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The Role of Resource Allocation in Understanding Reproductive Patterns

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Introduction

Foraging by organisms results in resource intake; those resources are then allocated to life-history traits including reproduction, survival and growth (Figure 1). Resources can also be used to obtain more resources via allocation to foraging. Foraging and life-history traits are thus dynamically linked via allocation processes.

For some time, students of life-history traits have called for studies combining foraging and life-history trait information, to gain a more complete understanding of reproductive and survival patterns of organisms under natural conditions, where resource availability may vary (e.g. Pianka, 1976). Given the dynamic link between foraging and life-history traits forged by allocation, we must understand allocation processes to both life-history traits and foraging in order to gain that predictive ability about reproductive and survival patterns of organisms (e.g. Boggs, 1981; Mooney and Chiarello, 1984; Gatto, Matessi and Slobodkin, 1989). Allocation has often been used in the past as an implicit conceptual framework for understanding life-history patterns; we now need to continue building explicitly on that framework in order to understand the dynamics of allocation per se.
Initial attempts at predictive understanding of reproductive patterns in particular focused on trade-offs, recognize the interdependencies among life-history traits which are mediated by allocation. If resources from a limited pool are allocated to reproduction, those resources are not available to be spent on growth or survival (e.g., Gadgil and Bossert, 1970; Cohen, 1971; Snell and King, 1977; Reznick, 1985). The relative distribution of resources, which could be quantified by reproductive effort (Tinkle, 1969), thus determined the temporal pattern of reproduction. Reproductive effort and hence reproductive patterns, should vary with age, probability of juvenile or adult mortality, environmental variability, etc. (e.g., Gadgil and Bossert, 1970; Pianka and Parker, 1975). The idea of a limited resource pool is critical to this type of analysis, and seems not unreasonable if considered over an organism’s entire life span. However, allocation to foraging can vary with resource demand, making the size of the limited resource pool a variable rather than a constant (Tuomi, Hakala and Haukioja, 1983; Abrams, 1991; Boggs, 1992). This has been demonstrated for Heliconius butterflies; as reproductive demand is experimentally increased, foraging also increases if resources are available in the environment (Woods, Boggs and Karlsson, personal observation).

More recently, dynamic models of allocation to life-history traits, including reproduction, have been developed. The most extensive of these have been applied to Daphnia (e.g., Gatto, Matessi and Slobodkin, 1989; Kooijman, van der Hoeven and van der Werf, 1989; Gurney et al., 1990; Hallam, Lassiter and Suarez, 1990; McCauley et al., 1990). Generally in these studies, fitness costs and benefits of allocation patterns to growth, storage, survival, reproduc-
tion and foraging are calculated, and dynamic optimization is used to determine allocation patterns to growth (or storage) and life-history traits which maximize life-time fitness.

Study of phenotypic plasticity of reproductive patterns must also be done in the context of allocation patterns. Phenotypic plasticity can result from differences in allocation in different environments. Examination of genotypic differences in allocation patterns under a diversity of environments is yielding intriguing results: for example, Sultan and Bazzaz (in press) have shown that, while allocation patterns in response to environmental variation can vary among genotypes, these patterns have been adjusted such that reproductive fitness does not vary among genotypes in a population of Polygonium persicaria.

Finally, study of the genetics underlying life-history traits, and the resulting constraints on life-history patterns, has begun to incorporate allocation processes explicitly. de Jong and van Noordwijk (1992) examined the genetic and phenotypic variances and covariances among life-history traits, in the context of genetic variation at an acquisition and an allocation locus. They further show that the optimal allocation fraction, and hence values of life-history traits, depends on primacy of resource allocation under this type of model.

This chapter focuses on two complications of the relationship between allocation dynamics and reproductive patterns which must be understood to build a predictive theory for any life-history trait, including how these traits interact with an organism's resource environment. First, resources may vary in availability throughout the life cycle of an organism, constraining expenditure of those resources on reproduction. That is, specific nutrient types may only be available from feeding at specific life stages, or times in the adult lifespan. This is true for holometabolous insects with different diets in the juvenile and adult stages, or for animals with nuptial gifts, a situation where the female receives nutrients from the male at mating (e.g. Thornhill, 1976; Boggs and Gilbert, 1979; Boggs, 1990). These nuptial gifts may include compounds limiting to reproduction (e.g. Pivnick and McNeil, 1987; Gwynne, 1988).

Second, allocation priorities to different expenditures (reproduction, growth, survival, storage, and foraging) will affect reproductive patterns and must be understood. Organisms could shift allocation priorities depending on stage in the life cycle or amount of resources available to be allocated. For example, growth could have precedence over reproduction if resources are limiting at one point in the life cycle, but reproduction could have precedence over survival at another point. Further, variation in available resources relative to demand for expenditure of those resources could affect allocation patterns. Such variation may occur not infrequently in nature: for example, drought stress within the flowering period of a plant may reduce nectar availability for a nectarivore, while demand for sugars to support flight remains high. Alternatively, selection for high levels of reproduction early in life may result in a high demand for resources early in life, compared with late life.

In what follows, then, example case studies examining the interaction between allocation priorities and constraints on reproduction due to the timing of resource availability are presented.
Study system

*Speyeria mormonia* (Lepidoptera: Nymphalidae) is a widespread montane North American butterfly. Populations are univoltine, with larvae diapausing over the winter as unfed first instars. Larvae feed on violets in the spring. Adults fly from early July to early September in the study site at Gothic, Gunnison County, Colorado, USA (Boggs, 1987a). Adults feed on nectar from flowers of Compositae, and both sexes also feed from mud, dung and carrion, presumably to obtain sodium (Boggs and Jackson, 1991). Females emerge as adults with a fixed number of oocytes (Boggs, 1986). No eggs are completely mature, but some yolk is already present in the most mature oocytes (Boggs, 1986). Adult and larval resources can thus both be used to make any or all eggs.

**Question 1: What is the pattern of reproductive use of resources available from either adult or juvenile feeding?**

Adult *S. mormonia* feed primarily on nectar, which contains sugars with small amounts of amino acids and other compounds (Boggs, 1987b). Some protein or amino acids may be obtained from feeding at dung, mud or carrion. However, the bulk of nitrogenous compounds used in reproduction must come from stores from larval feeding, while carbohydrates should be available from either larval stores or adult feeding. Thus the pattern of use of carbohydrates from larval vs. adult feeding could affect reproductive patterns under adult nutrient stress.

An adult butterfly theoretically has three options for priority of use of larval- vs. adult-derived carbohydrates:

1. Larval carbohydrates could be kept in reserve (storage) against the possibility of adult food shortages. In this case, the last formed eggs could contain a greater percentage of larval-derived carbohydrates, as stores are expended at the end of life.
2. Small amounts of larval-derived carbohydrates could be used in each egg, with the bulk of the carbohydrates coming from adult feeding. This tactic ‘strings out’ reserves stored from larval feeding. Some reserves will be available for use if adult food sources vanish.
3. Larval-derived carbohydrates could be used first in egg production, with adult resources phased in as larval-derived stores are exhausted. No reserves would be available for use if adult food sources vanish. However, the necessity of adult foraging would be reduced early in adult life, potentially decreasing mortality risks associated with foraging or allowing time for behavioural maturation or location of adult food sources.

These hypotheses were examined, using offspring of fieldcaught *Speyeria mormonia* (Boggs, personal observation). Double-label radiotracer techniques were used to examine the relative use of labelled glucose eaten by larvae as opposed to that eaten by adults. Both $^{14}$C and $^{3}$H were used for each of larval and adult sources, to control for any possible differential incorporation of label
into particular compounds from metabolism of glucose. Adults were maintained on *ad libitum* honey – water two times a day. This feeding regime results in maximum possible fecundity and survival, with no evidence of adult food stress (Boggs and Ross, 1993).

Radioactivity derived from labelled glucose fed to larvae started out high in the first day’s egg production by females, and then decreased until about day 5–7 of egg laying, after which it stabilized at a low level (Boggs, personal observation). Adult-derived label increased during the first 5–7 days, and then stabilized at a high level (Boggs, personal observation). These data suggest that larval resources are used initially in oocytes with yolk incorporated prior to adult emergence. Larval resources are then used at a low level in future eggs, although the label could have been incorporated prior to adult emergence rather than during final yolkling of the eggs. In any case, larval resources are not initially completely expended in reproduction, but are held in storage under optimal adult feeding conditions.

**Question 2: What are allocation priorities with respect to reproduction and survival, under adult food scarcity?**

*Speyeria mormonia* were again used to examine the effect of a quantitative reduction in adult food on allocation to survival and reproduction, including fecundity and egg size (Boggs and Ross, 1993). This work examined allocation priorities under nutrient stress.

The experimental design was controlled for possible effects on survival and reproduction of butterfly size and larval reserves, sex, and relative adult emergence date within the flight season. New adults were caught in the field, with females caught after mating. Butterflies were fed a 25% honey–water solution twice a day, using a Hamilton syringe so that amount eaten could be measured. Butterflies were grouped into threes of similar size and emergence date, with one individual in each group fed *ad libitum*, one fed half of what the *ad libitum* individual ate, and the third butterfly fed one third of what the *ad libitum* individual ate (Boggs and Ross, 1993).

Adult food restriction had no effect on lifespan or egg weight (Boggs and Ross, 1993; *Table 1*). However, fecundity decreased significantly with decreases in adult food intake, as demonstrated by analysis of covariance with lifespan as a covariate (Boggs and Ross, 1993; *Table 1*).

Shifts in allocation between reproduction and other uses can be measured more directly as well. Since females emerge with a fixed number of oocytes in the ovaries (Boggs 1986), any differences among feeding treatments in the sum of the number of eggs laid and the number of oocytes remaining in the ovaries at death (or potential fecundity) must be due to differences among feeding treatments in resorption of oocytes initially present at adult emergence. Oocyte resorption directly reflects reallocation of resources away from reproduction. Analysis of variance, with lifespan as a covariate, showed that feeding treatment had a significant effect on potential fecundity, with potential fecundity directly
Table 1: Means ± standard deviation of life-history traits of *Speyeria mormonia* females under various adult feeding regimes. All means are adjusted least squares means from ANOVAs or ANCOVAs with feeding regime, capture date, body size, year as variables and either lifespan or fecundity as covariates. Data are from Boggs and Ross (1993).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Feeding Regime</th>
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<tbody>
<tr>
<td></td>
<td>ad libitum</td>
</tr>
<tr>
<td>Lifespan</td>
<td>18.4 ± 6.9 days</td>
</tr>
<tr>
<td>Egg weight</td>
<td>0.22 ± 0.02 mg</td>
</tr>
<tr>
<td>Fecundity</td>
<td>267 ± 70 eggs</td>
</tr>
<tr>
<td>Potential fecundity</td>
<td>398 ± 23 eggs</td>
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<td></td>
<td>1/2 ad libitum</td>
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<tr>
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</tr>
<tr>
<td>Fecundity</td>
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<tr>
<td>Potential fecundity</td>
<td>194 ± 15 eggs</td>
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<tr>
<td></td>
<td>1/3 ad libitum</td>
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<td>Egg weight</td>
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<td>Fecundity</td>
<td>72 ± 18 eggs</td>
</tr>
<tr>
<td>Potential fecundity</td>
<td>127 ± 13 eggs</td>
</tr>
</tbody>
</table>

decreasing with decreasing food intake (Boggs and Ross, 1993; Table 1). Potential fecundity of females fed *ad libitum* did not differ significantly from the number of oocytes in the ovaries of newly emerged females (Boggs and Ross, 1993), indicating that no egg resorption was occurring in females fed *ad libitum*.

These results indicate a strong dependence of a nectarivore on adult food for reproduction. Lifespan was constant in the face of adult nutrient stress, while resources were allocated away from reproduction, presumably to support survival. The data thus suggest that survival has first claim on resources, with any 'surplus' going to reproduction. Previous studies on iteroparous organisms with more complex adult diets have yielded similar results (e.g. David, van Herweewege and Fouillet, 1971 for *Drosophila*; Reznick, 1983 for guppies); the finding of reallocation in an iteroparous nectarivore is surprising, given the incomplete nature of the adult diet and hence the possible role of larval resources as the constraint on reproduction.

Integration: Allocation patterns producing the observed results

There are two possible allocation scenarios that could produce the pattern observed in *Speyeria mormonia* under adult nutrient stress. First (*Figure 2a*), adult-derived resources may normally be used almost entirely for adult survival. Nectar is primarily carbohydrates, and sugars are expected to be needed to support flight, glycolysis, etc. Under adult resource stress, larval-derived nutrients are reallocated away from reproduction to support survival. Such reallocation may involve not only redirection of carbohydrates, but conversion of compounds not normally used in survival to compounds that could support survival. Adult feeding thus affects reproduction, without being a direct major contributor to reproduction.

Alternatively (*Figure 2b*), adult-derived resources may directly limit reproduction. In this case, little reallocation occurs under adult feeding restriction,
Figure 2. Alternative allocation patterns which could result in maintenance of lifespan at the expense of reproduction under conditions of low resource availability.

but reproduction is simply reduced in direct response to reduction in adult intake.

The radiotracer data presented for glucose support the second scenario: adult-derived resources were allocated directly to reproduction under food sufficiency, suggesting that under conditions of food restriction, reproduction should suffer directly. However, the egg resorption data suggest that resources allocated to reproduction prior to adult emergence may be reallocated away from reproduction under adult food stress, supporting the first scenario.

Reality may be a combination of the two scenarios, since what happens depends on the total scope of nutrient types, not just glucose. It seems most likely that reduction of adult food availability leads to a carbohydrate shortage. If there are not enough carbohydrates available to support both survival and egg production, survival has first priority. Eggs which are not fully formed because of lack of carbohydrates may then be resorbed, and the nutrients (including noncarbohydrates) used for other purposes.

Conclusions

Two factors have been illuminated as important to understanding the role of allocation in shaping reproductive patterns. First, the source and timing of nutrient availability are important in understanding allocation to reproduction. Nutrients available throughout the life cycle might be allocated differently than nutrients available only at one stage, resulting in different constraints on
reallocation in the face of nutrient stress. Second, allocation priorities both under nutrient stress and nutrient sufficiency will affect reproductive patterns. These two factors interact to produce observed reproductive patterns under a variety of food availabilities.

The findings presented here also show the need to include foraging activity in allocation models, as reflecting the timing and amount of nutrients available to be allocated. The dynamics of the entire diagram of foraging inputs and life-history trait outputs must be examined to generate an understanding of the factors controlling allocation priorities under different circumstances, if any sense at all is to be made out of the pattern of life-history traits, and in particular, reproductive patterns, of biologists' favourite organisms, be they aphids or butterflies.

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References


