

Adult feeding and reproduction in Lepidoptera

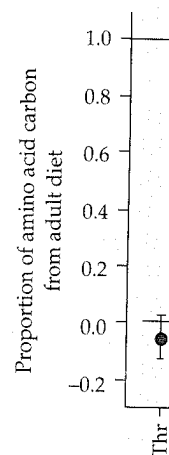
Butterflies provide excellent material for examining allocation of larval nutrients to reproduction or body building, which essentially means allocation to abdomen or thorax. In two species of Nymphalidae that feed only on nectar as adults, thorax mass decreased with age but abdomen mass decreased more, so flight ability was probably not impaired. In contrast, pollen feeding by a third nymphalid, *Heliconius hecale*, led to increases in both thorax and abdomen mass with age (Karlsson 1994). Pollen feeding among adult butterflies is unique to *Heliconius*, and is associated with long adult life and eggs laid singly over a prolonged period. Boggs (1981) predicted that the ratio of reproductive reserves to soma at eclosion would vary inversely with expected adult nutrient intake, and directly with expected reproductive output (assuming that organisms are equivalent in terms of larval nutrition). Her model was supported by data on nitrogen allocation in three species of closely related heliconiines, one of which does not collect pollen. Females obtain nitrogen from larval feeding, adult pollen feeding, and male spermatophores contributed during mating. Because the abdomen of a newly eclosed butterfly consists mainly of reserves stored in fat body, haemolymph, and developing oocytes, the ratio of abdomen total nitrogen to whole body total nitrogen can be used as an estimate of the allocation of larval resources to reproduction. Pollen feeding is unusual in butterflies, but predictions concerning larval and adult nutrient allocations to reproduction are supported by subsequent studies on other butterflies with different life histories (e.g. May 1992).

Nutrients acquired by adult foraging or from males during mating are renewable, while those accumulated during the larval stage are not. This leads to the distinction between capital breeders with non-feeding adults, and income breeders which accumulate resources for reproduction in both juvenile and adult stages. Nutrient allocation dynamics have recently been examined in more detail in nectar-feeding Lepidoptera in which proteins carried over from the larval stage play a major role in adult fecundity. Boggs (1997) used radiotracers to examine the use of glucose and amino acids acquired in larval and adult stages in

two nymphalid butterflies. Glucose and amino acids labelled with ^{14}C and ^3H were painted on leaves to assess larval contributions, or included in nectar solutions to assess adult contributions. Because the adult diet is carbohydrate-rich, incoming glucose is used in preference to stored glucose (storing and then remobilizing nutrients incurs additional costs). By contrast, nitrogen is scarce in the adult diet, and juvenile reserves of amino acids are used throughout adult life. Male nutrient donations at mating, assessed by mating females with males which were labelled as larvae, are less predictably allocated, being immediately used in egg production (Boggs 1997). Stable isotopes have provided information on the dietary sources of amino acids used in egg manufacture by a day-flying hawkmoth, *Amphion floridensis* (O'Brien *et al.* 2000, 2002). These authors fed larvae on grape leaves (*Vitis*, C_3 species) and adults on sucrose purchased as either beet sugar or cane sugar (C_3 and C_4 plants, respectively). C_3 plants are substantially depleted in ^{13}C relative to C_4 plants, so the dietary sources of the carbons in specific egg amino acids can be identified. Essential amino acids originate entirely from the larval diet, whereas nonessential amino acids are synthesized from nectar sugar (Fig. 2.16). Amino acids in nectar contribute insignificantly to egg provisioning. After initial use of larval carbon sources, adult nectar meals provide 60 per cent of the carbon allocated to eggs, but the need for essential amino acids places an upper limit on their use in reproduction. Note that aphids also derive amino acids from dietary sucrose (Fig. 2.12), but their symbionts can synthesize the carbon skeletons of essential amino acids.

Re-allocation of larval nutritional resources can occur after metamorphosis. Flight muscle may be histolysed to provide amine groups for synthesizing non-essential amino acids in egg manufacture (Karlsson 1994). Alternatively, longevity may be favoured at the expense of reproduction, and oocytes are then resorbed when adult food is limited (Boggs and Ross 1993).

Larval performance is more important in Lepidoptera that do not feed as adults. Even as immatures, the sexes differ in food consumption and other performance criteria. Stockoff (1993)



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