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NUTRITIONAL ECOLOGY

Understanding insect life histories and senescence through a resource allocation lens

Carol L. Boggs*

Department of Biology, Stanford University, Stanford, CA 94305, USA

Summary

1. Resource acquisition and allocation are the physiological mechanisms integrating foraging and life-history traits. An understanding of the patterns of acquisition and allocation in different environments and organisms is critical to a predictive theory of life history.

2. Here I develop an allocation framework, which provides a template for conceptualizing the interactions among resource acquisition, allocation and life-history traits. The framework describes the process through which food is taken in by an organism at specific life stages, then allocated to growth, survival (including maintenance, defence, dispersal, etc), reproduction and further foraging.

3. I use the allocation framework to examine allocation to life-history traits in insects under both benign and stressful environments. Stressful environments result from resource scarcity or harsh environmental conditions. I consider effects of consistent stress or variable stress across time.

4. Several broad generalizations emerge from empirical studies, viewed in the allocation framework. First, resource congruence, or the requirement for specific nutrient ratios in, for example, eggs, results in different limiting nutrients for each life-history trait. Second, the timing of resource acquisition affects both allocation patterns and the identity of limiting nutrients for a given life-history trait. Third, physiological trade-offs may occur across, not just within, life stages. Fourth, apparent trade-offs may be driven by differences among traits in resource congruence constraints and deleterious effects of excess nutrients on a particular trait. Fifth, allocation response to environmental stress shows age-specific and sex-specific patterns. Sixth, physiological trade-offs are often more pronounced under environmental stress. Finally, even within insects, there is considerable variability in allocation response to environmental stress. We do not yet have sufficiently diverse and thorough case studies to understand why this is so. Studies in the wild, or relating laboratory conditions to wild environments, are also needed.

5. Senescence can also be understood in an allocation framework. The present approach provides a necessary functional basis for understanding patterns of senescence in diverse organisms and environments.

6. The allocation framework fosters a mechanistic understanding of life-history patterns, and the beginning of an understanding of the processes underlying those patterns.

Key-words: nutritional ecology, resource acquisition, foraging, survival, fecundity, life-history trade-offs, environmental stress, constraints

Introduction

Nutritional ecology lies at the heart of life-history expression and evolution. What organisms eat, when they eat, and how they allocate what's eaten yield observed life-history and foraging traits, whether it be the role of royal jelly in determining the reproductive fate of a female bee (e.g., Haydak 1970; Lin & Winston 1998) or of plant quality affecting growth rate of an insect herbivore.

Several research foci have emerged within the study of resource allocation and life histories. These foci include the study of life-history physiological trade-offs and life-history evolution, and the study of senescence (especially in *Drosophila*), among others. These research foci are often rather disconnected. In particular, researchers interested in senescence and those studying other aspects of life histories

*Correspondence author. E-mail: cboggs@stanford.edu

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in non-dipteran insect orders are often seemingly unaware of the cross-connections between the two areas that are facilitated by a nutritional ecological approach (but see Lee *et al*. 2008).

Here I lay out a general allocation framework describing the nexus among nutritional ecology, resource allocation and life history. This framework serves as a template for structuring and conceptualizing research questions and theoretical modelling. I then examine emergent life-history patterns among and within species in benign environments, defined as those with *ad libitum* food of normal quality and no known reproductive or survival stresses. I next consider emergent life-history patterns in constrained, as well as variable, nutritional environments, or otherwise stressful environments. I include the effects of dietary restriction on senescence and life histories. Along the way, I highlight both conceptual and empirical challenges and puzzles. Throughout, my examples are not all-inclusive of those in the literature and are biased towards Lepidoptera, but serve to illustrate general concepts.

The allocation framework

OVERVIEW

Nutrients are taken in by an organism at various life stages and ages within those life stages. These are transformed by metabolism, then allocated as a function of age and sex to reproduction, maintenance, foraging, growth, storage, or other activities to produce the suite of life-history and foraging traits observed in a given environment (Fig. 1) (for earlier versions, see Boggs 1990, 1992, 2003).

For holometabolous insects, with complex life histories, allocation is a three-stage process corresponding to life stage. Maternal- and larval-derived nutrients are allocated during the larval stage to growth, maintenance, storage, foraging, and sometimes reproductive structures. During the pupal stage, available resources are re-allocated within this closed system to adult soma, maintenance, storage, and reproductive structures. In the adult stage, incoming nutrients along with larval-derived reserves and occasionally soma are then allocated to life-history and foraging traits, which integrate to determine fitness. At all stages, some fraction of nutrients is lost to waste.

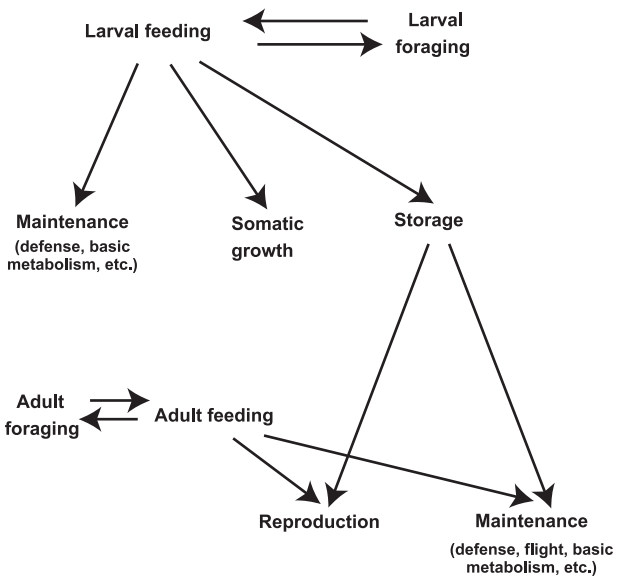

Fig. 1. Graphical illustration of the allocation framework. Each allocation is accompanied by waste, as allocations are not 100% efficient.

Allocation is less complex in hemimetabolous insects, with less complete re-organization between larval and adult stages. Nonetheless a distinct age-structured allocation pattern can be identified.

Allocation patterns at each stage are not independent and interact as well with the nutritional environment. For example, in a set of heliconiine butterflies, proportional allocation at metamorphosis to reproductive reserves as opposed to soma was correlated across species and sexes with mean expected future adult nutrient intake and reproductive output (Boggs 1981).

FOOD INTAKE

The first step in the process is food intake. This is of course zero in the pupal stage. But excluding the pupal stage, some species feed on the same food resource through life. These are usually hemimetabolous insects, of which orthopterans are an example. Alternatively, the quality and quantity of food may vary with life stage, particularly for holometabolous insects. At the extreme, some moth species are not known to feed as adults (reviewed in Jervis *et al*. 2005). Larval food is at least as nutritionally complete, if not more so, than adult food in most cases. For example, lepidopteran species are herbivorous as larvae, with a diet that contains diverse compounds, including carbohydrates and nitrogen. As adults, some of these same species are nectivorous, with a diet that is high in carbohydrates but very low in other compounds. Differences in diet quality and quantity with life stage significantly affect allocation and life-history processes, as seen below.

Even within a species and life stage, different food types may be exploited in a sex- and age-specific manner. For example, *Speyeria mormonia* (Lepidoptera: Nymphalidae) feed both on nectar and on mud, dung or carrion (termed 'mud-puddling') as adults. Nectar intake varies with age (Boggs & Ross 1993; Boggs 1997), being higher in young adults than older adults. Mud-puddling, a source of sodium (Arms *et al.* 1974) and likely also of nitrogenous compounds for some species (Beck *et al.* 1999), is exhibited predominantly by young males, followed by older males and females, with young females rarely encountered (Boggs & Jackson 1991). As documented for *Thymelicus lineola* (Lepidoptera: Hesperidae) (Pivnick & McNeil 1987), sodium and possibly other compounds collected by mud-puddling males are transferred to the female at mating, consistent with the sex-specific behavioural patterns (but see Molleman *et al*. 2005).

In the extreme case of sex-specific feeding patterns, nuptial gifts are transferred from the male to the female at mating (reviewed in Boggs 1995; Vahed 1998). Such gifts can take the form of prey items, of salivary gland or reproductive accessory gland products, or in the most extreme cases, body parts or

haemolymph. These behaviours link male and female resource budgets, which may be important not only in division of foraging labour, but also in the face of constrained or variable environments (see below).

Insects are capable of diet selection and compensatory feeding in response to food availability and demand for nutrients, as elegantly illustrated by recent studies on *Drosophila melanogaster* (Diptera: Drosophilidae) (Lee *et al*. 2008) and *Teleogryllus commodus* (Orthoptera: Gryllidae) (Maklakov *et al*. 2008). Such behavioural responses also occur with nuptial gifts; *Heliconius cydno* (Lepidoptera: Nymphalidae) females show a population-level trade-off between number of matings (= spermatophores received) and adult pollen feeding, both sources of nitrogenous compounds (Boggs 1990). Mechanisms controlling such foraging behaviours will be genetic, neural, hormonal and environmental in nature, which have been best worked out for *Apis mellifera* (Hymenoptera:Apidae) (reviewed in Page & Erber 2002).

ALLOCATION TO LIFE-HISTORY TRAITS, INCLUDING FORAGING

In the second step in the framework, nutrients and energy from ingested food are assimilated and allocated to various life-history traits, further foraging activity, storage, or lost to waste (Fig. 1). Assimilation can be affected by food composition, gut symbionts (Douglas 2009), etc., influencing resources available to be allocated. The nutritional requirements differ for each life-history trait to which nutrients are allocated, and can change with age or allocation duration. For example, the first eggs laid by *Eupelmus vuilletti* (Hymenoptera: Eupelmidae) are composed of 52% lipids, 22% carbohydrates, and 26% proteins. The composition changes with subsequent eggs laid by females (Giron & Casas 2003), with percent lipids remaining relatively constant, while percent carbohydrates and proteins shift in dominance. Similarly, flight in long-distance fliers such as locusts is first fuelled solely by carbohydrates in the energy-intensive take-off phase of flight, and then by lipids for longer duration flight (reviewed in Candy *et al.* 1997).

Food intake for any given life stage is not necessarily matched to life-history trait requirements for that life stage, particularly for organisms whose diets differ with life stage. Thus, stored reserves can be important sources of allocated nutrients. Allocation has sometimes been simplified as the expenditure of capital (resources stored from earlier life stages) or of income (resources more or less directly expended upon acquisition) (Stearns 1992; Parker *et al.* 2009). However, any given activity may require both capital and income resource expenditure, as outlined below.

An important general aspect of allocation is the necessity of matching available nutrients to the nutrient requirements of life-history traits, on an age- and sex-specific basis. Life span, reproduction, or other life-history traits are proximally constrained by one or more crucial limiting nutrients, due to the need for resource congruence (sensu Bazzaz 1996), that is, matching of nutrients in a specific ratio for a unit output (e.g., an egg). Note that the identity of the limiting nutrient can differ among life-history traits, and can change under different nutritional conditions. For example, if *S. mormonia* is well-fed on nectar as an adult, then nitrogenous stores from larval feeding may constrain possible total fecundity. However, if adult feeding on carbohydrates is limited, then availability of carbohydrates provides the proximal constraint on reproduction (Boggs & Ross 1993). Thus, multiple nutrient types must be considered simultaneously in this framework (see also Jervis *et al.* 2008).

How broadly or narrowly to classify nutrient types will depend on the type of question addressed. For example, it may be sufficient to use carbohydrates, proteins and lipids as nutrient types when considering trade-offs among some reproductive and survival characters, but for understanding defence, alkaloids or other compounds may be critical. Likewise, simply examining sources of amino acids allocated to eggs in nectivorous lepidopteran species will be misleading, since essential and non-essential amino acids derive from different sources (O'Brien *et al.* 2002; see also Wolf *et al.* 2009).

LIFE-HISTORY TRADE-OFFS

The above discussion considers one trait at a time. However, the need to simultaneously allocate nutrients to multiple traits can generate physiological trade-offs among those traits, if a particular nutrient type is limited. Classic trade-offs have been documented among growth, survival and reproduction, usually in a pair-wise manner (reviewed in Roff 2002). However, trade-offs may occur at a smaller trait scale, as between egg number and size (Smith & Fretwell 1974). Additionally, trade-offs may vary through time within a given individual (e.g., Fischer *et al*. 2006). Note that there is nothing in this schema that precludes physiological trade-offs among $n > 2$ traits, and in fact this may be the case more often than we have realized.

Physiological trade-offs may occur across time, including across life stage boundaries. In these cases, the trade-offs are mediated by timing of allocation relative to the amount of stored nutrient reserves, or of foraging. For example, in a short-lived caddis fly species, *Odontocerum albicorne* (Trichoptera: Odontoceridae), increased investment in larval defence results in shifts in allometry of adult investment in abdomen vs. thorax mass and wing length, increasing investment in abdomens (Stevens *et al*. 1999). This likely preserves reproduction at the expense of adult flight capability in this species.

Recent work by Lee *et al*. (2008) on *D. melanogaster* offers the fascinating suggestion that trade-offs may not always result from competition for resources among allocation targets, including competition for limiting nutrients, but rather may result from the need for resource congruence. That is, the need to increase consumption of a food type containing a limiting nutrient for a particular allocation target (say, eggs) may result in excess consumption of nutrients that are toxic to another allocation target (say, survival). Thus, trade-offs may be a function of the packaging of nutrients available as food in the environment. Intriguingly, long-term exposure to

increased carbohydrate : protein ratios in larval food resulted in the evolution of lowered adverse excess fat storage, which otherwise results from excess carbohydrate intake, in *Plutella xylostella* (Lepidoptera: Plutellidae) (Warbrick-Smith *et al*. 2006). This suggests that trade-offs resulting from deleterious effects of excess nutrients acquired 'inadvertently' can be subject to selection.

RELATIONSHIP TO OTHER APPROACHES

The allocation framework outlined above provides a conceptual tool for understanding the physiological and ecological interrelations between foraging and life-history patterns, including senescence. It is amenable to modelling (as in Casas *et al*. 2005; Lee *et al*. 2008). Since the results of allocation directly affect fitness, various fitness optimization approaches can be used to predict suites of life-history and foraging traits expected to occur in particular nutritional environments, given appropriate genetic variation. Other environmental factors, such as predation pressure, extent of reproductive opportunities, metabolic costs due to abiotic environmental factors such as temperature, can also be accounted for if desired as fixed draws or constraints on allocation.

At least two sets of extant modelling approaches in particular fit within the allocation framework, but with different degrees of success. First, the 'y-model' (van Noordwijk & De Jong 1986; de Jong & van Noordwijk 1992) is a life-history model based on acquisition and allocation of resources to two, or a very few, life-history traits, hence the 'Y'. Although the model has served as a useful starting point, as generally implemented, it does not allow for consideration of the complexities of multiple traits competing for resources at once, or of multiple resource types or resource congruence. Second, the geometric framework (see Raubenheimer *et al.* 2009 and references therein) is a graphical model, with axes being two or more nutrient types or food components. Resource congruence is thus explicitly built into the model. Variables modelled within this graphical framework can include a diversity of performance measures, including body composition, growth rate, etc. Response surfaces for these variables, plotted for the specific sets of nutritional axes, describe the array of possible performance outcomes, and can be used to determine the combination of nutrient acquisition and performance values yielding maximum fitness. Beyond predicting suites of life-history traits, such models have been used successfully to explore the role of nutritional ecology in explaining the mechanistic basis of population (Simpson *et al*. 2006) and community phenomena (Behmer & Joern 2008; Raubenheimer *et al*. 2009).

The allocation framework treats the mechanisms controlling allocation as a black box. Mechanistic approaches to understanding factors controlling insect life-history traits have included study of hormonal or other biochemical and physiological control mechanisms and constraints (reviewed in Zera & Harshman 2001). Study of the role of major genes coding for central metabolic pathway enzymes has also been important (e.g., Watt *et al.* 1985; Watt 1992; Watt & Dean 2000; Haag *et al*. 2005; Zera & Zhou 2006). These mechanisms are both mediated and influenced by the nutritional environment. For example, an insect's physiological state, influenced by nutrition, determines the alternative splicing profile of troponin-t RNA, affecting allocation as a plastic response to environmental conditions (Marden 2008). An integration of these mechanisms into the allocation framework is sorely needed. Such integration will provide a synthetic conceptual understanding of how allocation works, and if and how it acts to constrain life-history plasticity or affects life-history evolution in response to variable environments.

Allocation to life history in benign environments

Understanding allocation patterns in benign environments provides the baseline for understanding life-history responses to nutritional or physiological stress. Below, I outline the effects of allocation decisions made in benign environments at the larval/pupal, and adult stages, and explore the integration of allocation decisions across life stages. This sets the stage for further consideration of what happens in constrained or variable environments.

LARVAL/PUPAL STAGE ALLOCATION DECISIONS

The primary allocation decision affecting life-history traits during the larval stage is how much to allocate to growth, storage and defence. The decision as to when to stop foraging, hence transition out of the larval stage, is also critical. These decisions determine both the stored reserves carried over from the larval stage that is available for adult reproduction and other activities, and an upper limit to possible body size. Body size influences available space for reproductive organs, hence places an upper limit to the rate of reproductive output.

Allocation between growth and storage in larval stages has been studied within species by experimental manipulation of diet quality or quantity, which will be addressed below when I consider stressful environments. With the exception of work on polyandrous vs. monandrous *Pieris napi* (Lepidoptera: Pieridae) (Välimäki & Kaitala 2007), essentially no attention has been paid to variation in allocation within populations under benign conditions. Comparative studies across populations or species in benign environments are also scarce and should be informative.

Other activities compete with growth and storage for allocated nutrients during the larval stage, including defence, in the form of colouration, behaviour, secretions or immune response. Such allocation can occur in either the larval or pupal/adult stages. As one example of effects of allocation to defence in larvae, consider immune response, reviewed by Cotter *et al*. (2004). Juvenile stages of several orders, including orthopterans, phasmids and lepidopterans, exhibit population outbreak dynamics. Dense 'gregarious' phase juveniles are often more melanic than solitary phase juveniles. Cotter *et al*. (2004) showed that larvae of *Spodoptera littoralis* (Lepidoptera: Noctuidae) raised on *ad libitum* food in high densities have higher immune function than do those raised at low densities,

but at the cost of decreased larval mass and haemolymph protein on entry to the last instar. Additionally, they found trade-offs within immune function as well: darker larvae had higher phenol oxidase activity and encapsulation response to foreign objects inserted in the haemocoel than did paler larvae, but lower anti-bacterial activity. Larval age can also influence immune response, hence allocation (Eleftherianos *et al*. 2008). Immune competence decreases markedly in wandering pre-pupal last instar *Manduca sexta* (Lepidoptera: Sphingidae).

Allocation at the larval and pupal stages also determines the resulting adult body structure. Allometry of adult body parts results from allocation of larval resources to imaginal disks (reviewed in Shingleton *et al*. 2007). Such allometries may provide significant constraints on adult life-history and foraging traits. In holometabolous insects, this allocation generally occurs after larval feeding largely ceases, during the pre-pupal and pupal stages. Nijhout & Wheeler (1996) modelled allocation to imaginal disks using the Gompertz growth equation and assuming a closed system, as in a pupa. They showed that disks exhibit correlated responses to change, such that when allocation to one disk (e.g., flight muscle) is altered, other disks show compensatory changes in nutrient uptake. Their model explained allometric changes in caste morphology within ants. Moczek & Nijhout (2004) showed further that competing disks need not be located next to each other, and competition levels among disks can vary over time.

One can also think of allocation to adult body parts on an aggregated scale. Among related butterfly species with similar larval diets and developmental patterns, allocation to soma vs. non-soma is a function of the expected completeness of the adult diet plus expected costs of reproduction or survival (Boggs 1981; Karlsson & Wickman 1989). Intra-specific variation in allocation to soma and non-soma remains virtually unexplored. What are the consequences of such variation? How much of it is a plastic response to larval/pupal resource environments, due to maternal effects, or genetic?

ADULT STAGE ALLOCATION DECISIONS

The timing and quality of adult food intake, in combination with oogenesis patterns and the amount of reserves from larval feeding, strongly influence observed life histories in benign environments. Lepidoptera are excellent exemplars here. Across related species, as the adult diet becomes more complete, hence larval reserves are less constraining, the fecundity curve flattens and lengthens (Boggs 1986). Likewise, the daily survival rate increases. The ovigeny index, that is, the proportion of oocytes mature at adult emergence, also decreases with increasing completeness of adult diet, allowing more oocytes to be made from adult-derived resources (Jervis *et al*. 2005).

Adult diets can be more complete in one of two ways. Insects can eat a rich resource, as happens with adult herbivory or granivory. Alternatively, insects can eat a heterogeneous diet, with multiple food resources. The latter is the case for pollen feeding members of the lepidopteran genus *Heliconius*, which feed on nectar and pollen as adults (Gilbert 1972), or for nectivorous or frugivorous butterflies which also feed on mud, dung, or carrion as adults. In cases such as mud-puddling, the role in the allocation budget is not well-understood. Clearly, salts can enhance male virility (Lederhouse *et al.* 1990), but effects of sodium on egg hatchability are not generalized (Molleman *et al.* 2004). Mud-puddling may also not be a unitary behaviour, with all species seeking the same nutrients. This idea is supported by the phylogenetic signal seen in substrate preferences (Boggs & Dau 2004). An integrated view of foraging habits such as mud-puddling behaviour, given by the allocation framework, will help us understand variation among species in foraging strategies on heterogeneous resource bases.

The timing and amount of adult feeding also interacts with use of male nuptial gifts. This is seen with pollen feeding by female *Heliconius* (Boggs 1990). Female *H. charitonius*, which generally mate only once, delay pollen feeding as adults until the spermatophore has been absorbed, suggesting that the spermatophore is used in preference to foraging for new income in this species. Female *Kawanaphila nartee* (Orthoptera: Tettigoniidae) exhibit a related behaviour. Mate choosiness/competition switches between the sexes, depending on the availability of pollen (Simmons & Bailey 1990), suggesting a trade-off between resources derived from nuptial gifts vs. pollen.

Nutrients available from adult feeding (or larval reserves) are then allocated to various life-history traits, including egg production. Egg composition varies among species, as a result of differences in reproductive allocation decisions. For example, egg C : N ratios differ by nearly a factor of two across a set of nymphalids and pierids (O'Brien *et al*. 2004). Compositional differences may be driven by any number of factors. For *S. mormonia*, the relatively high carbon content of eggs may reflect the need for carbon compounds as anti-freeze for diapausing first instar larvae. Egg composition in other lepidopteran species is tied to dessication tolerance (Pivnick & McNeil 1987). In general, the relationship between foraging patterns and specific resource requirements for reproduction or survival is not well-studied, and will certainly affect organisms' response to environmental variation (see below).

Adult allocation to traits other than reproduction also varies within and among species. Loss or reduction of flight ability results in striking adult allocation differences within some groups of insects. The allocation framework predicts that flight loss should be associated with lower food quality and/or increased reproductive investment and/or longevity. A comparative study on beetles (Coleoptera: Silphidae: Silphinae) supports this prediction (Ikeda *et al*. 2008). Similarly, summer generation *P. napi* female butterflies in Sweden have larger thoraces, greater flight bout duration, and lower egg output than do females of the spring generation (Karlsson & Johansson 2008). In a wing-dimorphic cricket, *Gryllus rubens*, female long-wing morphs convert assimilated nutrients into biomass less efficiently, and their ovaries gain less mass over the first 14 days of adult life than do short-wing morphs (Mole & Zera 1993). This suggests there are energy costs to flight maintenance that translate both into overall

mass gain and reproductive function. This effect of flight is supported by further work on the differences in the metabolic fate of lipids and amino acids in both morphs (Zera & Zhou 2003, 2006).

Within species, sex differences may also occur in adult allocation. This is seen in allocation to defence response under benign conditions (reviewed in Zuk & Stoehr 2002), although the pattern is not uniform among species. *Drosophila melanogaster* showed no sexual dimorphism in immune response under ample food conditions and no reproductive opportunities, but stronger immune suppression in males when mating opportunities were present (McKean & Nunney 2004). Similarly, Stoehr (2007) found that wild males (with mating opportunities in the wild) had greater immune response than females in *Pieris rapae* (Lepidoptera: Nymphalidae), and that immune response correlated positively with body mass. Under captive conditions, with reproductive opportunities, male immune response was still stronger than that of females, and immune response varied with adult age. This argues that there are sex-specific allocation patterns, depending on resource draw to different life-history traits, consistent with the allocation framework. Quantification of the resource budget in relation to immune response is needed.

Investment in life-history traits also varies with age. For example, mg carbon allocated to eggs per day decreases over the life span of nectivorous butterfly species (O'Brien *et al*. 2004). These effects are not limited to females; male spermatophore mass changes with age in virgin males, and with time since last mating in non-virgins in *Danaus plexippus* (Lepidoptera: Nymphalidae) (Oberhauser 1988). Evidence for changes with age in investment in maintenance in insects, as measured by age-specific metabolic rates or age-specific flight costs, is rare. However, oxygen consumption rates of resting male *Acheta domesticus* (Orthoptera: Gryllidae) decreased with age between 7 and 81 days of adult life, independent of body mass and trial date (Hack 1997), and the same is true in *Drosophila* (reviewed in Hack 1997).

INTEGRATION OF ALLOCATION DECISIONS ACROSS LIFE STAGES

Allocation at the adult stage derives from a mix of adult and larval sources. In general, we think of larval-derived sources as having been stored in fat body or in various storage compounds in the haemolymph and elsewhere. However, resources can also be re-allocated from oocytes or other tissues as a routine matter in benign environments, even in the adult stage. This is highlighted by species that resorb wing muscles as adults, using recycled nutrients in reproduction and other activities. Homoptera, Diptera, Coleoptera, Heteroptera, Orthoptera, and Hymenoptera all contain species capable of wing muscle resorption, which in general happens after dispersal and with the onset of reproduction (reviewed in Stjernholm *et al.* 2005).

Use of thorax-derived resources, which likely result from resorption and re-allocation of wing muscle resources, also occurs to a lesser extent in Lepidoptera, suggesting that it may be more widespread among insects than previously suspected (Karlsson 1994, 1998; Stjernholm & Karlsson 2000, 2006; Norberg & Leimar 2002; Stjernholm *et al*. 2005). In the best studied case, *P. napi* (Lepidoptera: Pieridae), resorption of thorax muscle is stimulated by female re-mating (Stjernholm & Karlsson 2000); re-mating also increases fecundity (Wiklund *et al*. 1993). Degree of polyandry is a heritable trait in this species (Wedell, Wiklund & Cook 2002), suggesting that reliance on male nuptial gifts and adult resource re-allocation are linked traits. Polyandry in fact is likely associated with a suite of life-history changes in this species. Välimäki and Kaitala (2007) showed that growth rate of female offspring was correlated with mother's degree of polyandry, with those with polyandrous mothers exhibiting a faster larval growth rate than those from monandrous mothers. As a result, female offspring from polyandrous mothers had a shorter development time in directly developing generations, and a larger adult size in over-wintering generations under benign conditions. The relationship broke down under conditions of larval resource stress.

This points up a significant conceptual issue: when should resorption/re-allocation occur as a matter of course in benign environments, with ample food, reproductive opportunities and high survival rates, and under what circumstances should feeding and 'normal' storage sources provide all resources for current life-history activities? The answer will need to include the role of senescence, since senescence is defined as loss of function, which itself can be caused by resorption and re-allocation.

The integrated pattern of allocation to egg production from larval and adult resources was studied in several lepidopterans and in *D. melanogaster* (Diptera: Drosophilidae), using carbon stable isotopes and mixing models (O'Brien *et al.* 2000, 2003, 2004, 2005; Fischer *et al.* 2004; Min *et al*. 2006) The results indicate that allocation of bulk carbon to egg production fits a two-compartment mixing model for both nectivores and frugivores. In this model, the two compartments are larval- and adult-derived carbon. In Lepidoptera, oocytes present at emergence contained only larval-derived carbon. As adult resources were taken in, they were mixed with larval carbon reserves. Egg isotopic composition reflected that mixture. The ratio of adult: larval carbon in eggs increased with female age, reaching a plateau with eggs composed of that larval-derived carbon present in oocytes at adult emergence and the rest of the egg made up of adult-derived carbon (O'Brien *et al*. 2004). Additionally, carbon derived from adult nectar feeding was incorporated into synthesized amino acids in eggs, with only essential amino acids retaining a completely larval carbon isotope signature (O'Brien *et al*. 2002, 2003, 2005). In *D. melanogaster*, eggs produced late in life were composed only of adult-derived carbon. Most intriguingly, turn-over from larval- to adult-derived carbon also occurred for somatic tissues in the adults, with approximately 75% of somatic carbon at older ages derived from sucrose fed on by adults (Min *et al*. 2006). This implies significant amounts of somatic tissue turn-over during adult life in Diptera, more so than in Lepidoptera given the difference in egg carbon

sources at older ages. This may be one factor underlying differences in senescence patterns described below.

Finally, nearly all the work on allocation in benign environments has been empirical, examining patterns of variation among species in different environments. However, the stage is set for modelling of the allocation framework, using the empirical data, to explore constraints on combinations of foraging and life-history traits, including the major questions highlighted above.

Allocation to life history in consistently stressful environments

Environments are often not benign, but stressful. Allocation patterns will be a function of the type of environmental stress (including effects of stress in maternal environments), along with the degree of plasticity vs. genetic constraint on resource acquisition and allocation.

How does allocation to life histories change in consistently resource-poor environments, or conditions of semi-starvation? Are some traits preserved at the expense of others, resulting in observable, or predictable, trade-offs? Or are all trait values suppressed? Do effects of semi-starvation at different life stages differ, and if so, how and why?

These questions have been addressed by manipulating food and/or reproductive opportunities (e.g., Boggs & Ross 1993; Tatar & Carey 1995; Chapman & Partridge 1996; Messina & Fry 2003; Boggs & Freeman 2005; Hahn 2005; Partridge *et al.* 2005). In general, these studies provide support for the hypothesis that resource congruence is important, and resource types are not always freely interchangeable. As a result, the identity of the limiting nutrient for a given life-history trait varies, depending on the environment for resource availability and demand (see also Lee *et al*. 2008). Effects of resource limitation on life-history traits may be seen across life stages, such that food restriction in the larval stage affects longevity and/or reproduction in the adult stage, for example.

For insects that feed in both the larval and adult stages, but whose diet differs between the two, the effects on adult life-history traits differ depending on which stage experiences restricted feeding. For example, for the butterfly *S. mormonia*, food stress in the larval stage affected adult survival, independent of body mass, whereas food stress in the adult stage affected only adult reproduction (Boggs & Freeman 2005; see also Bauerfiend & Fischer 2005). In contrast, adult food restriction reduced adult male survival as well as spermatophore dry mass, while increasing spermatophore water content in the butterflies *Bicyclus anynana* and *P. napi* (Ferkau & Fischer 2006). Presumably these differences depend on whether the limiting resources for adult survival and reproduction are acquired in the larval or adult life stages, but this remains to be tested.

For insects that feed on similar foods at both life stages the story is somewhat different. In these cases, adult food deprivation can generate observed trade-offs in life-history traits, including fecundity, survival, and defence, where none may have existed under benign food environments. This is seen in a stored grain pest, *Callosobruchus maculatus* (Coleoptera: Bruchidae), for example (e.g., Messina & Fry 2003 and Tatar & Carey 1995; references therein). Messina & Fry (1996) provided support for a difference in the role of population-level variation in resource acquisition vs. resource allocation in producing this pattern. Under conditions of abundant seeds for adults, adult food is effectively available *ad libitum*, since adults feed little. The role of variation in allocation is small, and variation in acquisition ability (whether adults feed at all) is more important in determining observed trade-offs. In an environment without seeds for adults, the importance of variation in acquisition decreases, and variation in allocation of scarce resources dominates, producing population-level trade-offs between reproduction and longevity. This work is based on a genetic and phenotypic analysis; analysis of the actual food intake and allocation patterns is needed.

Variation in acquisition and allocation is also important in stress responses of *D. melanogaster*, as demonstrated by Chippendale and co-workers. They used fly lines selected for dessication and starvation resistance (Chippendale *et al*. 1996; Chippendale *et al*. 1998; Djawdan *et al*. 1998). Dessication resistant lines had greater water and carbohydrate stores primarily carried over from larval feeding, while starvation resistant lines had greater lipid and carbohydrate stores. These stores buffered poor adult environments. The authors argue that these patterns are due to differences in acquisition in the larval stage, but differences in allocation between storage and other uses by larvae must also play a role, given observed effects on larval development time and pre-adult mortality.

Food acquisition differences between the sexes can also play an integral role in sex-specific buffering of food–poor environments, if allocation demands differ between the sexes. For example, *Araschnia levana* (Lepidoptera: Nymphalidae) females, but not males, prefer nectar containing amino acids. Mevi-Schütz & Erhardt (2005) raised larvae on poor vs. good quality host plants. Fecundity of adults from poor host plants was preserved only when adults were fed sugar solutions with a mix of amino acids. Fecundity of females raised on good quality plants was unaffected by the presence of amino acids in the adult diet (reviewed in Jervis & Boggs 2005).

Related patterns of response to larval food stress occurred between katydid males and females (Gwynne 2004). Under larval food stress, female *Kawanaphila nartee* maintained body mass, but male mass decreased. In this species, females compete for matings, hence nuptial gifts from males, under poor resource environments. Relatively large body size is beneficial in such competitions. In contrast, male *Conocephalus nigropleurum* (Orthoptera: Tettigoniidae) maintained body mass to a greater extent than did females. In this species, males compete for mates, regardless of environmental conditions, and large male body size is advantageous. Whether these patterns are the result of allocation or acquisition differences is unknown.

Other sex-specific changes in allocation patterns result from larval food restriction in particular. Adult body allometry changes in females, but not males, of the butterfly *S. mormonia*

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(Boggs & Freeman 2005), and the caddisfly *Agrypnia deflate* (Trichoptera: Phryganeidae) (Jannot *et al.* 2007). This may influence dispersal ability, and its interaction with fecundity.

Finally, given that male and female resource budgets are linked in some species via nuptial gifts, can these buffer female life-history traits in poor food environments? This could occur through an increase in number of matings by females, hence an increase in nuptial gifts (Boggs 1990; Gwynne 2004). However, Bergstrom & Wiklund (2002) found that smaller females of the butterfly *P. napi* cannot use increased numbers of nuptial gifts to compensate for reduced fecundity associated with smaller size, even though females decrease body mass more than do males under poor larval food conditions. A fuller understanding of the relationship between male and female resource budgets is clearly needed. For which types of life cycles and under what conditions can nuptial gifts buffer bad adult or larval environments experienced by females?

Allocation to life history in variably stressful environments

Environments are often not constant, but vary either predictably or stochastically over various time scales. The frequency and amplitude of variability in environmental conditions, along with the degree of predictability, influence organismal responses (e.g., Boyce *et al*. 2006; Boggs 2003). For example, reproductive diapause in the adult stage is a mode of coping with predictable, seasonal variation in resource availability. Note that if the variation occurs on a time scale matching the length of part of the life cycle, that is, the egg, juvenile, and adult stages, then such variation will be seen by individuals as a constant environment. What are the effects, however, of variation in the resource environment, or in reproductive opportunities or survival stress, within a life stage?

The answer should depend on the balance among incoming resources, stored resources and the expenditure on life-history traits at any given time. Indeed, in *S. mormonia*, low food availability early in adult life can be compensated by apparent draw-down of larval-derived reserves to maintain reproductive output, if such reserves are available (Boggs, unpublished data). Compensatory feeding, when possible, can also be significant. For example, in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae), early larval food restriction is followed by compensatory feeding. Such feeding yields adults of normal size, but larval mortality is increased during the period of compensatory feeding, and adult mortality is higher in response to late life food stress (Dmitriew & Rowe 2007). The exact allocation patterns associated with consequences of compensatory feeding remain to be discovered and will allow us a better predictive understanding of the effects of periodic food restriction.

We have only begun to understand what happens in variable environments, particularly as experienced in the wild, and studies are relatively scarce. Both stress responses and the extent to which compensation is possible are not well-studied. This becomes ever more urgent with changes in variance in climate parameters, along with changes in means (Boyce *et al*. 2006).

Senescence

Senescence has been defined as 'the age-related decline in fitness traits that arises due to internal physiological deterioration' (Rose 1991; Burger *et al*. 2007). In practice, senescence has often been measured in terms of demographic variables, usually fecundity and longevity. However, functional traits are also subject to senescence. These include muscle or nerve function, or traits related to resilience to environmental challenges, such as immune response, or starvation, dessication, thermal, or oxidative stress resistance. Such functional traits will combine to yield the demographic variables, but functional traits need not change in unison with age.

As should be evident by now, allocation rates or amounts to various life-history traits, including functional traits, do not always result in collapse of the entire organism's physiology at once at the end of life. This is particularly true in stressful environments, where there may be advantages to preserving wing muscles at the expense of fecundity, for example.

Thus, we expect rates and extents of senescence of demographic variables and functional traits to differ in different environments and organisms. Indeed, while dietary restriction in adult *D. melanogaster* can extends life span, functional traits showed deterioration in function, in an age-dependent manner (Burger *et al*. 2007). Further, Lee *et al*. (2008) showed that diet composition, rather than simply caloric restriction, determines life span extension and values of functional traits. However, not all insects behave like *D. melanogaster* in response to dietary restriction; some butterflies show no increase in life span, for example, under adult stress (Boggs & Ross 1993). Why these differences occur requires an understanding of the processes governing allocation, and in particular, of the suites of traits that are favoured by selection (see Arking *et al*. 2002; Lee *et al*. 2008).

Using the allocation framework, we also expect that, for experiments with dietary restriction, whether the quantity or quality of the diet is reduced will make a difference to observed senescence. Likewise, the timing of dietary restriction will be important. These factors should affect resource congruence for a given trait, as a function of the timing of dietary restriction and allocation needs for that trait. The allocation framework thus gives us a predictive framework for understanding the effects of dietary restriction on senescence of different traits.

Researchers exploring senescence have used the 'y-model' of allocation described earlier as one possible rubric for understanding resource acquisition or allocation effects on senescence. However, the broader view of the allocation framework proposed here is needed, given multiple traits and resource types.

Alternative models include accumulated damage as responsible for senescence of a particular trait or physiological function. An interesting possibility is that accumulated

damage may influence allocation itself, hence senescence. Likewise, re-allocation of resources can result in senescence. Resorption of oocytes or of wing muscles results directly in a reduction in fecundity or flight ability, for example.

A broader perspective on acquisition and allocation is thus called for in understanding senescence patterns in diverse environments. Genetic structure and direct physiological controls (such as hormones) do play a role in a complete understanding, but we need to understand senescence at the level of allocation as well.

Conclusions

The allocation framework developed here provides a template for integrating foraging with life-history traits via allocation. This yields a holistic approach to the ecological, physiological and, eventually, evolutionary study of life history. The framework gives us a context for asking several key questions: What combinations of life-history traits can occur under benign environmental conditions? Under what circumstances should we expect acquisition or allocation processes to constrain life histories? Under what general circumstances is a particular life-history trait buffered against resource variation or stressful conditions? Does this come at the expense of other life-history traits? Do the answers vary among insect orders or habitats, and if so, why?

We have made significant progress in beginning to answer these questions. However, there are a number of areas crying out for more work, many of which were highlighted above. In particular, three areas are critical: (i) quantification of resource acquisition and allocation, rather than only observational studies of the outcomes of allocation; (ii) attention to the possible effects of diets provided to study organisms; and (iii) more effective translation of laboratory studies to environmental conditions and resulting acquisition and allocation patterns found in the wild. Additionally, further work on the allocation processes themselves is needed.

To accomplish these tasks, we must study diverse insect groups, particularly if we want to fully understand senescence. *Drosophila melanogaster* is an excellent model system in many respects, but its ecology is little known, and it is apparent that not all insects behave as it does. Other groups, including Lepidoptera, Orthoptera, Coleoptera and Trichoptera, are increasingly under study, which should yield significant additional insights.

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