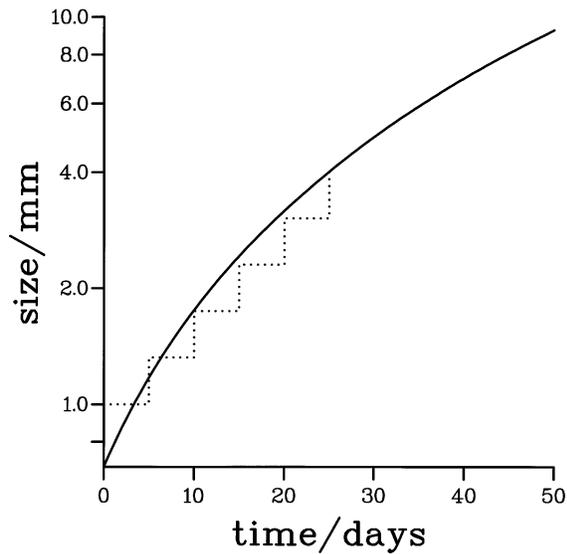


Figure 4. A locus of options (solid line). Each point on the locus corresponds to a particular time taken to attain maturity and assumes that moulting decisions are optimal given this time constraint. Consequently the locus shows the adult sizes attainable for each time spent growing (parameters as in figure 5a). The dotted line shows the actual optimal trajectory taken by an animal to attain one particular point on this locus.

paper. However, if x_N/x_0 increases, at least one growth ratio must have increased. For the case of the power-law growth equation and size-independent mortality this implies that all u_i will have increased. Similarly, for this case, an increase of $t_N - t_0$ implies that all d_i have increased. The situation is more complex when the number of instars is also allowed to be optimised (see §8).

(a) Loci of maximum size attainable within a growth period

For the moment let us consider only cases in which mortality is independent of size and the number of instars is fixed. If it were optimal for the final moult to occur at some particular time, we suppose that the optimal life history would maximize size given this time constraint. We can plot the maximum size attainable against the time allowed (figure 4). We call this line a locus of options. Note that the locus is not the trajectory taken by any one animal as it grows; it is the collection of endpoints of an array of distinct trajectories, each optimal given its time constraint and all with the same parameters of the growth equation.

The locus will be the same whatever fitness function we specify (so long as fitness increases with size). What the fitness function does affect is which point of the locus is optimal. We first consider how changing parameters of the growth equation changes the positions and shapes of these loci. Later we will superimpose the loci onto a landscape of fitness values; this allows us to visualize how these changes in the loci, or changes in the fitness functions, will affect which point of the locus is optimal.

When $\alpha = 1$ it is optimal to spend equal times in

each of the N juvenile instars (Appendix 2), so the locus is

$$x_N = x_0[\epsilon + f(t_N - t_0)/N]^N \quad (3)$$

or

$$\ln(x_N) = \ln(x_0) + N \ln[\epsilon + f(t_N - t_0)/N].$$

We consider these loci plotted on a graph of $\ln(x_N)$ against t_N . The solid lines in figure 5b show how altering x_0 , t_0 and f changes these loci. Increasing x_0 translates the graph vertically, increasing t_0 translates it horizontally, and increasing f increases the slope.

Figures 5c and 5d show the loci for $\alpha = 0.67$ and $\alpha = 1.33$, which we calculated numerically. For values of $\alpha \leq 1$ the loci resulting from a power-law growth equation are all markedly concave-down curves. In fact α has to be appreciably larger than 1 for the locus to be concave up. When $\alpha = 1.33$ the locus is concave down when the efficiency of moulting is low (e.g. $\epsilon = 0.2$), but in part concave up when $\epsilon = 0.8$. Increasing t_0 still merely translates the locus horizontally (because we have assumed that food availability does not depend on the time of year), and increasing f again increases the slope. Increasing x_0 now does affect the slope of the locus: when $\alpha < 1$ the gradient decreases, when $\alpha > 1$ the gradient increases, although the main effect is still a translation upwards.

(b) Fitness functions

We will suppose that fitness depends both on adult size (x_N) and on how long it takes to mature ($t_N - t_0$). A plausible set of fitness functions that we will consider first are

$$F(x_N, t_N) = kx_N^\beta \exp[-\theta(t_N - t_0)]. \quad (4)$$

Here k is an arbitrary positive constant.

Fitness depends on the probability of surviving to adulthood multiplied by the expected number of offspring produced once adulthood has been reached. $\exp[-\theta(t_N - t_0)]$ describes the probability of surviving to adulthood; an increased risk of not reaching adulthood is the penalty of maturing late. We are assuming that mortality before maturation occurs at a constant rate of θ per day independent of size. This term can be simplified to $\exp(-\theta t_N)$, since the rest is a constant factor independent of t_N and so can be subsumed into k .

x_N^β describes how the rate of production of offspring scales with adult mass (x_N); this represents the benefit of maturing at a larger size. Reiss (1989) reviews studies of β , reporting a coefficient for *Asellus* of 0.77 and for an aphid species of 0.47 and 0.62. In fact we expect β to vary in similar ways to the coefficient α , which described how the rate of accumulation of reserves scaled with size, only in this instance reserves are converted to offspring rather than to growth. At least for many hemimetabolous insects, α and β might often be considered equal. From the rate of production of offspring we need to convert to the expected number of offspring produced over the lifetime of the adult. If adults die with a constant probability ρ per unit time,

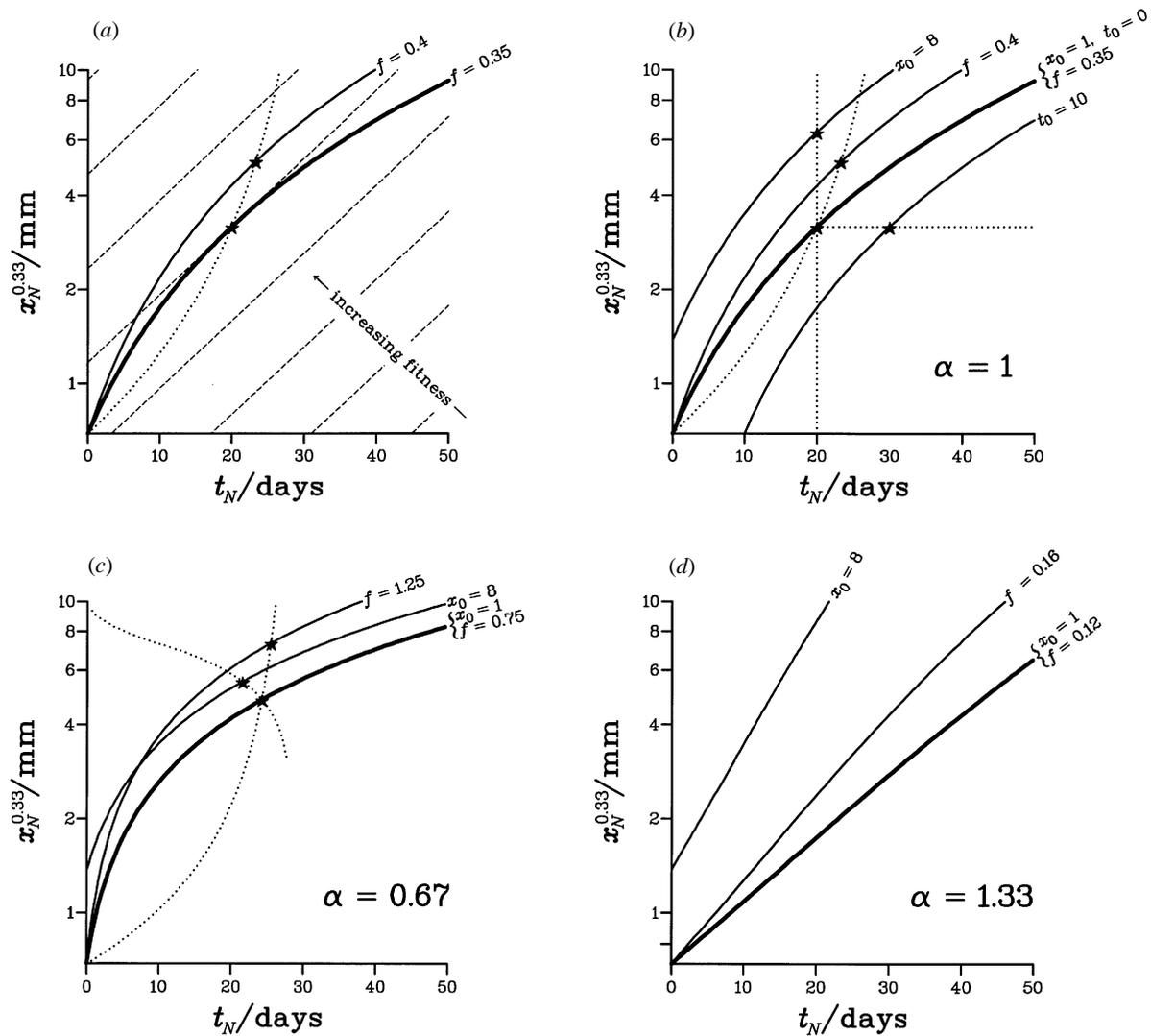


Figure 5. Loci of options and norms of reaction, on a plot of size of adult (x_N) against time of emergence of adult (t_N). (a) Two loci of options, each for a different food availability f (solid lines). The dashed lines are contours of equal fitness (where $\theta/\beta = 0.15$ in equation (4)). Where these form a tangent to a locus is the optimal time and size to become adult; this point is marked with a star. The dotted line is the norm of reaction, connecting all such points obtained for different values of f ; (b) is for the same parameter values but with two extra loci showing the effect of changing initial size (x_0) and initial time (t_0); the norm of reaction from varying x_0 is the vertical dotted line and that from varying t_0 is the horizontal dotted line; (c) similarly shows the effect of varying f and x_0 , but when $\alpha = \frac{2}{3}$ (in (a) and (b) $\alpha = 1$); the norm of reaction from varying t_0 is not shown but again would be horizontal. Here $\theta/\beta = 0.09$. (d) The corresponding loci when $\alpha = \frac{4}{3}$, but the norms of reaction are not shown because for most parameter values it is optimal to mature either immediately or never. In all cases $N = 5$ and $\epsilon = 0.8$. Values of f shown are in units of mm^3/day , of x_0 are in mm^3 , and of t_0 in days.

the expected number of offspring produced is x_N^β/ρ . In equation (4) the factor of $1/\rho$ is subsumed into the constant k .

With such fitness functions the fitness landscape over the $[\ln(x_N), t_N]$ plane is described by contours that are straight parallel lines of the form

$$\ln(x_N) = (\theta/\beta) t_N + \ln(G/k)/\beta,$$

where G is the fitness value on that contour (figure 5a). Moving along a contour, the benefits of the increase in size exactly compensate the costs of the longer delay.

Now consider superimposing concave-down loci onto such a fitness landscape (figure 5a). The point with the highest fitness on any locus will be where the tangent has the same gradient as the contours of equal

fitness. Anywhere along the locus to the left of this point, where t_N is smaller, the gradient of the locus is steeper, so that the benefits of an increase in size outweigh the costs of a delay. Conversely at points to the right of this point the gradient of the locus is shallower, so that the benefits of a size increase are outweighed by the costs of delay; consequently it is better to mature earlier.

In figure 5 the points on the loci where fitness is maximized are shown by stars. The dotted lines joining these stars are the norms of reaction. For $\alpha = 1$ (figure 5b), when x_0 is increased, the optimal t_N is unchanged but x_N increases proportionately, so that x_N/x_0 is unchanged. Thus both u_i s and d_i s are unchanged. When t_0 is increased, the optimal x_N is unchanged, t_N

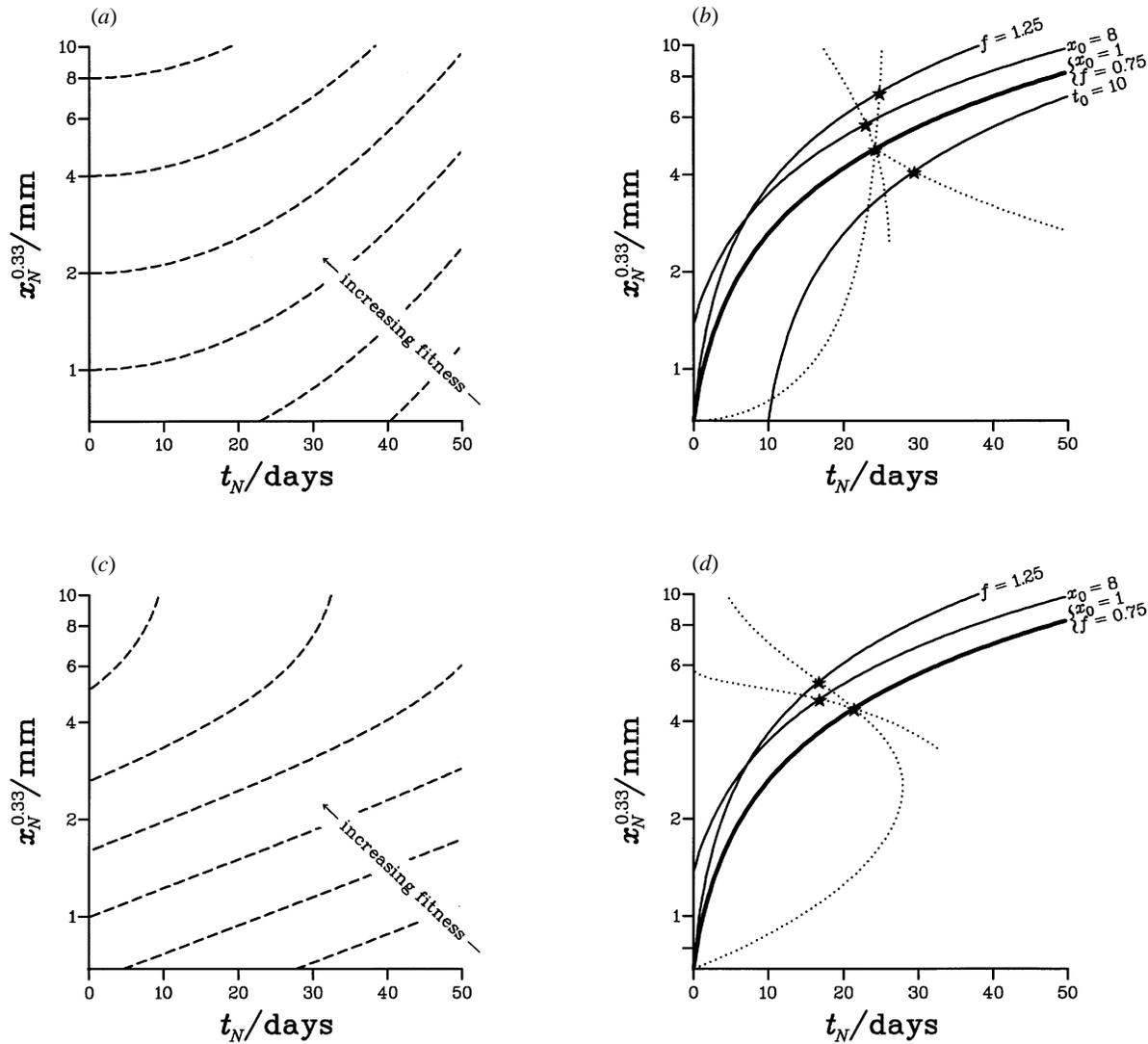


Figure 6. Fitness contours and norms of reaction for two fitness functions. (a) and (c) show contours of equal fitness; contours are spaced evenly on a log scale but three times as widely in (c). (a) Extra penalty on late emergence: $F = \exp(-0.0012 t_N^2 x_N^2)$. (c) Sigmoidal increase in fitness with size: $F = \exp(-0.06 t_N x_N / (x_N + 125))$. (b) and (d) show norms of reaction (dotted lines) corresponding to the fitness functions of (a) and (c) respectively; the loci (solid lines) in both are the same as in figure 5c (where, for comparison, the norms of reaction correspond to the fitness function $F = \exp(-0.06 t_N x_N^2)$). The norm of reaction due to variation in t_0 is only shown in (b), because with the other fitness function it is horizontal (as in figure 5b).

increases, but $t_N - t_0$ is unchanged, so again both u_i s and d_i s are unchanged. Less obviously, increasing f means that both x_N and t_N increase.

For the case of $\alpha = 1$ and a fitness function of the form of equation (4) it is straightforward to prove the generality of these results algebraically. (Because all u_i s and d_i s are then equal, x_N can be substituted by an algebraically simple function of t_N (equation (3)); the fitness function can then be differentiated with respect to t_N so as to locate the maximum.) Here we outline another proof that gives a better intuitive understanding of the direction of the reaction norms. Consider the gradient of the loci when $\alpha = 1$. From equation (3),

$$d[\ln(x_N)]/dt_N = N/[\epsilon/f + (t_N - t_0)/N].$$

If f is increased, the gradient at any particular value of t_N increases. At the time when with the lower f the

benefits of increased size matched the costs of increased delay, the steeper gradient means that now by increasing the delay the increase in benefits more than compensates for the increase in costs. The optimum is thus to mature later when f is increased. A similar argument shows that it is also optimal to mature at a larger size.

(c) Other shaped loci and fitness functions

With the loci for values of $\alpha \neq 1$ (figure 5c, d) increasing f still increases the slope of the locus, again meaning that the optimum time to mature and the size at maturity both increase. The main effect of increasing x_0 is again to translate the locus upwards, but now the gradient is also affected. When $\alpha < 1$ the gradient decreases and consequently the norm of reaction due to variation in x_0 is different in direction to the norm of reaction due to variation in f : large sizes are predicted

to be associated with short times to maturity. (Increasing x_0 decreases x_N/x_0 , so both u_i s and d_i s will decrease.)

The situation is intriguing, because an animal that has reached a particular instar at a larger size than normal, because of a good food availability earlier, should then aim to mature earlier than normal. But if this earlier food availability is indicative of future food availability, the increase in f would favour maturing later than normal. Which argument wins will depend on a variety of factors, but really a full stochastic model is necessary.

The norms of reaction in figures 5*b* and *c* arise because the locus is concave down. When the locus is a straight line or concave up, its gradient will never decline to that of the linear fitness contours, and so it will always be better to continue to grow. (Conversely, for concave-down loci the locus would never attain the gradient of very steep fitness contours, in which case it is optimal to mature immediately.) Even with concave-down loci, many possible slopes of the fitness contours would result in the optimum not occurring until size increases and the time elapsed to maturity are unrealistically huge. We believe this does not happen in real life because real fitness contours curve up at large values of x_N and t_N . Being very late attracts extra penalties (e.g. the onset of winter, senility) and being very big is no longer such a benefit (for instance, fitness may show a sigmoidal relationship with size, or there may even be an optimal size above which fitness decreases, particularly perhaps in insects which could get too heavy to fly properly; Bernado 1994).

In figure 6*a* we therefore show fitness contours when the mortality rate increases with t^2 (an arbitrary concave-up function of t), rather than with t as before. This could also apply to the situation when offspring born late are less likely to survive. Now the norm of reaction due to variation in t_0 is no longer horizontal, but x_N decreases as t_N increases (figure 6*b*). Figure 6*c* shows fitness contours when fitness shows a sigmoidal relationship with x_N . In this case the norm of reaction due to variation in f is qualitatively changed: increased x_N is associated with decreased t_N (figure 6*d*), whereas with previous fitness functions it was associated with increased t_N .

Norms of reaction are also affected by size-dependent mortality. Then the graphical approach presented here is not applicable, so results have to be obtained numerically by the method of Appendix 1.

Of course many other fitness functions are possible, just as real growth equations will be more complex and give rise to different shaped loci of options. At present there is no point in us exploring more of these infinite possibilities. Now that we have demonstrated that the nature of these relations can affect what life-history strategy is optimal, it is up to empiricists to measure the necessary parameters for their individual populations.

(d) Norms of reaction with other moulting strategies

Are the predicted norms of reaction qualitatively different if an animal follows a different moulting

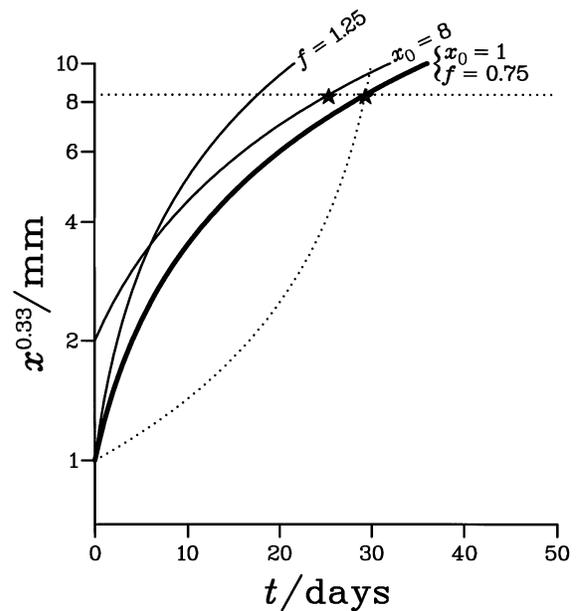


Figure 7. Loci (solid lines) and norms of reaction (dotted) when growth is continuous and $dx/dt = fx^\alpha$. Here $\alpha = \frac{2}{3}$, and the other parameters are also as in figure 5*c*.

strategy than we have predicted to be optimal (perhaps because constrained by one of the other adaptive influences mentioned in our review of earlier work)? Once again as an example we suppose that the animal might keep its growth ratio constant between instars (Dyar's Rule). Under this policy, when $\alpha \neq 1$, the loci and norms of reaction will differ from those under the optimal policy. In this example we continue to consider norms of reaction when the fitness function is given by equation (4). Under the suboptimal strategy an increase in x_0 should now slightly increase x_N and t_N for most reasonable values of α and ϵ ; the direction of this norm of reaction differs qualitatively from that when $\alpha < 1$ and the policy is optimal (see figure 5*c*). The norm of reaction due to variation in food availability does not differ qualitatively when growth ratios are kept constant from when growth ratios are optimized, but of course the shape will differ quantitatively and in the case of other fitness functions may also differ qualitatively. Observations of the norms of reaction could therefore provide a test of our model, so long as the form of the fitness function is also known.

(e) Comparison with continuous growth

For comparison, in figure 7 we show loci of options when growth is not discontinuous but continuous ($dx/dt = fx^\alpha$). (In this case the locus of options and the growth trajectory are identical.) Note that the shapes of these loci differ from the shapes of the loci when food assimilation rate scales with the same value of α but changes discontinuously. For instance when $\alpha = 1$, in the continuous-growth case the locus of options is linear when $\ln(x_N)$ is plotted against t_N , whereas the discontinuous-growth locus was concave down. If α is increased the loci still change from concave down to concave up, and the changes of the loci when food or

initial size is altered also appear qualitatively similar to the discontinuous-growth case. But although increasing initial size (x_0) still increases or decreases the optimal time to maturity (t_N) depending on whether α is greater or less than 1, the optimal adult size (x_N) is now unchanged. Thus the optimal norms of reaction under discontinuous growth can differ qualitatively from those under continuous growth (cf. figures 5c and 7).

8. OPTIMIZING NUMBER OF INSTARS

Except where we considered size-dependent mortality, our optimization criterion has been to maximize adult size given a specified time to mature, which is equivalent to minimizing the time taken to achieve a specified adult size. So far we have in addition specified a fixed number of instars and we have optimized just the duration of each instar, but in reality we expect natural selection to optimize also the total number of instars utilized.

Often the number of moults undergone by animals reared in identical conditions in the laboratory differs between the sexes, or between winged and wingless morphs, or between populations from different environments, or between otherwise similar individuals from the same population (Wigglesworth 1972; Daly 1985; and references therein). It may also vary facultatively; for instance diet, temperature, day length, size of egg and generation can all alter the number of moults (Wigglesworth 1972; Daly 1985). Some insects kept on a low diet will even continue moulting indefinitely (Sehnal 1985) until a better diet enables them to reach the critical size to become adult.

The same Investment Principle that we used to explain how long should be spent in each instar also

implies that there is an optimal number of instars. If an animal moults too little, it is not making use of a frequent increase in size to increase its feeding rate (in figure 1 it would obviously be suboptimal to continue till the final time as a first instar with that instar's low rate of reserve accumulation). Conversely, if it moults too often, the animal is wasting its accumulated reserves by losing them as discarded skins.

Should we then all along have been considering only moulting strategies that also optimized the number of instars? Only to an extent. Our earlier predictions for how u_i and d_i change as the animal grows remain true whatever the number of instars. Furthermore, as you cannot have half an instar, over some ranges of parameters the number of instars, even if optimized, does not change. Also arthropods are not always infinitely plastic about how many moults they undergo; in many species the number of instars is constrained to a single number or narrow range whatever the environment. For instance no mutation of *Drosophila* is known which has a different number of instars, and constancy of the number of instars is the rule generally in Diptera and Hymenoptera (Sehnal 1985). (Part of the reason for this may be that moults not only serve to increase size, but also to change shape, so the animal may be ready shape-wise to become adult after the set number of instars even if it is the wrong size.)

(a) The effect of environmental parameters

We first predict how the parameters f and x_0 affect the optimal number of instars (and thus the growth ratios and instar durations). Figure 8a shows how the locus of options changes if we fix the number of instars

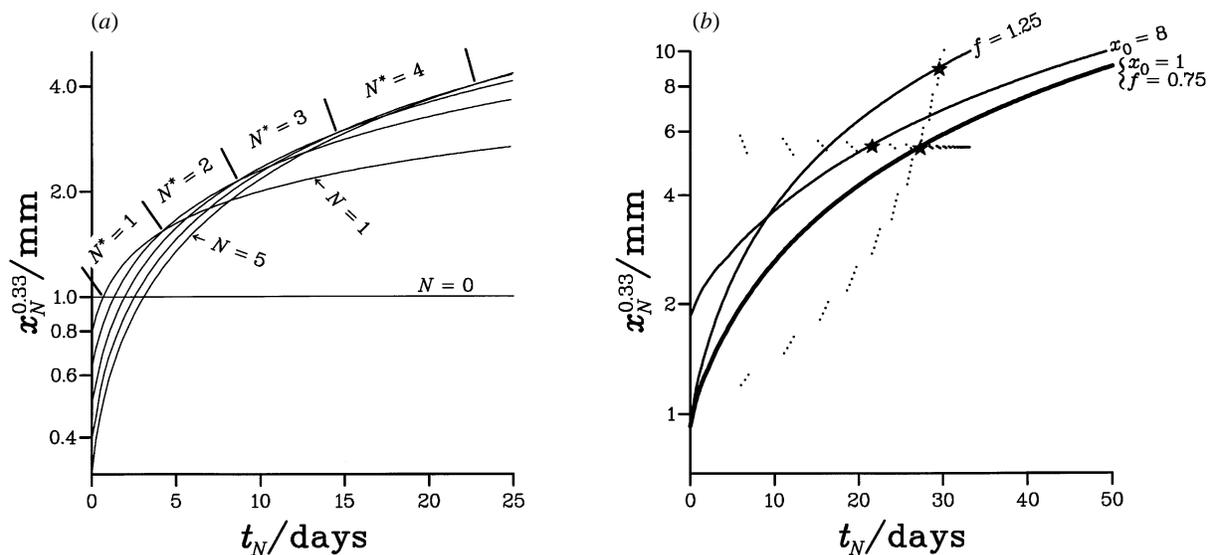


Figure 8. Loci (solid lines) and norms of reaction (dotted) when the number of instars is optimized. (a) The different norms of reaction when N is fixed. Different values of N are optimal (shown as N^*) depending on how long is spent reaching adulthood. The locus when N is optimized is thus a combination of segments from the fixed- N loci. ($\alpha = \frac{2}{3}$, $\epsilon = 0.5$, $f = 0.35 \text{ mm}^3/\text{day}$, $x_0 = 1 \text{ mm}^3$.) (b) The parameters are now identical to those in figure 5c, but N is optimized rather than fixed at 5.

at different values. These loci intersect, so that at different values of t_N it is a different locus that results in the largest size, implying that a different number of instars would be optimal. If we do allow the number of instars to be optimized, the locus of options therefore becomes a combination of segments from the loci for fixed numbers of instars. The shape of the locus when the number of instars is optimized is thus somewhat different from the locus when the number of instars is fixed (figure 8*b*).

Figure 8*b* also shows the norms of reaction resulting from variation in f and x_0 . These consist of disjointed segments of the norms-of-reaction curves when N is fixed. As x_0 is decreased, x_N decreases and t_N increases so long as it is not optimal to change the number of instars; but at some point the optimal number of instars increases, whereupon x_N and t_N both increase in a sudden jump. This would be confusing to the field entomologist with data on adult size and time of emergence but not on the number of instars. Such sudden reversals in the direction of the norm of reaction may also happen if one is considering the growth ratio or duration of a particular instar. Ebert (1994) did observe discontinuous jumps in the size at maturity of *Daphnia* as a result of extra moults, but supposed that they arose because earlier instar durations were not adjusted optimally (only a correct deduction if size and time do not both affect fitness).

In figure 8*b* the norm of reaction due to variation in x_0 converges to a horizontal line, with no further decline in x_N , in contrast to the fixed instar case (figure 5*c*). This is because, having attained a particular size at some intermediate instar, the animal can act subsequently just as if this were its size at the first instar. It can add moults indefinitely and the time already spent growing has affected only the total mortality not the subsequent rate of mortality. (For large N the situation becomes more comparable with continuous growth; compare figure 7.) With fitness functions in which time spent growing is more severely penalized we expect the norm of reaction to decline.

In figure 8*b* the effect of a decrease in food availability is a decrease in the number of instars used. This is the opposite of what is probably the most common response to less food (Calvert 1929; Gaines & Campbell 1935). However, we have already seen that we can easily predict quite different norms of reaction with different fitness functions (e.g. figure 6*d*).

(b) Predictions of growth ratios; the effect of α and ϵ

It is obvious how some other parameters in our model will affect the optimal number of instars. The higher α , the greater the benefits once size has increased, so the more instars. Mortality associated with moulting will tend to decrease the optimal number of instars, as will any extra time taken up by moulting when the animal is unable to feed. The loss of resources in the ecdysed skin is also a penalty on moulting, so the smaller ϵ is, the fewer the instars.

We now quantify these predictions, making the same assumptions as in §3 so as to find solutions analytically.

Consider any two consecutive instars of an animal following an optimal growth strategy with a fixed number of instars. In Appendix 4 we analyse under what conditions it is better to spend the same amount of time as spent in these two instars in one instar instead, skipping the intermediate moult. It turns out that one instar is better if the first growth ratio under the two-instar strategy is less than a particular value that depends only on α and ϵ (we are not considering time or mortality penalties on moulting). If the growth ratio is less than this, and the number of instars is unconstrained, the two instars should amalgamate into one, so that the consequent growth ratio will lie above the critical value. Thus a prediction from the Investment Principle is that observed growth ratios lie above the values tabulated in table 5*a*.

Conversely it is also true that if growth ratios are above a particular value it is better to replace one moult by two moults and an extra instar. Each of these two moults has a lower growth ratio of course, so another prediction is that growth ratios above the values tabulated in table 5*b* should not be observed. Thus values in tables 5*a* and *b* bracket the range of growth ratios predicted if the number of instars is optimized.

These limits can be made more stringent. Even if it is not optimal to spend the time spent in two instars in one instar instead, it may still be better to spend the time spent in three consecutive instars in two instars instead, or to replace four instars by three, etc. It turns out that when $N > 2$ there is still a critical growth ratio dependent only on α and ϵ (and independent of size or food availability) below which it is better to undergo one less moult (see Appendix 4). Conversely there is another such critical growth ratio above which it is better to undergo an extra moult. We explain in Appendix 4 how to calculate these limits numerically. Table 5*c* gives the range of permissible growth ratios if five moults are optimal. The most extreme values apply to u_0 (when $\alpha < 1$) or u_4 (when $\alpha > 1$), so one could also derive more stringent limits for growth ratios at other instars. The minimum values in table 5*c* also apply when more than five moults are used, but then it is again possible to derive stricter limits; conversely the maximum values also apply when less than five moults are used. The larger the number of instars used, the narrower the ranges of growth ratio predicted. However, the narrowing of the range is not dramatic once N is not very small: for instance, when $\alpha = \frac{2}{3}$ and $\epsilon = 0.8$, the minimum growth ratio is 1.199 for five instars and 1.210 for 10 instars; the maximum is 1.277 for five instars and 1.268 for ten instars.

(c) Tests of the influence of ϵ on growth ratio

ϵ , the efficiency of moulting, is probably greatest in maggot-like and thin-skinned holometabolous insects, which suggests that they should use more instars and have lower growth ratios to attain the same increase in size as hemimetabolous insects. In fact holometabolous insects tend to have fewer instars and higher growth ratios (Cole 1980; and our reanalysis of the same dataset). One potential explanation for this would be if

Table 5.

<i>(a) Lower bound on growth ratio ($u^{\frac{1}{3}}$) if number of instars can be optimized (for $N \geq 2$)</i>								
	ϵ							
α	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
1.33	1.189	1.180	1.170	1.158	1.145	1.129	1.109	1.081
1.00	1.237	1.225	1.211	1.195	1.177	1.157	1.131	1.096
0.67	1.268	1.256	1.241	1.225	1.206	1.183	1.155	1.114
0.33	1.315	1.303	1.290	1.274	1.255	1.232	1.200	1.152

<i>(b) Upper bound on growth ratio ($u^{\frac{1}{3}}$) if number of instars can be optimized (for $N \geq 1$)</i>								
	ϵ							
α	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
1.33	1.444	1.419	1.391	1.360	1.326	1.286	1.237	1.172
1.00	1.531	1.500	1.466	1.428	1.386	1.338	1.279	1.201
0.67	1.678	1.637	1.592	1.543	1.489	1.426	1.351	1.251
0.33	2.004	1.942	1.875	1.801	1.719	1.625	1.512	1.363

<i>(c) Lower and upper bounds on growth ratio ($u^{\frac{1}{3}}$) when $N = 5$, if number of instars can be optimized</i>								
	ϵ							
α	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
1.33	1.246	1.233	1.220	1.204	1.187	1.166	1.140	1.103
	... 1.355	... 1.334	... 1.312	... 1.287	... 1.258	... 1.226	... 1.187	... 1.135
1.00	1.315	1.297	1.278	1.257	1.233	1.205	1.170	1.124
	... 1.399	... 1.376	... 1.351	... 1.323	... 1.292	... 1.256	... 1.213	... 1.154
0.67	1.348	1.331	1.312	1.291	1.266	1.236	1.199	1.147
	... 1.548	... 1.513	... 1.476	... 1.435	... 1.390	... 1.339	... 1.277	... 1.197
0.33	1.375	1.363	1.349	1.332	1.311	1.284	1.248	1.191
	... 1.904	... 1.843	... 1.778	... 1.707	... 1.628	... 1.540	... 1.435	... 1.302

the insect families that used the most instars tended to spend a long time as larvae (e.g. Plecoptera), so that they may be moulting not to increase in size but to renew a worn-out skin. Some such other function of moulting is also suggested by those instances where moulting does not cause a size increase, for instance when certain insects are kept on a starvation diet (other examples in Calvert 1929). The limited ability of rigid-skinned hemimetabolous insects to change shape at a moult, and especially the lack of a pupal stage in which a complete reorganization is possible, may be another reason why they require more moults to mature into adults. Also caterpillars and maggots are vulnerable to predation and desiccation because of their thin skins, and often exploit resources that quickly disappear, so the extra delay associated with moulting is another factor that will curtail how many instars they should utilize.

We do have measurements of ϵ for some species, so we can also check quantitatively whether their observed growth ratios are compatible with the predicted limits in table 5. Unfortunately we do not know the value of α , but we might assume that it lies between 0.33 and 1.33. Vollrath's data on females of *Nephila* fed a poor diet suggested a mean value of ϵ of 0.77 ranging between 0.68 and 0.82. Table 5c suggests that we should then not observe growth ratios below about 1.14, nor above about 1.54. In fact the observed mean growth ratio is 1.35 with the minimum of 47

observations being 1.20 and the maximum 1.48. Our prediction is thus supported. Also encouraging is that the higher estimate of ϵ (0.97) from Przibram & Megušar's data (1912) is associated with some lower growth ratios (minimum = 1.03).

(d) Dyar's Rule explained?

The predicted ranges in growth ratio in table 5 all include $u^{\frac{1}{3}}$ (the value for which our model predicted no change in growth ratio through development; see figure 2). This implies that both increases and decreases in growth ratio through development are still to be expected. However, because the limits to these ranges are quite close to $u^{\frac{1}{3}}$ we do not expect to observe dramatic changes in growth ratio through development when the number of instars is optimized. For instance when the number of moults is five, $\alpha = \frac{2}{3}$ and $\epsilon = 0.8$, the maximum change in growth ratio is either from 1.199 to 1.222 or from 1.277 to 1.255. Such small changes in empirical data subject to measurement error would tend to be interpreted as constancy of growth ratio. Therefore, the Investment Principle provides an adaptive explanation for Dyar's Rule, providing the number of instars is optimized.

The argument may still apply to a lesser extent if the number of instars does not vary facultatively, but is subject to evolutionary optimization. The fixed number of instars that has evolved will be one that is

optimal given average ecological parameters. As just noted, the Investment Principle predicts that the optimal number of instars is one in which the growth ratio is close to $\hat{u}^{\frac{1}{3}}$. Thus under near-average environmental conditions the growth ratio will not change much through development, although extreme environmental conditions will result in growth ratios beyond the limits that we have just calculated (when a slightly different number of instars would be optimal but is not realized). Even then, however, the range of growth ratios will be less than had the number of instars been fixed at some other value.

It is worth emphasizing that it is not obvious why \hat{u} lies within the limits in table 5. Before calculating these limits we wondered if, for some parameter values, \hat{u} would lie outside the limits, in which case growth ratios would always either decrease or increase. We still have no intuitive explanation for why in fact \hat{u} does lie within the limits and thus why a moulting pattern close to Dyar's Rule is optimal.

When there is a risk of mortality associated with moulting, or if there is a time penalty associated with moulting, fewer moults will be optimal and thus larger growth ratios are predicted. However, the Investment Principle will still favour an extra instar being incorporated if growth ratios would otherwise be particularly large, so it will still tend to restrict the range of growth ratios; Dyar's Rule may still appear to be observed. But because growth ratios are larger than they would be without these extra costs to moulting, growth ratios will tend to be above $\hat{u}^{\frac{1}{3}}$. As α is usually below 1 (as evidenced by the usual increase in instar durations through development, see above), growth ratios will thus usually decline through development. Roughly constant growth ratios, but with a marked tendency to decline slightly through development, is exactly the pattern that we observed from table 4. Again this argument still works if the number of instars does not now vary facultatively but if the fixed number used has been evolutionarily optimized.

(e) *Robustness*

We checked how robust these patterns were when the growth equation incorporated a metabolic cost scaling with size differently to energy assimilation. As described in an earlier section, over a fivefold change in linear dimensions, metabolic costs were changed from 25% to 45% of energy assimilation (or vice versa). With a fixed number of instars, as the time taken to mature is increased a monotonic increase in growth ratio with each moult changes to a monotonic decrease; the intermediate case is a non-monotonic change (see §6*a*). When the number of instars is optimized, as the time taken to mature is increased it can become optimal to fit in an extra instar before the monotonic decrease arises (with the extra instar, growth ratios again are smaller and increase each moult). Thus, in such cases we would mostly observe increases in growth ratio each moult. This is opposite to the trend observed in nature (table 4), but we have not checked enough growth equations to be sure that others do not predict that mostly decreases should be observed.

With non-power-law growth equations and optimized number of instars, the range of growth ratios predicted with a particular number of instars is no longer independent of x_0 . However, with the growth equations investigated, a twofold change in x_0 only affected these ranges at the third decimal place.

Size-dependent mortality will also affect the ranges in growth ratio predicted in table 5 and whether increases in growth ratio are more or less likely than decreases.

9. CONCLUSIONS

We have explained how the Investment Principle means that there is an optimum duration of each instar and an optimum number of instars. The question is whether this is what determines instar durations in nature; our review of the literature explained other factors that might have a more important influence on instar durations and growth ratios. In some arthropods the Investment Principle may be totally inapplicable, because their feeding rate does not depend on the size of structures that grow discontinuously (Reynolds 1990).

One line of evidence is our calculation that the selective advantage of following an optimal strategy is typically about 1% over following Dyar's Rule. This is potentially enough to drive animals away from Dyar's Rule, but suggests that other selective consequences could outweigh the Investment Principle. On the other hand, the selective advantage of the Investment Principle optimum will be much higher compared with some alternative policies (e.g. equal time in each instar), so we would expect the Investment Principle to be important in restricting what other moulting strategies can evolve.

Our observational evidence for the Investment Principle was not particularly strong. The relation between one growth ratio and the next differed between different diets in the *Nephila* data, and there were frequent exceptions to our prediction of monotonic trends in growth ratio and instar durations. It is impossible to say how much this failure of our predictions is a result of poor data collected for other purposes and of the absence of data on, for instance, size-dependent mortality; better data would permit a more sophisticated model and more specific predictions. A tendency for animals to moult only at a particular time of day will also be expected to introduce considerable noise. Given this constraint on time spent in an instar, it could still be the Investment Principle that determines how many days are spent in an instar, yet the patterns of growth ratios need not correspond very closely to that predicted by our analytic results. We also showed how the Investment Principle would affect the norms of reaction expected as environmental conditions vary or are manipulated. But it was impossible to make general predictions because the results depended so much on parameters that will vary between species and have rarely been measured. The same lack of data broadened the range of growth ratios that we predicted if the number of instars is optimized, but these predictions did look promising. In particular

we now have another adaptive explanation for why Dyar's Rule is often observed and why deviations from it are most commonly in the direction of a reduction of growth ratio through development.

Only partial agreement with our predictions is to be expected with simple models: real life is complex. This paper has demonstrated that, in realistically complicated models, parameters can be chosen to make the Investment Principle generate realistic moulting patterns. Therefore we hope that this paper will inspire empiricists to gather the data to test the Investment Principle more stringently. All there is at present are fragments of relevant data collected on hundreds of species, but in no species is the whole picture well understood. Moreover, data on more than one species are required; the answer will not be that the Investment Principle is right or wrong, but that it is important in this type of animal, less important in that type, and inapplicable in others. When further data are available it will be worth developing the theory further, in particular to incorporate stochasticity in the food availability.

Thanks to Steve Simpson, Dieter Ebert and several referees for commenting on the manuscript. J. M. C. H. was funded by an SERC research grant to J. M. McN.

REFERENCES

- Bennet-Clark, H. C. 1971 The cuticle as a template for growth in *Rhodnius prolixus*. *J. Insect Physiol.* **17**, 2421–2434.
- Bernardo, J. 1993 Determinants of maturation in animals. *Trends Ecol. Evol.* **8**, 166–173.
- Bodenheimer, F. S. 1933 The progression factor in insect growth. *Q. Rev. Biol.* **8**, 92–95.
- Brown, V. & Davies, R. G. 1972 Allometric growth in two species of *Ectobius* (Dictyoptera: Blattidae). *J. Zool.* **166**, 97–132.
- Calow, P. 1977 Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* **52**, 385–409.
- Calvert, P. P. 1929 Different rates of growth among animals with special reference to the Odonata. *Proc. Am. phil. Soc.* **68**, 227–274.
- Clarke, K. U. 1957 On the increase in linear size during growth in *Locusta migratoria* L. *Proc. R. ent. Soc. Lond. A* **32**, 35–39.
- Cole, B. J. 1980 Growth ratios in holometabolous and hemimetabolous insects. *Ann. ent. Soc. Am.* **73**, 489–491.
- Daly, H. V. 1985 Insect morphometrics. *A. Rev. Entomol.* **30**, 415–438.
- Dyar, H. G. 1890 The number of moults of lepidopterous larvae. *Psyche, Camb.* **5**, 420–422.
- Eadie, J. McA., Broekhoven, L. & Colgan, P. 1987 Size ratios and artifacts: Hutchinson's rule revisited. *Am. Nat.* **129**, 1–17.
- Ebert, D. 1994 A maturation size threshold and phenotypic plasticity of age and size of maturity in *Daphnia magna*. *Oikos* **69**, 309–317.
- Enders, F. 1976 Size, food-finding, and Dyar's constant. *Environ. Ent.* **5**, 1–10.
- Freeman, J. A. 1990 Molt increment, molt cycle duration, and tissue growth in *Palaemonetes pugio* Holthius larvae. *J. exp mar. Biol. Ecol.* **143**, 47–61.
- Gaines, J. C. & Campbell, F. L. 1935 Dyar's rule as related to the number of instars of the corn ear worm, *Heliothis obsoleta* (Fab.), collected in the field. *Ann. ent. Soc. Am.* **28**, 445–461.
- Griffiths, D. 1992 Size, abundance and energy use in communities. *J. Anim. Ecol.* **61**, 307–315.
- Hutchinson, G. E. 1959 Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159.
- Hutchinson, G. E. & Tongring, N. 1984 The possible adaptive significance of the Brooks-Dyar rule. *J. theor. Biol.* **106**, 437–439.
- Jones, D., Jones, G. & Hammock, B. D. 1981 Growth parameters associated with endocrine events in larval *Trichoplusia ni* (Hübner) and timing of these events with developmental markers. *J. Insect Physiol.* **27**, 779–788.
- Klingenberg, C. P. & Zimmermann, M. 1992 Dyar's rule and multivariate allometric growth in nine species of waterstriders (Heteroptera: Gerridae). *J. Zool.* **227**, 453–464.
- Lampert, W. 1977 Studies of the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. II. The dependence of carbon assimilation on animal size, food concentration and diet species. *Arch. Hydrobiol. (Suppl.)* **48**, 310–335.
- Ludwig, D. 1934 The progression factor in the growth of the Japanese Beetle (*Popilla japonica* Newman) (Coleop.: Scarabaeidae). *Ent. News* **45**, 141–153.
- Lynch, M. 1989 The life history consequences of resource depression in *Daphnia pulex*. *Ecology* **70**, 246–256.
- MacNally, R. C. 1988 On the statistical significance of the Hutchinsonian size-ratio parameter. *Ecology* **69**, 1974–1982.
- Nijhout, H. F. 1979 Stretch-induced moulting in *Oncopeltus fasciatus*. *J. Insect Physiol.* **25**, 277–281.
- Nijhout, H. F. 1981 Physiological control of molting in insects. *Am. Zool.* **21**, 631–640.
- Peet, W. B. Jr 1979 Description and biology of *Nidicola jaegeri*, n. sp., from southern California (Hemiptera: Anthocoridae). *Ann. ent. Soc. Am.* **72**, 430–437.
- Peters, R. H. 1983 *The ecological implications of body size*. Cambridge University Press.
- Press, W. H., Flannery, B. P., Teukolsky, S. A. & Vetterling, W. T. 1988 *Numerical recipes in C*. Cambridge University Press.
- Przibram, H & Megusar, F. 1912 Wachstumsmessungen an *Sphodromantis bioculata* Burm. 1. Länge und Masse. *Arch. EntwMech. Org.* **34**, 680–741.
- Reiss, M. J. 1989 *The allometry of growth and reproduction*. Cambridge University Press.
- Reynolds, S. E. 1990 Feeding in caterpillars: maximising or optimizing food acquisition? In *Animal nutrition and transport processes. I. Nutrition in wild and domestic animals* (ed. J. Mellinger), pp. 106–118. Basel: Karger. *Comp. Physiol.* **5**, 106–118.
- Rice, A. L. 1968 Growth 'rules' and the larvae of decapod crustaceans. *J. nat. Hist.* **2**, 525–530.
- Richards, O. W. 1949 The relation between measurements of the successive instars of insects. *Proc. R. ent. Soc. Lond. A* **24**, 8–10.
- Rummel, J. D. & Roughgarden, J. 1985 A theory of faunal buildups for competition communities. *Evolution* **39**, 1009–1033.
- Schroeder, L. A. 1981 Consumer growth efficiencies - their limits and relationships to ecological energetics. *J. theor. Biol.* **93**, 805–828.
- Sehnal, F. 1966 Kritisches Studium der Bionomie und Biometrik der in verschiedenen Lebensbedingungen gezüchteten Wachsmotte, *Galleria mellonella* L. (Lepidoptera). *Z. wiss. Zool.* **174**, 53–82.
- Sehnal, F. 1985 Growth and life cycles. In *Comprehensive insect physiology, biochemistry and pharmacology* (ed G. A. Kerkut & L. I. Gilbert), pp. 1–86. Oxford: Pergamon Press.

- Sheldon, R. W., Prakash, A. & Sutcliffe, W. H. Jr 1972 The size distribution of particles in the ocean. *Limnol. Oceanogr.* **17**, 327–340.
- Simpson, S. J. & Simpson, C. L. 1990 The mechanisms of nutritional compensation by phytophagous insects. In *Insect-plant interactions*, vol. 2 (ed. E. A. Bernays), pp. 110–160. Boca Raton, Florida: CRC Press.
- Solow, A. R. & Faber, D. B. 1995 A test of Prizbram's rule. *J. Zool.* **237**, 159–161.
- Stork, N. E. & Blackburn, T. 1993 Abundance, body size and biomass of arthropods in tropical forest. *Oikos* **67**, 483–489.
- Tanaka, A. 1981 Regulation of body size during larval development in the German cockroach, *Blattella germanica*. *J. Insect Physiol.* **27**, 587–592.
- Tanaka, K. 1992 Size-dependent survivorship in the web-building spider *Agelena limbata*. *Oecologia* **90**, 597–602.
- Vollrath, F. 1983 Relative and absolute growth in *Nephila clavipes* (Arachnida: Araneae: Argiopidae). *Verh. naturw. Ver. Hamb.* **26**, 277–289.
- Wigglesworth, V.B. 1972 *The principles of insect physiology*, 7th edn. London: Chapman and Hall.

Received 15 February 1996; accepted 29 September 1996

APPENDIX 1

This section describes the principles behind the numerical calculation of optimal instar durations and number of instars. We hope that workers with their own observations can reconstruct or amend our computer program so as to further test the ideas in this paper. (The program is available from J.M.C.H.) The main principle utilized is dynamic programming.

The idea is to deal with each instar at a time, starting with the last instar and working backwards. We consider a restricted range of calendar times and sizes at which the animal can start each instar; $0 \leq t \leq t_{\text{MAX}}$, $0 \leq x \leq x_{\text{MAX}}$. Within these ranges we consider a discrete two-dimensional grid of equally spaced points. For each such point we associate a fitness ($F_i(x, t)$) with moulting to start instar i at size x and time t . In the case of the last (N th) instar, we directly specify this fitness, for instance as

$$F_N(x, t) = x^\beta \exp(-\theta t).$$

Fitness values of earlier instars are calculated as explained presently.

It is necessary to interpolate fitness values between the grid points. We do this by means of cubic splines. Programs given in Press *et al.* (1988) calculate the second derivatives of $F_i(x, t)$ at all grid points, so that it is then fast to interpolate fitness values at intermediate sizes and times. Cubic splines will only function satisfactorily for our purposes if the fitness function specified shows no sharp discontinuities and no large areas of uniform value (otherwise the function reconstructed by the cubic spline may oscillate between the grid points, which disrupts the localization of true maxima). Thus it is best not to specify $F_N(x = 0, t) = 0$, unless this is compatible with adjacent fitness values. Also, the range of the grid must extend well beyond the optimal x or t values. It is often more accurate to make x_{MAX} twice as large as the optimal final size than to use

the same number of grid points in a finer grid extending less widely. To guard against artefacts caused by using cubic splines we report only results that are consistent when finer and wider grids are used.

Once we have thus specified the fitness values of starting the last instar at any size and time, we consider in turn each grid point, each specifying a starting size and time for the penultimate instar. For each grid point we search the range of possible instar durations to find the maximum fitness value achievable. Each duration will determine the time of the subsequent moult and the size of the next (last) instar, given which we calculate $F_i(x, t)$ using the cubic-spline interpolation. This value is discounted by predation over the duration of the instar or at the moult, giving the fitness value associated with a particular instar duration.

We now express this more formally in terms of the dynamic programming equations. The fitness resulting from spending a duration of d in the i th instar, when that instar is commenced with a size x at time t , is

$$H_i(x, t, d) = e^{-\theta(x)d} F_{i+1}(s(x, d), t + d).$$

Here $\theta(x)$ is the size-dependent mortality rate. If the animal enters one instar at size x and spends a duration d in that instar, $s(x, d)$ is the size of the next instar; equation (1) is an example of such a function. When no skipping of instars is allowed the fitness under the optimal policy is simply

$$F_i(x, t) = \max_a H_i(x, t, d).$$

The duration giving the maximum fitness is found using the routine `brent()` given in Press *et al.* (1988). This routine requires the optimum duration to be bracketed. For one end of the range we use a duration of 0, and the other end is usually limited by the size of the grid (i.e. $0 < d < t_{\text{MAX}} - t$). `brent()` also requires a value from which to start the search; we normally use the optimum duration for an adjacent grid point. A limitation of this numerical approach is that any local optimum may prevent location of the true optimum. This means that only unimodal fitness functions can be specified for the final instar; for instance, we would have to amend the program for an animal that produces some offspring if it matures in the autumn, no offspring if it matures in the winter and some offspring if it matures in the following spring.

Having found the optimal duration, we have the option then to compare the associated fitness value with the fitness value if a moult was missed completely (i.e. the fitness value if the animal started the next instar at the same size and time as the present instar). This is not the same as the fitness value of moulting after a duration of 0, as there is a cost to moulting in terms of material lost or extra mortality. By providing this option we can simultaneously find the optimal number of instars as well as the optimal duration in each (so long as we allow so many instars that at least one is skipped).

For each starting x and t for the i th instar we store the optimal duration (or whether it is better to skip the instar) and the corresponding fitness value. This new

array of fitness values is then fitted by cubic splines and used to find the optimal durations for all starting sizes and times in the $(i-1)$ th instar. The process is repeated, working backwards one instar at a time, until the optimal policies for all starting sizes and times in every instar have been calculated.

Having used dynamic programming to find the optimal policy in all states, we then work forward in time from a chosen size and time in the first instar. Given a particular size and time of moulting into one instar, we can read (from the stored table of optimal policies just calculated) the appropriate duration to be spent in that instar; this is used to calculate the size and time of moulting into the following instar. Dynamic programming calculates the optimum policy only when starting each instar at a grid point, so optimal durations for values of size and time of moult between grid points must be found by interpolation. Here we use linear interpolation. For simplicity, when the optimal policy at any of the four surrounding grid points is not a duration but the decision to skip an instar, we skip an instar.

In the main text we point out that it is likely that many arthropods are constrained to moult at a particular time of day. If we incorporate this constraint, the dynamic programming is simplified considerably. The time grid is now in units of 24 hours and there is no need to construct cubic splines or to find the maxima by successive approximation. Instead it is simple to test out all possible numbers of days to be spent in each instar up to a maximum $t_{\text{MAX}} - t$. Unlike with cubic splines this method is unaffected by sharp discontinuities and multiple local optima in the fitness function, and so might be used even when moulting can occur at any time of day. The time grid would then be made finer than 24 hours.

APPENDIX 2

(a) Optimal change in growth ratio

We initially generalize the power-law growth equation (1) to

$$x_{i+1} = \epsilon x_i + h(x_i) d_i,$$

where $h(x_i)$ is some function of x_i .

Consider an arthropod whose instar durations $d_0, d_1 \dots d_{N-1}$ are optimal. By this we mean that adult size is maximized given that a specified total time is available for growth. Let x_0 be the initial size after hatching and $x_1, x_2 \dots x_N$ be the sizes after successive moults under this optimal strategy. Focus on any instar i where $0 \leq i \leq N-2$. Then the size of the i th instar is x_i and the total duration of that instar and the next is $d_i + d_{i+1}$. We define T to be this total duration. Any instar durations D_i and D_{i+1} (not necessarily optimal) such that $D_i + D_{i+1} = T$ must give a size X_{i+2} of the $(i+2)$ th instar which is less than or equal to x_{i+2} given by the optimal durations d_i and d_{i+1} .

For given D_i and $D_{i+1} = T - D_i$ the sizes of the $(i+1)$ th and $(i+2)$ th instar are X_{i+1} and X_{i+2} , where

$$\begin{aligned} X_{i+1} &= \epsilon X_i + h(X_i) D_i, \\ X_{i+2} &= \epsilon X_{i+1} + h(X_{i+1})(T - D_i). \end{aligned} \tag{A 2.1}$$

Differentiating these with respect to D_i gives

$$\begin{aligned} X'_{i+1} &= h(X_i), \\ X'_{i+2} &= \epsilon X'_{i+1} + h'(X_{i+1}) X'_{i+1} (T - D_i) - h(X_{i+1}). \end{aligned}$$

Eliminating X'_{i+1} gives

$$X'_{i+2} = h(X_i)[\epsilon + h'(X_{i+1})(T - D_i)] - h(X_{i+1}).$$

When $X'_{i+2} = 0$, X_{i+2} is maximized, implying that $D_i = d_i, D_{i+1} = d_{i+1}, X_{i+1} = x_{i+1}$, and $X_{i+2} = x_{i+2}$. So we set $X'_{i+2} = 0$, to give

$$h(x_i)[\epsilon + h'(x_{i+1})(T - d_i)] = h(x_{i+1}).$$

Rearranging (A 2.1), and putting instar durations and sizes to their optimal values, also gives

$$(T - d_i) = (x_{i+2} - \epsilon x_{i+1}) / h(x_{i+1}).$$

Thus, substituting this into the preceding equation,

$$\begin{aligned} \epsilon + (x_{i+2} - \epsilon x_{i+1}) h'(x_{i+1}) / h(x_{i+1}) &= h(x_{i+1}) / h(x_i) \\ \Rightarrow \epsilon + (x_{i+2} / x_{i+1} - \epsilon) x_{i+1} h'(x_{i+1}) / h(x_{i+1}) &= h(x_{i+1}) / h(x_i). \end{aligned}$$

In the special case of the power-law growth equation (1), $h(x) = fx^\alpha$

$$\begin{aligned} \Rightarrow \epsilon + (x_{i+2} / x_{i+1} - \epsilon) \alpha &= (x_{i+1} / x_i)^\alpha \\ \Rightarrow x_{i+2} / x_{i+1} &= \epsilon + [(x_{i+1} / x_i)^\alpha - \epsilon] / \alpha \\ \Rightarrow u_{i+1} &= \epsilon + (u_i^\alpha - \epsilon) / \alpha. \end{aligned} \tag{A 2.2}$$

We define the function $g(u)$ as

$$g(u) = \epsilon + (u^\alpha - \epsilon) / \alpha,$$

so that, under the optimal policy, $u_{i+1} = g(u_i)$. It is straightforward to prove the following if $\epsilon < 1$ (animal loses mass when it moults) and $u > 1$ (animal is growing):

- (i) if $\alpha = 1$, then $g(u) = u \Rightarrow$ growth ratios constant;
- (ii) if $\alpha < 1$, then $g(1) > 1, g'(u) < 1$, and $g'(u) \rightarrow 0$ as $u \rightarrow \infty$ (which implies that the graph of $g(u)$ against u starts above and then crosses the identity line once as in figure 2a);
- (iii) if $\alpha > 1$, then $g(1) < 1, g'(u) > 1$, and $g'(u) \rightarrow \infty$ as $u \rightarrow \infty$ (which implies that the graph of $g(u)$ against u starts below and then crosses the identity line once as in figure 2b).

It is then apparent from figure 2 that when $\alpha < 1$ u_i s will converge to \hat{u} , and when $\alpha > 1$ u_i s will diverge from \hat{u} .

(b) Optimal change in instar duration

We now consider how durations change. The power-law growth equation (1) is

$$\begin{aligned} x_{i+1} &= \epsilon x_i + f x_i^\alpha d_i \\ \Rightarrow d_i &= (x_{i+1} - \epsilon x_i) / (f x_i^\alpha) \\ &= (x_{i+1} / x_i - \epsilon) / (f x_i^{\alpha-1}) \\ &= (u_i - \epsilon) / (f x_i^{\alpha-1}) \end{aligned} \tag{A 2.3}$$

$$\Rightarrow d_{i+1} / d_i = u_i^{1-\alpha} (u_{i+1} - \epsilon) / (u_i - \epsilon). \tag{A 2.4}$$

But equation (2) states:

$$u_{i+1} = \epsilon + (u_i^\alpha - \epsilon) / \alpha.$$

Thus

$$\begin{aligned} d_{i+1}/d_i &= u_i^{1-\alpha} [(u_i^\alpha - \epsilon)/\alpha]/(u_i - \epsilon) \\ &= (1/\alpha)(u_i - \epsilon u_i^{1-\alpha})/(u_i - \epsilon). \end{aligned}$$

We define the function $B(u)$ as

$$\begin{aligned} B(u_i) &= d_{i+1}/d_i - 1 \\ \Rightarrow B(u_i) &= [u - \epsilon u^{1-\alpha} - \alpha(u - \epsilon)]/[\alpha(u - \epsilon)] \\ &= [\alpha\epsilon + (1 - \alpha)u - \epsilon u^{1-\alpha}]/[\alpha(u - \epsilon)]. \end{aligned}$$

Now $\alpha(u - \epsilon) > 0$ (because we consider only $\alpha > 0$, $u > 1$ and $\epsilon < 1$).

Therefore $B(u_i) > 0 \Leftrightarrow b(u) > 0$, $B(u) < 0 \Leftrightarrow b(u) < 0$, and $B(u) = 0 \Leftrightarrow b(u) = 0$, where

$$b(u) = B(u) [\alpha(u - \epsilon)] = \alpha\epsilon + (1 - \alpha)u - \epsilon u^{1-\alpha}.$$

Now

$$\begin{aligned} b(1) &= (1 - \alpha)(1 - \epsilon) \\ \Rightarrow b(1) &> 0 \text{ if } \alpha < 1, b(1) < 0 \text{ if } \alpha > 1, \text{ and} \\ b(1) &= 0 \text{ if } \alpha = 1 \text{ (because } \epsilon < 1). \end{aligned} \quad (\text{A 2.5})$$

Also, differentiating with respect to u ,

$$\begin{aligned} b'(u) &= (1 - \alpha)(1 - \epsilon u^{-\alpha}) \\ \text{and} \\ (1 - \epsilon u^{-\alpha}) &> 0 \text{ (because } \epsilon < 1, u > 1 \text{ and } \alpha > 0), \\ \Rightarrow b'(u) &> 0 \text{ if } \alpha < 1, b'(u) < 0 \text{ if } \alpha > 1, \text{ and} \\ b'(u) &= 0 \text{ if } \alpha = 1. \end{aligned} \quad (\text{A 2.6})$$

Therefore, taking (A2.5) and (A2.6) together, for all $u > 1$,

- (i) $\alpha < 1 \Rightarrow b(u) > 0 \Rightarrow B(u) > 0 \Rightarrow d_{i+1} > d_i$
- (ii) $\alpha > 1 \Rightarrow b(u) < 0 \Rightarrow B(u) < 0 \Rightarrow d_{i+1} < d_i$
- (iii) $\alpha = 1 \Rightarrow b(u) = 0 \Rightarrow B(u) = 0 \Rightarrow d_{i+1} = d_i$

APPENDIX 3

This appendix develops a statistical test to investigate whether consecutive growth ratios relate to each other as specified by equation (2), and in particular to test the prediction that the parameters of the relationship do not differ between individuals or instars. We explain in the main text that the essence of our approach is to fit curved lines through a scatter plot such as figure 3, and to compare the residual mean squares as in an analysis of covariance.

Suppose that data exist recording sizes of successive instars in J animals. Let $u_{i,j}$ denote the ratio of sizes (weights) of instar $i+1$ to instar i for the j th animal. The data on all J animals need not be complete and/or different individuals may go through different numbers of instars before maturity. We suppose that for animal j the n_j instar ratios $u_{1,j}, u_{2,j}, \dots, u_{n_j,j}$ are recorded.

Under the exact model in the text

$$\begin{aligned} u_{i+1,j} &= \kappa + u_{i,j}^\alpha/\alpha \quad \text{for } i = 1, \dots, n_j - 1, \\ &\text{and for } j = 1, \dots, J \end{aligned} \quad (\text{A 3.1})$$

where $\kappa = \epsilon - \epsilon/\alpha$. There are various ways in which this relationship might be subject to error, and hence

various ways a statistical analysis might be performed. If there is measurement error one might assume that the relationship (A 3.1) is exact and one is observing $v_{i,j}$ rather than $u_{i,j}$ where $v_{i,j} = u_{i,j} + \eta_{i,j}$ and $\eta_{i,j}$ is the measurement error. We do not take this approach here. Instead we assume that equation (A 3.1) is not exact and that there is error in the true growth increments such that

$$\begin{aligned} u_{i+1,j} &= \kappa + u_{i,j}^\alpha/\alpha + \delta_{ij} \quad \text{for } i = 1, \dots, n_j - 1, \\ &\text{and for } j = 1, \dots, J \end{aligned} \quad (\text{A 3.2})$$

where the $\delta_{i,j}$ s are independent error terms. Under this assumption an error in the growth increment in one instar affects the size and hence growth ratios in subsequent instars, but given a particular growth ratio, $u_{i,j}$, subsequent growth is independent of past errors.

(a) Estimation of α and κ

Assuming model (A 3.2) we can estimate α and κ by regressing u_{i+1} on u_i for all instars and animals, finding parameter values which minimize error sum of squares. If α and κ are estimated by a and k respectively, the error sum of squares is

$$S(a, k) = \sum_{j=1}^J \sum_{i=1}^{n_j-1} [u_{i+1,j} - (k + u_{i,j}^a/a)]^2.$$

Let $\tilde{k}(a)$ be the value of k which minimizes this quantity for fixed a . By setting $\delta S(a, \tilde{k}(a))/\delta k = 0$ it is easily seen that

$$\tilde{k}(a) = \frac{1}{M} \sum_{j=1}^J \sum_{i=1}^{n_j-1} [u_{i+1,j} - (k + u_{i+1,j}^a/a)]$$

where

$$M = \sum_{j=1}^J n_j - J. \quad (\text{A 3.3})$$

Having minimized over k for fixed a , we can treat $S(a, \tilde{k}(a))$ as a function of the single variable a and seek the value $\hat{\alpha}$ of a which minimizes this function. That is

$$S(\hat{\alpha}, \tilde{k}(\hat{\alpha})) = \min_a S(a, \tilde{k}(a)).$$

This minimization needs to be computed numerically because $S(a, \tilde{k}(a))$ is an awkward non-linear function of a . The least-squares estimates of α and κ are then $\hat{\alpha}$ and $\hat{\kappa} = \tilde{k}(\hat{\alpha})$. The residual sum of squares after fitting the best regression line is $Q_0 = S(\hat{\alpha}, \hat{\kappa})$.

Note that model (A 3.2) assumes that $u_{i+1,j}$ is an increasing function of $u_{i,j}$ whatever the values of α and κ . In the limit as $\alpha \rightarrow -\infty$, $u_{i+1,j}$ becomes constant. The model cannot fit a negative relationship between $u_{i+1,j}$ and $u_{i,j}$.

(b) Testing for other forms of the dependence of u_{i+1} on u_i

Model (A 3.2) assumes that there is no effect of instar on the relationship between consecutive growth ratios. To test for an effect of instar we test

H_0 : α and κ constant (i.e. model A 3.2)

versus H_1 : α and κ depend on i .

Under hypothesis H_1 the model is

$$u_{i+1,j} = \kappa_i + u_{i,j}^\alpha / \alpha_i + \delta_{i,j}.$$

Let J_i denote the number of animals for which the two instar ratios $u_{i,j}$ and $u_{i+1,j}$ are recorded. The appropriate estimates for α_i and κ_i can be made separately for each i as follows. For given a_i set

$$\tilde{k}_i(a_i) = \frac{1}{J_i} \sum_j (u_{i+1,j} - u_{i,j}^\alpha / \alpha_i)$$

where the sum is over all animals for which $u_{i,j}$ and $u_{i+1,j}$ are recorded. Set

$$S_i(a_i, \tilde{k}_i(a_i)) = \sum_j [u_{i+1,j} - (\tilde{k}_i(a_i) + u_{i,j}^\alpha / a_i)]^2.$$

Then the least-squares estimate $\hat{\alpha}_i$ for α_i satisfies

$$S_i(\hat{\alpha}_i, \tilde{k}_i(\hat{\alpha}_i)) = \min_{\alpha_i} S_i(a_i, \tilde{k}_i(a_i))$$

and the least-squares estimate for κ_i is given by

$$\hat{\kappa}_i = \tilde{k}_i(\hat{\alpha}_i).$$

To form the residual sum of squares let

$$I = \max_j n_j.$$

Then α_i and κ_i have been estimated for $i = 1, \dots, I-1$. Set

$$Q_1 = \sum_{i=1}^{I-1} S_i(\hat{\alpha}_i, \hat{\kappa}_i).$$

Then to test H_0 versus H_1 test

$$\frac{(Q_0 - Q_1) / (2I - 4)}{Q_0 / (M - 2)} \quad \text{as} \quad F_{2I-4, M-2}$$

where M is given by equation (A 3.3).

One can instead allow α and κ to differ between animals rather than between instars. In this case one calculates estimates for α and κ separately for each animal. The residual sum of squares is then the sum of the residual sum of squares for each animal.

APPENDIX 4

This derives the minimum value of u that should be observed if the animal can optimize the number of moults as well as how long to spend in each instar. The assumption is that the only penalty on moulting is the energy and material wasted.

Consider any two consecutive instars under an optimal strategy constrained by a fixed number of moults. The animal starts off at size x_i , moults once to size x_{i+1} and will attain size x_{i+2} after the second moult. The durations of the two instars are d_i and d_{i+1} . Thus

$$x_{i+1} = \epsilon x_i + x_i^\alpha d_i$$

and

$$x_{i+2} = \epsilon x_{i+1} + f x_{i+1}^\alpha d_{i+1}.$$

Suppose now that the animal can skip one moult; this will be optimal if by spending $d_i + d_{i+1}$ in the i th instar its size after a single moult exceeds x_{i+2} . That is, one instar is better than two if:

$$\begin{aligned} x_{i+2} &< \epsilon x_i + f x_i^\alpha (d_i + d_{i+1}) \\ &\Rightarrow \epsilon x_{i+1} + f x_{i+1}^\alpha d_{i+1} < x_{i+1} + f x_i^\alpha d_{i+1} \\ &\Rightarrow f d_{i+1} (x_{i+1}^\alpha - x_i^\alpha) < x_{i+1} (1 - \epsilon) \\ &\Rightarrow f d_{i+1} x_{i+1}^\alpha (1 - u_i^{-\alpha}) < x_{i+1} (1 - \epsilon) \\ &\Rightarrow (x_{i+2} - \epsilon x_{i+1}) (1 - u_i^{-\alpha}) < x_{i+1} (1 - \epsilon) \\ &\Rightarrow (u_{i+1} - \epsilon) (1 - u_i^{-\alpha}) < 1 - \epsilon \\ &\Rightarrow (u_i^\alpha - \epsilon) (1 - u_i^{-\alpha}) < \alpha (1 - \epsilon) \end{aligned}$$

(since under the optimal policy, from (A 2.2), $u_{i+1} = \epsilon + (u_i^\alpha - \epsilon) / \alpha$)

$$\Rightarrow (u_i^\alpha)^2 - [1 + \epsilon + \alpha(1 - \epsilon)] u_i^\alpha + \epsilon < 0. \quad (\text{A 4.1})$$

This is a quadratic in u_i^α ; the larger root is of interest to us and we call it w_i .

If a u_i is less than w_i it would be better to amalgamate the two instars into one. This is only the case if the next instar exists to be amalgamated, so it might be possible for the ratio of sizes at the last moult (u_{N-1}) to be less than w_i . Now w_i turns out to be always less than \hat{u} . When $\alpha < 1$ successive u_i s converge to \hat{u} ; thus u_{N-1} cannot be less than w_i if u_{N-2} is greater than w_i , and u_i s less than w_i should not be observed. (The values of this limit w_i are given in table 5a). But when $\alpha > 1$, u_i s diverge from \hat{u} , so u_{N-1} can be less than w_i without u_{N-2} being less than w_i , and thus without amalgamation being advantageous. To allow for this we put w_i into equation (A 2.2) to calculate a critical value for w_{i+1} ; this is the predicted lower limit for all u_i (used in table 5a where $\alpha > 1$).

The product of w_i and w_{i+1} is a growth ratio over two moults. For these critical values this is the same as the growth ratio obtainable by a single moult when the two instars are replaced by a single instar taking the same total time. This is the largest growth ratio that is optimal before it is better to split the instar into two. Table 5b gives these predicted upper limits.

We now go on to generalize this result, by comparing the size attainable in a particular time using N moults with that attainable using $N-1$ moults. A simple analytic solution is only possible when $\alpha = 1$. In other cases we find solutions numerically using the procedure described below. (The computer programs are available from J.M.C.H.) The aim is to find an initial growth ratio $w_0^{\frac{1}{N}}$ which, using N moults in total, leads to the same size increase in the same time as does an initial growth ratio of $v_0^{\frac{1}{N-1}}$ when only $N-1$ moults are used.

First we take an arbitrary value for w_0 and using equation (A 2.2) calculate successive values of w_i up to w_{N-1} . The product of these gives the overall growth increase after N moults. We then search for a value v_0 such that, when we have similarly calculated successive values of v_i using equation (A 2.2), the product of v_0 to v_{N-2} gives the same product as w_0 to w_{N-1} . To find v_0 we use the algorithm `zbrent()` given by Press *et al.* (1988).

We now have a pair of initial growth ratios that yield the same final size after either N or $N-1$ moults.

However, the two strategies will normally take different times. The time taken in the initial instar is calculated from equation (A 2.3), using arbitrary values for x_0 and f . The time in successive instars can then be calculated from equation (A 2.4) and these times summed to give the overall time taken to reach adulthood. Having calculated the time taken under both strategies, w_0 is adjusted successively until the difference in the times taken is zero. We again use `zbrent()` to find this root. Of course every time w_0 is adjusted a new v_0 achieving the same size increase must be calculated. (Note that x_0 and f appear in equation (A 2.3) but not in equation (A 2.4), so that whatever their values the times taken using both N moults and

$N-1$ moults are affected by the same factor. We are interested in the growth ratios when the two strategies take the same time, so x_0 and f do not affect the result.)

When both the final sizes and times taken are the same under the two strategies w_0 gives the lowest u_0 predicted if N moults are used and v_0 gives the highest u_0 if $N-1$ moults are used. As with $N=2$, it turns out that always $w_0 < \hat{u} < v_0$; thus when $\alpha < 1$ w_0 and v_0 are also the lower and upper limit for all u_i . When $\alpha > 1$, the lower and upper limit for all u_i are given by w_{N-1} and v_{N-2} . Table 5c gives the range of u_i predicted when five moults are used.