Resource Allocation: Exploring Connections between Foraging and Life History

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ESSAY REVIEW

Resource allocation: exploring connections between foraging and life history

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Foraging determines an organism’s intake of resources (water, nutrients or energy), while life-history patterns (survival, reproduction, growth) result from resource expenditure on fitness-related activities. Allocation of a limited resource pool among competing life-history traits links foraging and life-history strategies (Fig. 1). Although foraging, allocation and life history can be studied independently, they must be integrated in order to understand an organism’s ecology and population dynamics in contrasting or variable environments (Pianka 1976; Boggs 1981; Mooney & Chiarillo 1984; Gatto, Matessi & Slobodkin 1989). In particular, integration allows us to study ecological dynamics via the effects of input and output variation on the whole system through time.

Allocation is arguably both the most important and least understood element in the chain from foraging to life-history strategy. The physiological processes and the life-history effects of allocation have been studied extensively, but they have generally been examined separately. For example, life-history studies have examined correlations between offspring size and number, or among reproduction, storage, maintenance and growth, but have assumed a given resource intake and utilization efficiency (e.g. Cohen 1971; Smith & Fretwell 1974; Snell & King 1977; Reznick 1985; Parker & Begon 1986; Lloyd 1987; Reekie & Bazzaz 1987a–c). Physiological studies have focused on efficiencies of resource utilization, and resultant rates of growth or reproduction, but usually do not relate the results to integrated life-history strategies (e.g. Lei & Armitage 1980; Milne 1987; Briegel 1990; Glazier 1990). Foraging studies have considered patterns of resource intake in variable environments, but generally do not address resource use, even on further foraging effort (e.g. Chapin 1980; Real & Caraco 1986; Hutchings 1988; Tuttle, Wulffson & Caraco 1990). Here I argue that these three sorts of studies must be blended and expanded if we are to understand life-history strategies in variable resource environments.

Much life-history and resource allocation work has recently focused on the evolution of specific strategies, for which an understanding of the underlying genetic architecture is necessary (e.g. de Jong & van Noordwijk 1992). Ultimately, however, to integrate foraging, allocation and life-history traits, we need to understand not only the underlying genotypic covariance structure affecting allocation and hence constraining the relationships among traits, but also the ecological dynamics produced by relationships among traits in variable environments, and the physiological and developmental mechanisms producing those relationships. The primary focus of this paper is on ecological dynamics and considers phenotypic traits, but the reader should remember that genetic and developmental constraints are important.

To develop a framework that integrates foraging, allocation and life-history strategies in variable resource environments, I begin by reviewing what we know about ecological and physiological aspects of allocation. I consider effects of allocation decisions on life history and demography, and note biological constraints affecting these allocation decisions. Effects of environmental variation on foraging decisions, and hence on resource input to be allocated, are outlined. I then examine the physiology of allocation, focusing on the relationship between rates and efficiencies of growth or reproduction. With this background, I suggest an approach to understanding allocation that is based on physiological and ecological considerations, and conclude with ideas about how this can be used to understand an organism's life strategy.

A note on translating between plants and animals

Cross-fertilization of ideas concerning allocation between zoologists and botanists has not always been optimal. Difficulties arise from terminology differences that are due to differences between plants and animals in structure and function. The terminology used here tends to follow that of zoologists, since I belong to that group. ‘Resources’ include light, carbon, water and minerals for plants, or energy and specific nutrients for animals. ‘Foraging’ from a plant’s viewpoint includes photosynthesis as well as water and mineral uptake by roots.

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Life history and demography: theoretical studies of allocation effects

Resource availability and allocation control the life history of individuals, and hence demography of whole populations. Several theoretical approaches have been used to study the impacts of allocation decisions on life-history traits and hence on demography. One is based on physiological measurements of nutrient gain efficiency and allocation to life-history traits for specific organisms; a second is based on resource pools, using acquisition and allocation to study the relationships among life-history traits; a third is based on alterations in the underlying allocation trade-offs as a result of environmental stress; a fourth is based on covariation between survival and reproduction, which implies specific allocation trade-offs; and a fifth reverses the sequence, predicting allocation decisions associated with life-history traits.

First, demographic models specific to particular organisms have been developed, based on nutrient gain efficiency and allocation to growth, storage, maintenance or reproduction (e.g. Chiarello & Roughgarden 1984; Kooijman 1986; Hon 1988; Gatto et al. 1989; Iwasa & Cohen 1989; Kooijman, van der Hooven & van der Werf 1989; Gurney et al. 1990; Hallam, Lassiter & Suarez 1990; McCauley et al. 1990). The authors generally are seeking mechanistic explanations for observed fluctuations in population density or for life-history phenology of the organism in question. However, Gatto et al. (1989) go beyond this by delineating sets of strategies expected of any organism with a simple life cycle and minimal age structure in environments with differing frequency and duration of nutritional stress.

A second set of models has been formulated in response to the observation that some life-history traits can include a foraging component. Life-history strategies can only be understood in these cases in the context of the impact of these traits on the organism’s resource pool. For example, if males donate nuptial gifts to females at mating, then mating includes a meal for females. I have examined the effects of such gifts on female reproductive and foraging strategies, in the context of the female’s reproductive resource budget (Boggs 1990).

Also included within this type of model is recent work by de Jong & van Noordwijk (1992). They examine the life-history impact of variation at an ‘acquisition’ locus and at an ‘allocation’ locus, which divides resources between two traits. Aside from detailed analysis of genetic and phenotypic variances and covariances resulting from this scenario, de Jong & van Noordwijk show that polymorphisms at the acquisition locus are unlikely to be evolutionarily stable. Further, life histories in this system depend on primacy of resource allocation — whether resources are first used for reproduction, with the remainder allocated to survival, or vice versa. If reproduction has primacy, allocation is predicted to be all to one trait or the other at stability. If survival has primacy, the fraction allocated to each trait depends on the amount of resources present and population age structure and growth rate. This approach admirably combines a population-level genetic analysis with a physiological base, and points to the need for better understanding of allocation processes.

A third approach considers the effects on life history of environmental stress that alters the shape of life-history trade-off curves themselves. For example, Sibly & Calow (1989) examine factors that reduce growth rate or impose increased mortality. These factors not only result in alteration of energy expenditure on growth or defence, but may also alter the shape of the life-history trade-off curve since the organism no longer possesses its original physiological characteristics. Fitness maximization is then used by Sibly & Calow to determine new allocation patterns that are expressed as new optimal life-history trait combinations.

Fourth, models that only implicitly incorporate allocation have been developed. These ignore physiology but assume covariation between reproduction and survival in variable environments. For example, Orzack (1985) considers organisms with particular covariances between survival and reproduction, and with age-specific reproductive value curves. He asks whether reproductive plasticity (and implicitly, allocation shifts between survival and reproduction) is selectively favoured as a result of environmental stress occurring at a particular age. The stress is of specified duration and may be either positively or negatively autocorrelated with previous environmental stresses. The model does not assume a simple life cycle, but does assume that reproductive plasticity is governed by one locus.

Finally, some models consider the allocation decisions accompanying particular life-history strategies, rather than the reverse. For example, I predicted allocation of larval-derived resources to reproductive storage vs body building during metamorphosis in
holometabolous organisms, based on the expected resource intake and expenditure on life-history traits by the resulting adults (Boggs 1981).

Life history and demography: generalizations from empirical work

Empirical work has yielded two further generalizations about the relationship between life history and variation in resource availability. The first concerns the life-history effects of resource deprivation, and the second concerns the timing of the expression of those effects relative to the occurrence of the stress.

First, a quantitative reduction in availability of resources generally leads to a decrease in lifetime fecundity (even though the short-term response is to increase reproduction and die in some cases), but the effect on survival varies tremendously. In insects, reduction in available resources may result in an increase in life-span (possibly due to lowered basal metabolic rate) (e.g. Slansky 1980), no change (e.g. Wiedenmann & O'Neill 1990; Boggs & Ross 1992), a decrease (e.g. Adler 1989), or a variable response (e.g. Hill & Pierce 1989). This range of effects on survival suggests that allocation responses to resource variation differ among species, although variation in other processes, such as efficiencies of resource use in survival or control of metabolic rate, could also be important (D. Gordon, personal communication).

Several factors may account for the observed variation in survival in response to resource depression. These are not mutually exclusive.

1. In some studies, food was available ad libitum, but concentration varied. Thus, the relative amounts of different available nutrient types were altered. The results in these cases could be due to qualitative, rather than quantitative, diet changes.

2. Variation among species may be due to evolutionary history. Species may differ in normally experienced variability in the resource environment, such that selection may have favoured different survival strategies. This explanation has been proposed to account for observed life-history differences within and among species of water strider (Gerridae) in response to food stress (Kaitala 1987).

3. The timing of nutrient stress relative to developmental processes, including egg maturation, can affect life-history response, and might have differed among studies. The degree to which resources are re-allocated between survival and reproduction may depend on the baseline proportion of resources being allocated to reproduction and survival when the stress occurred. For example, timing of carbon limitation in an annual plant relative to the state of inflorescence development affects subsequent allocation patterns (Pyke 1989).

4. Resource intake varies through the life cycle, so that the actual intensity of a set stress may also vary with age. In at least two insect species, females alter either the quality or quantity of resource intake voluntarily in response to varying demand throughout a reproductive cycle (Haslett 1989; Schal & Bell 1982).

The second generalization derived from empirical work is that the relationship between timing of a nutrient stress and life-history expression of that stress varies. Costs of increased allocation to a particular life-history trait such as reproduction might be measured as decreases in values for another life-history trait, such as growth. These costs may be assessed on the organism's life-history immediately. Alternatively, the cost assessment may be delayed and expressed as decreased resilience to a new environmental stress either on the organism itself or on its offspring (e.g. Miao & Bazzaz 1990; Primack & Hall 1990). For example, de Souza Santos & Begon (1987) found that survival of female grasshoppers was affected by both past and present reproduction, indicating that costs can be assessed both immediately and on a delayed basis. In contrast, using male Drosophila, Partridge & Andrews (1985) found that survival costs of reproductive activity were short term only.

The relative timing of resource uptake and allocation to reproduction may determine the timing of expression of reproductive costs. Details of the costs of reproduction, then, might depend on whether an organism is an 'income' or 'capital' breeder, expending resources on reproduction as those resources are received or storing resources and expending them on offspring later (Sibly & Calow 1984, 1986).

A parallel argument can be made for costs of survival. A relatively long life-span may entail allocation both to building a sturdy body (Karlsson & Wickman 1989), and to maintenance metabolism. These extra demands could result in decreases in other life-history traits. Again, the impact and timing of the costs may depend on the relative timing of resource intake and expenditure on survival.

Life-style constraints affecting allocation and life history

The studies outlined above generally address life histories that are not biologically complicated. For many organisms, however, the relationship between allocation and life-history strategy can be constrained by what I term 'life styles'. These include occurrence of complex life cycles, commitment to production of highly durable body, unusual food sources or requirements, specialized defences and body size constraints on reproduction.

In organisms with complex life cycles, resources allocated to adult processes may derive from foraging in the juvenile and/or adult stages. The timing of resource acquisition may affect the life-history
strategy. For example, lepidopteran species range from those not feeding at all as adults to those feeding on very complex diets (Boggs 1987). This difference in the completeness of the adult diet, and hence in reliance on resources derived from larval feeding, is reflected in differences in age-specific reproductive patterns. Among species, as the adult diet becomes more complex, the age-specific fecundity curve lengthens and flattens (Boggs 1986). Details of the mechanistic causes of this relationship are as yet unknown, as are impacts on other life-history traits.

Life styles that require a commitment of resources to particular organ systems can constrain allocation and/or life-history strategies under normal or stressed nutritional conditions. For example, insects with reduced wings or no wings in the adult stage show an increase in fecundity or egg size and, in some cases, life-span as compared with winged individuals of the same species (e.g. Zera 1984; Kaitala 1988; Denno, Olimstead & McCloud 1989; Groeters & Dingle 1989; Zera & Rankin 1989). Commitment to the maintenance costs of diapause, or of long life-span in general, may also force increased allocation to maintenance and/or growth. Simply living an extended period of time, even if part of that time is at a reduced metabolic rate, may increase total basal metabolic costs. Organisms living longer periods may require sturdier bodies to withstand the wear and tear accompanying a longer life; longer-lived holometabolous insects increase allocation to somatic tissues at the expense of reproductive tissues during reorganization during metamorphosis (e.g. Boggs 1981; May 1985; Karlsson & Wickman 1989). Finally, Kindlmann & Dixon (1989) have postulated that a limit on developmental rate determines the optimum allocation ratio of resources to reproduction vs growth during larval development in an aphid.

A requirement for a scarce nutrient for successful reproduction, growth or survival may constrain allocation ratios among these traits. Suppose some scarce nutrient is needed for reproduction; amount of reproduction is limited by the availability of the scarce nutrient. The amounts of other nutrient types allocated to reproduction will be limited by the total amount of reproduction, so more nutrients will be available for other functions. Alternatively, organisms may shift foraging strategies, or alter storage patterns as a buffer against asynchrony in supply of particular resources. The buffering capacity of storage over several different time scales (e.g. daily, weekly, seasonal) has been considered in particular detail in plants (e.g. Bloom, Chapin & Mooney 1985; Chapin et al. 1987; Chapin, Schulze & Mooney 1990).

Survival depends on both body maintenance and defence. The requirement for allocation to defence should be dependent on life-span as well as environmental hazards, with longer life-span and larger hazards resulting in greater defence expenditures. Allocation to defence can also be dependent on both mean resource availability (e.g. Coley, Bryant & Chapin 1985) and on short-term environmental conditions. Bryant et al. (1987) showed that expenditure on defence by juvenile Alaska paper birch was lower under conditions of high soil nutrients or shading, whereas defence expenditures by juvenile green alders was not affected by these manipulations. The authors point out that these results support the idea that plant species will vary in their defence allocation flexibility, with early successional woody species normally found in good soils being more flexible than those found on poor soils.

Individual size may constrain allocation to growth, reproduction, maintenance and/or storage [see Calder (1984) for a thorough review]. Growth, even when exponential, depends on current body size or leaf area if surplus resources are available in the environment, since mouth size or leaf area limit intake rates. Thus, most analyses of insect growth rates for example, use mass-specific measures. Storage and reproduction can be limited by space available within the organism or strength of the supporting tissue. For example, Dunlap-Pianka (1979) showed that maximum daily fecundity is correlated with female body size in Heliconius charitonius butterflies, most likely due to space limitations in the ovaries. In a survey of tundra plants, Chapin & Shaver (1988) found that patterns of storage were affected by the ratio of storage tissue to new leaf tissue, among other factors. Maintenance expenditures related to survival, such as thermogenesis, can also be dependent on body size and shape, since heat loss is a function of those parameters.

Non-nutritional constraints due to limited opportunities for reproduction or growth may also affect allocation patterns. Pollination can limit reproductive allocation in some plant species (e.g. Snow 1986), and opportunity to mate, nest or lay eggs may limit reproductive allocation in some animal species (e.g. Springer & Boggs 1986). Likewise, a lack of vacant larger shells may constrain growth in hermit crabs that move into larger shells as the crabs get bigger (Bertness 1981).

**Foraging: source of resources to be allocated to life history**

I next consider foraging. Rate of resource input to an organism will depend on resources allocated to foraging activity and resource availability in the environment (Fig. 1). Extensive work on foraging in the context of allocation has been done for plants (e.g. Chapin 1980), but much less is known for animals and little has been generalized to all organisms. Nonetheless, there are at least three interesting avenues for research concerning the links between allocation and foraging. First, allocation to foraging could be affected by metabolic demand and age of the
while we can talk about number of offspring produced per unit time, reproductive efficiency measured as (number of offspring produced)/(number of offspring taken in) is nonsensical except in cases of cannibalism of offspring.

An allocation thus consists of input turned into output with some efficiency and at some rate. We can thus ask what the relationship is among resource input rate, efficiency of conversion to output and output rate. I define:

\[ P = \text{productivity} = \text{output to a given life-history trait}; \]
\[ A = \text{input to be allocated}; \]
\[ T = \text{time over which } P \text{ and } A \text{ are measured for a given organism}. \]

Then the rate of a particular trait (e.g. reproduction) is \( P/T \), the efficiency of that trait is \( P/A \), and the rate of input to be allocated is \( A/T \). The rate of input times efficiency equals the rate of output. Note that \( A \) must be assimilated energy or nutrients, in order not to confound rate and efficiency of assimilation with those of the trait under examination.

In the simplest case, input rate, \( A/T \), is constant (Fig. 2); then efficiency \( (P/A) \) is a linearly increasing function of output rate \( (P/T) \) and the slope is equal to \( T/A \), or the time over which a given resource input occurs. The line must go through the origin, since when either rate or efficiency is 0, \( P = 0 \), and both rate \( (P/T) \) and efficiency \( (P/A) \) must be 0.

How does changing the rate of resource input \( (A/T) \) affect the relationship between rate and efficiency of an allocation? Since the slope is equal to the inverse of the rate of resource input, increasing resource input rate will decrease the slope of the regression (Fig. 3). This means that, for a specified amount of output, at higher rates of input, rates of output are higher with lower efficiencies. If we were to examine reproductive rates and efficiencies for a single individual over a variety of resource input rates but with a maximum fecundity imposed by body size in all cases, we might therefore see a negative or no relationship between reproductive rate and efficiency.

Rates and efficiency of output both affect fitness

**Allocation: the relationship between power and efficiency**

I consider last our understanding of allocation, the central link in the foraging-allocation-life-history chain. Allocations, as based on metabolic processes, are associated with characteristic efficiencies and output rates. Power is the rate of output, e.g., of growth, offspring production, accumulation of stored nutrients, etc. Efficiency is the proportion of input converted into output. Measurement currency for allocation must be in units of nutrients or energy;

![Fig. 2. Graphical derivation of the relationship between rate and efficiency for a given rate of resource input (A/T).](image)

![Fig. 3. Relationship between rate and efficiency for different rates of resource input (A/T).](image)
Table 1. Relationships among rates and efficiencies of allocation to life-history traits. Equations were constructed using data from Lei & Armitage (1980). ‘Growth’ includes both their ‘growth’ and ‘exuvia’. Efficiencies were subject to arcsin-square root transformation to normalize distributions.

<table>
<thead>
<tr>
<th>Efficiency</th>
<th>Value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult reproductive efficiency</td>
<td>4487</td>
<td>(adult reproductive rate)</td>
</tr>
<tr>
<td></td>
<td>$F_{1,10} = 21.8, P = 0.0009$</td>
<td></td>
</tr>
<tr>
<td>Adult growth efficiency</td>
<td>9819</td>
<td>(adult growth rate)</td>
</tr>
<tr>
<td></td>
<td>$F_{1,10} = 40.5, P = 0.0001$</td>
<td></td>
</tr>
<tr>
<td>Juvenile growth efficiency</td>
<td>1698</td>
<td>(juvenile growth rate)</td>
</tr>
<tr>
<td></td>
<td>$F_{1,11} = 38.5, P = 0.0001$</td>
<td></td>
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</tbody>
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and thus are subject to natural selection to the extent that they are heritable. Smith (1976) suggested that natural selection can only maximize power at the expense of efficiency and vice versa. However, Watt (1986) showed that, within some limits, selection can act to maximize simultaneously power and efficiency of either a metabolic pathway or allocation to life-history traits, although selection need not operate this way.

Data available in the literature have not been collected with these ideas in mind, but nonetheless some of these propositions are supported. Lei & Armitage (1980) studied the energy budgets of *Daphnia ambigua* under a variety of temperatures and food availabilities. Genotype was not controlled, and some data are averages among genetically dissimilar individuals. Nonetheless, their data are consistent with the model developed above: adult reproductive efficiencies, growth efficiencies and juvenile growth efficiencies all are significantly positively dependent on their corresponding rates (Table 1). Urabe & Watanabe (1991) provide further evidence that growth rates and efficiencies in *Daphnia* change with food availability. Finally, to my knowledge, no definitive experiments examining effects of selection for power on evolution of efficiency (or vice versa) have been done.

Measurement of efficiency can be complicated if organisms store resources for later use in reproduction, growth or maintenance, particularly if both stored and newly acquired resources are used simultaneously. For example, Briegel (1990) showed that female mosquito reproductive rate and efficiency of utilization of a blood meal for oogenesis covary positively. However, if females used both the blood meal and stored reserves for egg production, the relationship between reproductive rate and efficiency was no longer positive — but estimated efficiencies were sometimes over 100%, because the calculations were not adjusted to take account of input from storage as well as current feeding.

There are two possible ways to address the problems posed by storage for calculating efficiencies. One is to calculate life-time efficiencies and rates, although this loses the resolution gained by considering age structure. Storage efficiency will also be subsumed as a contributor to reproductive, growth, etc. efficiency in this calculation. Alternatively, storage can be considered as a trait, similar to reproduction or growth, to which resources are allocated, and which can then serve as a source pool like incoming resources for re-allocation. This approach is more accurate in assessing actual biological costs and benefits of resource use. It has been used in optimal control models (e.g. Chiarello & Roughgarden 1984), but may be more difficult to implement experimentally, especially for animals where growth and storage may be difficult to distinguish on the basis of weight gain alone.

Another common complication in determining reproductive rates and efficiencies derives from parental care of offspring, or, in plants, translocation of resources from larger to smaller ramets (e.g. Bazzaz et al. 1987). For example, reproductive efficiency in mammals is often measured as growth of the offspring, based on energetic expenditure by the mother in lactation. This means that both efficiency of milk production by the mother and efficiencies of assimilation and growth by the offspring are combined into one term — ‘reproductive efficiency’. While positive relationships between efficiency and offspring growth rate are often found (e.g. Milne 1987; Glazier 1990), exactly what these mean in the present context is not clear.

The resulting central problem

We thus know something about the demographic and life-history effects of different resource allocation patterns, about foraging patterns and about physiological constraints on allocation. However, these have not been well integrated to yield a general model of the impact of temporal patterning of resource input on life history and demography. In particular, complications due to resource storage must be addressed. Such an analysis would enable us to examine interactions among foraging, allocation and life history, and to detect ecological and physiological constraints arising from those interactions. In the following, I outline a proposed framework that combines foraging, allocation and life history.

Proposed solution

I hypothesize that observed trade-offs among life-history traits are constrained by the relationship between power and efficiency for each trait. I then assume that allocation to foraging determines total resource income. Finally, I suggest that risk analysis, or study of response to variance, could be used to determine allocation to foraging in variable resource environments. Coherent sets of lifetime foraging, allocation, and life-history strategies specific to a given resource environment could then be generated using dynamic optimization.
growth and reproductive rates will depend on the relative efficiencies of the two processes at the resource levels available for each process. Further, as resources are shifted away from growth and into reproduction, efficiencies as well as rates will change, and the summed output as reproduction and growth may vary even though the total amount of resources to be allocated between the two functions remains constant.

This analysis gives us the relationship between any two or more life-history traits for a set amount of resources to be allocated. Expanding the analysis to consider variation in total resource availability, the relationships among life-history traits can be plotted against total amount of resources to be allocated, hence resource intake or foraging reward (e.g., Slobodkin, Dunn & Bossert 1987). Because efficiency is specific to each trait, the shape of the trade-off curve between any two or more life-history traits may vary with total amount of resources to be allocated (Fig. 5). However, values for a given trait should be constant for a given amount of resource, whether that amount represents the large or small fraction of the total resource available. For example, suppose 100 units of resource are available. If 5% of these units were allocated to a given life-history trait, the value of that trait should be the same as if 10 units were available and 50% were allocated to that trait.

We now have a different picture of life-history trade-offs than we would see if the original allocation efficiencies (that is, the ratio of output to total intake) were used. In the latter case, the trade-offs would be constrained to be linear, with a negative slope, since the sum of the allocations to all traits would have to equal the total intake. This constraint is relaxed when we consider the efficiency of each process, since some resource is lost from the system in the allocation process. The degree of loss for each trait will determine the degree of departure of the trade-off from linearity. How important such losses are remains to be tested. I know of no work examining

To begin, the relationships among rate of nutrient input, efficiency and rate of output should hold not only for total assimilated resources, but also for the subset of resources allocated to a specific life-history trait. That is, \( A \) was defined as assimilated resource available to be allocated among all traits, but could equally well have been defined as assimilated resource input to a single trait, such as reproduction. Efficiency then becomes the ratio of output to resources actually allocated to that trait; the difference between the two terms in the ratio is that resource 'wasted' through the metabolic pathways leading to the output.

The shape of observed trade-offs among life-history traits should be determined by the nature of the relationship between rate and this narrowly defined efficiency for each trait (Fig. 4). For example, rate of reproduction is equal to the allocation to reproduction multiplied by the efficiency of use of those allocated resources in reproduction. The same will hold for growth. If a resource pool is split between growth and reproduction over some specified time interval, the actual shape of the relationship between

--- => nutrient income = 1
---- => nutrient income = 2
----- => nutrient income = 3
actual allocation to metabolic pathways leading to the expression of a trait and the output of such pathways. This work would be easiest done for reproduction.

In order to tie foraging to allocation and life history, foraging can be treated as are life-history traits — as another life-history axis in the multidimensional function relating trait values under different allocation strategies. Foraging then has associated efficiencies and rates of expenditure. Foraging is unique among allocation targets, however, in that it has a rate of return of resources associated with a given expenditure (Fig. 1). Incorporation of foraging in this way also facilitates the incorporation of time into the model, since expenditure on foraging yields (with some probability distribution) a given resource income that is then allocated among competing processes at the next point in time.

The level of fixed investment in foraging structures, as in, e.g., plants, will affect the relationships among foraging and life-history traits through time. Decisions concerning investment in structure may either constrain resource income (if investment in foraging structures is low) or depress early fitness (if early investment in foraging structures is high). Similar dichotomies can be drawn for organisms with size-dependent reproductive or survival success.

The approach outlined so far generates a graphical description of the life history and foraging options available to an organism, given a specific resource environment. However, resource environments vary in time and space. For particular cases, we need to consider both variation in the resource environment, and the age, or stage within the life cycle, of the organism. The degree of variance about a mean value of resource availability is a measure of the amount of risk an organism is exposed to. Previous studies have considered the risk associated with choosing a particular diet item given a limited time budget, under a variety of social and physiological conditions (e.g. Real & Caraco 1986). In this case, we need to examine the risk, measured as variance in the rate of resource income, associated with particular levels of allocation to foraging. We then need to consider the circumstances under which organisms are risk insensitive (allocate without regard to the level of variation in return), risk averse (allocate more to foraging only when variation in return is low) or risk prone (allocating more to foraging when the return is highly variable). Age may play an important role in the analysis, since Engen & Stenseth (1989) suggest that the mortality probability an individual is willing to incur for a given nutritional pay-off varies with reproductive value, and hence age. If the food items in the environment are associated with particular mortality probabilities, then diet may vary with age. In short, we need to ask under what circumstances organisms are willing to risk a large allocation to foraging, which may depend on both current fitness and risk to lifetime fitness.

Size or investment in foraging structures may affect resource intake. Investment in structure may be different in a constant as opposed to variable resource environment. Thus, the level of such investment also needs to be examined in the context of risk sensitivity. Under what circumstances do organisms risk high investment in foraging structure or growth in a variable environment?

Analysis of foraging risk must also take into account amount of stored resources present. Although stored resources are already ‘on hand’, it is less efficient to funnel resources through storage rather than use them in fitness-related activities immediately. This is because conversion of incoming resources to a storable form and stored resources to a utilizable form do not occur with 100% efficiency. Resources should only be allocated to storage if there is an expectation that resource supply will be limited in the future (e.g. Chapin et al. 1990), if future foraging is expected to be risky and the organism is risk averse — or if it is more costly to discard a resource that is available in excess than it is to store it. This hypothesis has not been fully explored empirically.

The framework described here should produce models describing the interactions among foraging, allocation and life-history traits in variable resource environments. Such models could be manipulated in a variety of ways, including using dynamic optimization (e.g. Houston & Mcnamara 1988; Gladstein et al. 1991) to give predictions concerning optimal associations between specific resource environments, and foraging, allocation and life-history patterns. Such predictions could then form the basis for further experimental tests; if violations of the predictions are found, they might suggest directions of profitable enquiry into constraints due to the underlying genetic architecture, to phylogenetic history, etc.

### Needed empirical and theoretical studies

Both empirical and theoretical studies are needed to explore fully the framework set out here. Empirical studies need to ask, first, the extent of resource losses in metabolic processing, in order to examine the non-linearity of life-history trade-offs. Do particular types of processes involve greater loss? Is relative loss the same at high and low resource availability? Second, what are the actual effects of differing allocation to foraging structure at different ages on resource return and on allocation to other traits? Third, how risk sensitive in response to variation in resource availability are organisms when allocating resources to foraging? Do the same rules apply as for diet choice? Does risk sensitivity actually vary with age, due to experience, mortality probability associated with a given level of foraging effort, overall
nutrient demand (hunger level), or amount of stored resources? Theoretical studies are needed to explore further the dynamics of models incorporating foraging as an allocation, and hence incorporating a rate of nutrient intake. Models that incorporate differing levels of risk sensitivity are also needed to explore foraging, allocation and life history in variable resource environments. Finally, more empirical studies will be needed to validate the results of the modelling efforts.

Conclusions

What I thus propose is an approach to integrate ecological and physiological aspects of the study of allocation. This is necessary to bring us closer to understanding the role of variable environments in shaping life-history strategies, organizing the functional details of specific organisms’ ecologies within a comprehensive evolutionary scheme. I suggest that the relationship between the rate and efficiency of various allocation processes will determine the shape of life-history trade-offs at specific resource levels. If foraging effort is treated as the result of an allocation, we could generate a model that includes time. Finally, risk analysis, already used in studies of foraging strategy, needs to be more broadly applied to determining foraging effort, rather than just diet choice, in variable environments. The building stones of this overall model are understood, but the shape of the whole structure needs experimental and theoretical tests.

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