NUTRITIONAL AND LIFE-HISTORY DETERMINANTS OF RESOURCE ALLOCATION IN HOLOMETABOLOUS INSECTS

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The "decision" by an organism as to when and how much to reproduce will affect the extent of its genetic contribution to future generations, and is thus of critical evolutionary importance. Factors affecting the evolution of the array of reproductive options available to an organism may be divided into three categories. First, the life table parameters will play a role. That is, any particular decision concerning current reproductive expenditure will affect expected future survivorship and reproduction (i.e., residual reproductive effort). Both present and future reproduction must be taken into account if overall reproductive success is to be maximized (Pianka and Parker 1975). Second, since the decision concerns the expenditure of resources, the status and dynamics of the organism's nutrient/energy budget are important. Included here are patterns of past resource allocation and expenditure, as well as expected levels of future resource acquisition and expenditure. Finally, the degree of environmental variation, including habitat stability and the predictability of mate availability, affects the evolution of possible reproductive options. This last category could be subsumed into the life table analysis, if terms were included giving the potential variation in survivorship and fecundity probabilities at any given age.

The current body of work dealing with reproductive strategy includes examinations of life history tactics (e.g., Gadgil and Bossert 1970; Taylor et al. 1974; Bell 1976; Giesel 1976; Stearns 1976; Schaffner and Rosenzweig 1977), reproductive effort (e.g., Tinkle 1969; Goodman 1974; Schaffner 1974; Hirshfield and Tinkle 1975; Charlesworth and Leon 1976; Pianka 1976; Atkinson 1979), and resource allocation (e.g., Fitzpatrick 1973; Abrahamson 1979), including parental investment (e.g., Trivers 1972; Lawlor 1976; Thorhill 1976; Wilbur 1977; Howe 1978). These studies have concentrated on factors determined by the life table parameters of the organism or by the degree of environmental variation; factors relating to the status of the organism's nutrient/energy budget have generally only been dealt with in terms of growth or survival versus reproduction (e.g., Murdoch 1966; Law 1979). However, while each set of factors affecting the evolution of reproductive strategies is important by itself, such factors do not operate as isolated entities. In order to fully understand the reproductive strategy of an organism, the detailed interaction of the nutrient/energy budget dynamics with the life table and level of environmental variability must be understood.

The interaction between life histories and dynamics of the reproductive nutrient/energy budget is particularly complicated in organisms with complex life cycles, such as insects. Since many of these animals feed as adults, as well as during the immature stage, reproductive effort at any given age will involve a combination of larval-derived and adult-derived nutrients/energy. The proportion of larval-derived nutrients allocated to adult reproductive reserves as distinct from adult soma is determined during reorganization at metamorphosis. Thus, the life history is important in determining both resource allocation at metamorphosis and dynamics of reproductive utilization of larval-derived versus adult dietary nutrients.

A first step in understanding this interaction is to examine the effect of expected adult nutritional and reproductive patterns on the evolutionary allocation of resources during metamorphosis. One approach is to consider the potential reproductive effort (PRE) of such an organism at adult emergence. By extension of the definition of reproductive effort (Tinkle 1969), PRE will clearly depend on the proportion of larval resources allocated to reproductive reserves and on the overall proportion of adult nutrients expected to be allocated to reproduction. Further, PRE should be some monotonically increasing function of the total nutrients expended in reproduction. Therefore, I define

\[ \text{PRE} = a b N_r + b N_i, \]

\[ \text{PRE} = c N_r, \]

where

\[ a = \text{proportion nutrients at adult emergence allocated to reproductive resources versus soma}, \]

\[ B = \text{total body nutrient content at adult emergence}, \]

\[ b = \text{proportion adult dietary nutrients allocated to reproduction versus soma}, \]

\[ N_i = \text{overall adult nutrient intake}, \]

\[ c = \text{constant}, \]

\[ N_r = \text{overall reproductive output in terms of nutrients}. \]

Then,

\[ a b = c N_r - b N_i. \]

The value \( B \) is assumed to be constant, given that the organisms considered have equivalent larval nutrition and survivorship. Assuming that \( b \) is essentially constant, \( a \) should increase with an increase in \( N_i \) for a given \( N_r \) and \( a \) should decrease with an increase in \( N_i \) for a given \( N_r \). In other words, resource allocation during metamorphosis should be adjusted relative to expected adult nutrient intake and reproductive output in organisms with equivalent larval nutrition and survivorship.

The purpose of this study was to verify empirically the basic relationships between resource allocation at metamorphosis and mean adult nutrient intakes and reproductive outputs. The level of resolution was not such as to allow
TABLE I

ADULT NUTRITIONAL AND LIFE HISTORY CHARACTERISTICS OF Heliconius cydno, Heliconius charitonius, AND Dryas julia

<table>
<thead>
<tr>
<th></th>
<th>H. cydno</th>
<th>H. charitonius</th>
<th>D. julia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Longevity</td>
<td>long (max = 180 days in field)</td>
<td>long (similar to H. cydno)</td>
<td>short (max = 32 days in field)</td>
</tr>
<tr>
<td>Food resources</td>
<td>nectar + pollen; females collect more pollen than males</td>
<td>nectar + pollen; females collect more pollen than males; probably slightly less than H. cydno</td>
<td>nectar</td>
</tr>
<tr>
<td>Mating habits</td>
<td>both sexes mate multiply</td>
<td>females often mate only</td>
<td>both sexes mate multiply</td>
</tr>
<tr>
<td>Oogenesis</td>
<td>continuous throughout life</td>
<td>continuous throughout life; total no. oocytes fixed about once</td>
<td>at eclosion</td>
</tr>
<tr>
<td>Habitat</td>
<td>rain forest light gaps</td>
<td>succession</td>
<td>succession</td>
</tr>
</tbody>
</table>

* Summarized from Boggs (1979) and Dunlap-Planka et al. (1977).

examination of the exact relationship among the three variables. However, based on large scale differences in $N_1$ and $N_2$, predictions were made and tested concerning relative $a$ at eclosion in each sex of each of three species of closely related heliconine butterflies, the effect of body size on reproductive reserves, total body nutrients and $a$ in each sex of each species, and the relative degree of sexual dimorphism in $a$ in each species. Further, changes through time in the proportion of the adults' total nutrient content allocated to reproductive reserves were examined in the context of actual adult nutrient intakes and reproductive outputs.

CHOICE OF ORGANISM AND NUTRIENT PARAMETER

Three species of heliconine butterflies, Heliconius cydno Doub1., H. charitonius L., and Dryas julia Fabr. (Lepidoptera: Nymphalidae), were used in this study. These species are ideal for examining the relationship between larval resource allocation and adult nutritional and life history parameters, in that their larval feeding experiences are similar, while their adult nutritional and life histories are divergent (table 1). That is, all feed on species of Passiflora (Passifloraceae) and have a group of acceptable host plant species in common. However, the total number of acceptable host plant species differs among the three butterfly species (Benson et al. 1976; Smiley 1978). Heliconius cydno and D. julia lay eggs singly on young tendrils (H. cydno) or dead tendrils or old leaves (D. julia). Larvae may be cannibalistic, although they seldom encounter each other, at least in H. cydno, because females will not oviposit on a tendril already having an egg present (K. S. Williams and L. E. Gilbert, MS). Heliconius charitonius females deposit single eggs on meristems. More than one female may oviposit on a given meristem, and while larvae are not tightly gregarious feeders, they are not cannibalistic. Competitive interaction for food, therefore, should not differ dramatically among species. Total juvenile mortality is known to be approxi-

mately 95% in H. cydno at Finca La Selva, Costa Rica, and estimated to be of approximately equal magnitude in the two other species (Smiley 1978; Boggs 1979). The species differ, however, in the quality and quantity of adult nutrition, in the frequency and timing of mating, and in the patterns of numbers of eggs and weight of eggs laid during the life span (Gilbert 1972; Dunlap-Planka et al. 1977; Boggs 1979; see table 1).

Nitrogen was chosen as the nutrient to be examined for four reasons. First, vitellogenin (egg yolk) is a protein (Gellissen et al. 1976; Dejemal 1969; Chino et al. 1977). Second, spermatophores, which are absorbed by the female and represent male investment in egg production (Boggs and Gilbert 1979) have been shown to be primarily lipo-protein in those species examined (Khalifa 1949; Davey 1965; Gerber et al. 1971; Gadzama and Happ 1974; Boggs 1979; J. D. Rainbolt and C. L. Boggs, unpublished data). Third, adults of the genus Heliconius are unique in that they feed on pollen as well as nectar (Gilbert 1972), apparently obtaining free amino acids and other nitrogenous compounds thereby. Finally, heliconine butterflies exhibit no parental care aside from the manufacture of an egg and the careful placement of that egg in the environment. Thus, although it does not reflect the time or risk elements of parental investment, nitrogen expenditure may be used as a meaningful rough index of parental investment.

Nitrogenous reproductive reserves in insects are stored in fat body and hemolymph. The reproductive organs themselves may also be considered to contain reserves in the form of developing oocytes or spermatophore components. Since the abdomen of a newly eclosed butterfly consists primarily of reproductive organs, fat body, and hemolymph, with minor contribution from empty gut, empty malphighian tubules, and body wall, the abdomen may be considered to a first approximation as "reproductive reserves." Analysis of reproductive reserves will be less accurate for older adults than for teneral adults, because of the presence of gut and malphighian tubule contents. Variation among individuals due to gut and malphighian tubule contents was minimized by collecting all older individuals at the same point in the diurnal cycle, which was 1 h before sunset. The proportion of nitrogenous reserves earmarked for reproduction, then, may be estimated by the ratio of abdomen total nitrogen to total body total nitrogen, and is equivalent to $a$ in the equations.

MATERIALS AND METHODS

Animal rearing procedure.—All butterflies used in this study were from stock populations maintained along with larval and adult food plants in 6.5 m x 4 m greenhouses on the roof of Patterson Laboratories at the University of Texas at Austin. The Heliconius cydno individuals were descended from individuals captured at Finca La Selva, Heredia Province, Costa Rica, while the H. charitonius individuals were descendents of individuals captured at La Virgen de Sarapiqui, Heredia Province, Costa Rica. Dryas julia individuals were descended from butterflies caught in Austin, which annually move in from south Texas or Mexico.

To obtain newly emerged adults, pupae were removed from the greenhouse and held in cups until eclosion; or larvae were raised in cups on normal host plant, or
on normal host plant in a controlled environment chamber, with 85% humidity, 24.5°C and a 12:12 light:dark cycle. The teneral adults were frozen after releasing all pupal waste products. Wing length from the basal sclerite to the tip of the forewing was recorded for each individual. Analysis was done on individuals with a range of wing lengths in each sex and species.

In order to obtain adults of known age, individuals in the greenhouse populations were numbered the day after emergence, and sex and wing length were noted. Pollen load sizes were noted each day for as many individual Heliconius as possible, using a subjective scale of 0–3; Dries do not collect pollen. (Pollen is collected daily soon after anther dehiscence, mixed with fluid and agitated as a wet mass on the Heliconius' proboscis for several hours before being discarded [Gilbert 1972]. The subjective scale was based on relative size of the wet pollen mass; periodic pollen grain counts, done in part to assure consistency of ratings, yielded approximately 10⁶ grains per index [Boggs 1979]). The greenhouse was searched every 2 h during daylight for mating pairs of all species. Identification numbers of mating individuals were noted. Individuals were removed from the greenhouse 1 h before sunset on the day they reached the desired age and immediately frozen.

Nitrogen analysis.—Abdomens and head-wings-thorax portions of adult butterflies were analyzed separately in each case, using a microKjeldahl nitrogen procedure adapted from that of McKenzie and Wallace (1954).

**EFFECT OF BODY SIZE ON NITROGEN CONTENT AND a AT EMERGENCE**

Predictions.—Abdomen and total body nitrogen will be correlated with body size at emergence for any particular sex and species, whereas a will not.

For organisms that have not yet reproduced, both "reproductive reserves" and "total body" should be strongly correlated to overall body size by either allometric or isometric growth patterns. However, if resource allocation at metamorphosis is dependent on sex- and species-specific expectations of adult nutrient intake and reproductive output, the proportion reproductive reserves to total body should be independent of general body size within a sex and species. In this study, this means that abdomen and total body N of newly eclosed individuals should be strongly correlated to wing length (one good measure of overall body size, as wing length is strongly correlated with pupal weight for a given sex and species; Smiley [1978] and personal communication), while a should be independent of wing length in all sexes and species.

Results.—Because of different patterns of input and output of nitrogenous compounds between the sexes as well as among species, each sex of each species was considered separately in examining the relationship at adult eclosion between wing length and any of abdomen nitrogen, total body nitrogen, or a. Correlation coefficients were calculated for each pair of data sets using the natural log of all values except those of a, which were left untransformed. For those groups in which skewness might have affected the calculated significance level in a parametric test, a Kendall's rank correlation coefficient was calculated to verify the conclusions resulting from the parametric test.

As expected, each sex of each species at adult eclosion exhibited a significant positive correlation between wing length and total body nitrogen, as well as between wing length and abdomen nitrogen (table 2). In general, the relationship between wing length and total body nitrogen appeared to be slightly tighter than the relationship between wing length and abdomen nitrogen, since most groups showed higher correlation coefficients for the former than the latter.

Further, no relationship between wing length and a was found for any sex of any species at adult eclosion, except D. julia males (table 2). This group yielded a correlation coefficient of -0.70 (.01 < P < .05), indicating that an increasing proportion of resources are allocated to reproductive reserves as body size increases. The reasons behind this relationship can only be elucidated by further work on the dynamics of the nutrient budget.

**EFFECT OF N₁ AND Nᵣ ON a AT ADULT ECLOSION**

General predictions.—At emergence a will vary inversely with N₁ and directly with Nᵣ across organisms with approximately equal larval nutritional and life histories.

In any set of organisms with approximately equivalent larval nutrition and survivorship, those organisms with high expected future nutrient intake should allocate more nutrients or energy at metamorphosis to a long-lasting, sturdy body, with the amount going into reproductive reserves being inversely related to the probability of obtaining a given consistent future intake. As the probability of
future nutrient intake declines to zero across the set of organisms, relative allocation to reproductive reserves should increase until the physiological life span of total body is approximately equal to the reproductive life span of reproductive reserves.

Specific predictions.—Translated into the heliconine system (table 1), \( a \) at adult eclosion should decrease across species with a sex with an increase in pollen feeding. Further, since mating constitutes a nitrogen intake for females (Boggs and Gilbert 1979; C. L. Boggs, MS), \( a \) in females should decrease across species with an increase in mating frequency. Finally, since differences in future expected reproductive output should be directly correlated with differences in the ratio of reproductive reserves to soma at eclosion, \( a \) in females should decrease across species with a decrease in expected egg nitrogen output, and \( a \) in males should decrease across species with a decrease in expected nitrogen output in spermatophores. Note that this last prediction reflects the only species differences in degree of male-male competition or relative male reproductive success among species that can be measured by nitrogen allocation.

In order to generate species rank orders of expected \( a \), estimates of the difference between expected adult intake of nitrogen and output of nitrogen in reproduction were made for each sex of each species. Greenhouse data on average pollen load sizes, longevity and number of matings combined with greenhouse data on the extractable nitrogen content of a size 1 pollen load and on the nitrogen content of each species’ spermatophore as well as the percentage of the spermatophore absorbed by the female (C. L. Boggs, MS and unpublished data) were used for females. Nitrogen from nectar feeding was assumed to be equivalent across species. The same data base was used for calculations involving males, except mean number of matings based on spermatophore counts of field-caught females were used for Heliconius cydno and Dryas julia (Boggs 1979). Since D. julia showed no significant difference in mean number of matings between the greenhouse and wild-caught females (Boggs 1979), use of field mean number of matings should not affect \( D. julia \) calculations. However, \( H. cydno \) maintained in greenhouses showed lower pollen feeding values and higher mean number of matings than observed in the field (Boggs 1979). All existing evidence shows no relationship between number of matings by male \( H. cydno \) and quantity or timing of male pollen feeding. Thus, mean number of matings from field data should be the best estimate of male expenditure in reproduction. Estimates of male intake of nitrogen should be low for the two Heliconius species; however, increasing estimates of pollen feeding should not alter the resulting species rank order. Greenhouse estimates of pollen feeding and number of matings were used for females, however, as the two parameters may interact in this sex. That is, evidence suggests that the size of the spermatophore mass in the bursa, sensed either through a stretch receptor or through the nutritional state of the female, determines the female’s willingness to remate (C. L. Boggs, MS). The rate of absorption of the spermatophore is potentially affected by the female’s pollen feeding habits. Thus, if the female has a low pollen feeding rate, spermatophores may be absorbed more rapidly and the female may mate more often. Since

<table>
<thead>
<tr>
<th>Females</th>
<th>MALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. cydno</td>
<td>H. charitonius</td>
</tr>
<tr>
<td>Pollen</td>
<td>0.09</td>
</tr>
<tr>
<td>Mating</td>
<td>0.24</td>
</tr>
<tr>
<td>Total</td>
<td>0.33</td>
</tr>
<tr>
<td>Reproduction</td>
<td>1.39</td>
</tr>
<tr>
<td>Inputs - outputs</td>
<td>-1.06</td>
</tr>
</tbody>
</table>

sequential observations of pollen load size on the same individual throughout its life are difficult to obtain in the field and pollen feeding habits change with age (Boggs et al. 1981), field estimates of average pollen load size are less reliable than greenhouse estimates. Therefore, in order to be consistent, greenhouse estimates of mating frequency and pollen feeding were used for females.

For females, mean output of nitrogen subtracted from mean input of nitrogen yielded \( -1.06 \) mg N for \( H. cydno \), \( -2.12 \) mg N for \( H. charitonius \), and \( -2.22 \) mg N for \( D. julia \) (table 3). Thus, for females, the expected rank order from low to high \( a \) is \( H. cydno \), \( H. charitonius \), \( D. julia \).

For males, however, mean output of nitrogen subtracted from mean input of nitrogen yielded \( -2.7 \) mg N for \( H. cydno \), \( -0.83 \) mg N for \( H. charitonius \), and \( -3.4 \) mg N for \( D. julia \) (table 3). Thus, for males, the expected rank order from low to high \( a \) is \( H. charitonius \), \( H. cydno \), \( D. julia \).

Note that flight expenditures are not part of reproductive output when nitrogen is the nutrient being measured. Flight does not use up nitrogen per se in Lepidoptera, except in the sense of “wear and tear” of proteins (Sacktor 1975; Bailey 1975), which is subsumed under “maintenance.” Further, if nitrogenous compounds are utilized as flight fuel, the nitrogen will be transaminated from amino acids and shunted elsewhere. Therefore, differences in flight between sexes and species have not been examined for effect on the ratio of reproductive reserves to soma.

Results.—Mean \( a \) was compared (within sexes) among species using an analysis of variance, since \( a \) was normally distributed and there was no indication of deviation from constant slope regressing total body nitrogen on abdomen nitrogen for each sex and species. There were significant differences in \( a \) among all species within a sex, with the species ranked from highest to lowest \( a \) being \( D. julia \), \( H. cydno \), and \( H. charitonius \) for males, and \( D. julia \), \( H. charitonius \), and \( H. cydno \) for females (table 4). This rank order is consistent with the predictions for both sexes.
EFFECT OF $N_t$ AND $N_r$ ON SEXUAL DIMORPHISM IN $a$ AT ADULT ECOLSION

Predictions.—As the direction and degree of sexual dimorphism in $N_t$ approaches that of $N_r$ across a set of organisms, the sexual dimorphism in $a$ at emergence decreases.

A sexual dimorphism in reproductive output combined with an increase across species in sexual dimorphism in future expected intake should yield a corresponding decrease in sexual dimorphism in the ratio of reproductive reserves to soma. In other words, as the difference in reproductive output between sexes is more nearly met by a corresponding increase in sexual dimorphism in future expected intake, there is a smaller necessity for the difference in reproductive output to be covered by a dimorphism in current reproductive reserves.

Predictions as to relative degree of sexual dimorphism in $a$ in the heliconiines may be made by examining the magnitude of the difference in input minus output between sexes in each species. The value for $H. cydno$ is $-0.79$ mg N, for $H. charitonius$ is $-2.09$ mg N, and for $D. julia$ is $-1.88$ mg N (table 3). Thus, $H. cydno$ should exhibit the least sexual dimorphism, followed by $D. julia$ and $H. charitonius$.

Results.—The prediction that sexual dimorphism in $a$ should decrease with decreasing pollen feeding and/or decreasing mating frequency was examined by calculating a sexual dimorphism index (SDI) for each species, where SDI = (larger mean $a$ – $95\%$ confidence interval of the mean) – (smaller mean $a$ + $95\%$ confidence interval of the mean). Heliconius cydno showed no sexual dimorphism in $a$. Heliconius charitonius had an SDI equal to .07, and $D. julia$ had an SDI equal to .08. The results are consistent with the predictions except that the rank orders for $H. charitonius$ and $D. julia$ are the reverse of the expected order. This suggests that male $H. charitonius$ may have a larger nitrogen expenditure in reproduction than that represented solely by spermatophore nitrogen. Males of this species are known to pass odiferous compounds to females during mating (Gilbert 1976) that may be involved in maintaining female monogamy. No such system is known in $D. julia$ or $H. cydno$. Further, at least some lepidoptera transfer nitrogen as liquid glandular secretions at mating (Goss 1977), and it may be that the amount of non-spermatophore nitrogen donated by males varies from species to species.

CHANGES IN NITROGEN CONTENT AND $a$ THROUGH THE LIFE SPAN

Predictions.—Changes through the adult life in abdomen nitrogen, total body nitrogen and $a$ will depend on actual adult nutrient intakes and reproductive outputs of nutrients.

The exact pattern of change through the lifetime in the ratio of reproductive reserves to soma in an organism will depend on the patterns of intake and reproductive output of nutrients, as well as on the decay rate of total body caused by wear and tear. Ideally, both total body and reproductive reserves should arrive at approximately the same time at the point where further life and reproduction are no longer possible. However, the path by which that point is reached will
depend on intakes and outputs of nutrients, so that abdomen and total body nitrogen may fluctuate seemingly independently of each other.

Based on these ideas, various predictions can be made concerning which factors will affect rates of change in abdomen nitrogen, total body nitrogen, and $a$ in the heliconine species. That is, abdomen or total body nitrogen at any time in *D. julia*, which does not pollen feed, should depend on age (time), number of matings (representing either intake or reproductive output, depending on the sex), and wing length (as a measure of nitrogen at eclosion, or time 0). In the same species, $a$ should depend on number of matings and only potentially on age, for reasons discussed in the preceding paragraph.

The situation for pollen feeding *Heliconius* species is even more complex. First, since male pollen feeding habits are not correlated with mating patterns (C. L. Boggs, MS), input of nitrogen does not follow output of nitrogen and number of matings should have a significant effect on $a$ and abdomen nitrogen in males. Therefore, factors with a significant effect on abdomen and total body nitrogen through time should include age, wing length (as a measure of nitrogen at eclosion), pollen feeding, and number of matings (representing inputs and outputs). Changes in $a$ should be affected by all of the above except wing length. Second, decay of abdominal nitrogen through utilization of reserves may be greater in the first month or so, becoming progressively slower as pollen feeding increases with age (C. L. Boggs, MS). Finally, because of greater adult nutrient intake, both abdomen and total body nitrogen should decay at a slower rate in *Heliconius* than in *Dryas*.

**Results.**—Each sex of each species was again examined separately in testing the predictions concerning changes in $a$, abdomen, and total body nitrogen through the life span. In order to separate the effects of the possible variables, partial linear regressions were performed relating the parameters of interest to $a$, abdomen, and total body nitrogen. In instances where the independent variable had a skewed distribution, each dependent variable was tested separately using a Kendall rank correlation coefficient. Since sampling was destructive, the results are population values, rather than compiled values for a single individual through time.

As predicted, wing length had a significant positive effect independent of time in all sexes of all species on abdomen and total body nitrogen, but not on $a$ (Tables 5, 6, 7). Intriguingly, even *D. julia* male $a$ did not depend on wing length. When combined with the observation that early adult survivorship is higher in the greenhouse than in the field (Boggs 1979), this suggests that these males are allocating increasing amounts of nutrients to ready mobilized reserves as body size increases. Such reserves may then be expended early in life at a rate independent of general body size, either in mating or somatic maintenance.

Age, either by itself or in combination with number of matings, had a significant negative effect in all cases except male *H. cydno* and *H. charitonius* total body nitrogen or male *D. julia* and female *H. charitonius* $a$. However, both male *H. cydno* total body nitrogen, and male *D. julia* and female *H. charitonius* $a$, exhibited inverse relationships with mating number, which is correlated with age (C. L. Boggs, MS).
TABLE 6
Factors Affecting Total Body Nitrogen through Time

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Wing Length</th>
<th>Mating No.</th>
<th>Mating Age</th>
<th>Pollen Collecting Frequency</th>
<th>Mating No. + age</th>
<th>Pollen Collecting Frequency + Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heliconius cydno</td>
<td>δ</td>
<td>+5.297</td>
<td>−867</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 37</td>
<td></td>
<td>F = 48.35</td>
<td>P &lt; .005</td>
<td>.05 &gt; P &gt; .01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 22</td>
<td></td>
<td>F = 20.87</td>
<td>P &lt; .005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heliconius charitonius</td>
<td>δ</td>
<td>+2.608</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 29</td>
<td></td>
<td>F = 42.06</td>
<td>P &lt; .005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 29</td>
<td></td>
<td>F = 3.31</td>
<td>P &lt; .005</td>
<td>.05 &gt; P &gt; .01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dryas julia</td>
<td>δ</td>
<td>+5.758</td>
<td>−2.66</td>
<td>−.047</td>
<td></td>
<td></td>
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<tr>
<td>n = 25</td>
<td></td>
<td>F = 78.35</td>
<td>P &lt; .005</td>
<td>.025 &gt; P &gt; .005</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>n = 30</td>
<td></td>
<td>F = 46.25</td>
<td>P &lt; .005</td>
<td></td>
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</tr>
</tbody>
</table>

Note.—Wing length, mating number, and age were regressed on total body nitrogen for Heliconius cydno and Dryas julia; those factors plus pollen collecting frequency and average pollen load size were regressed on total body nitrogen for H. charitonius. Slopes and significance levels of the significant terms in the regression are shown.

As expected, the rates of decay of abdomen or total body nitrogen for Heliconius were significantly lower than the decay rates for Dryas julia females. In general, rates of decrease of either abdomen or total body nitrogen did not differ among sexes or species within the Heliconius group. The Dryas julia males and Dryas julia females did have a lower rate of decrease of abdomen or total body nitrogen than the Heliconius group. This suggests that there is no difference in rate of decrease of abdomen or total body nitrogen between the first month and later the when more pollen is collected.

Pollen feeding played no role in determining any of the Heliconius a, total body (male or female) nitrogen. However, frequency of pollen feeding (but not average pollen load size) had a significant negative effect on total body nitrogen of adult females. This result suggests that females pollen feed increasingly as larval reserves are drawn down, such that costs associated with finding and processing pollen are delayed until such time later in the adult life for learning the location of adult food resources.

Note.—Pollen collecting frequency and average pollen load size were regressed on a factor affecting 4 through time for H. charitonius. Slopes and significance levels of the significant terms in the regression are shown.
Values for _D. julia_ males were not significantly different from those for the _Heliconius_ species. However, greenhouse populations of _Heliconius_ spp. may not have been collecting as much pollen as their field counterparts, and certainly were shorter lived than those in the field (Boggs 1979). This suggests that perhaps rates of decay of abdomen or total body N through time should actually be lower than that observed in the greenhouse population, and therefore lower than those of _D. julia_ males.

**DISCUSSION**

**Evidence from Other Organisms**

Very little direct evidence addressing the predictions set forth here is available from other studies of organisms with complex life cycles, with the exception of studies of autogenous and anautogenous mosquitoes. Autogenous female mosquitoes do not require an adult blood meal prior to laying the first egg batch; anautogenous females do. Briegel (1969) showed that, given equivalent larval nutritional conditions, autogenous female _Culex pipiens pipiens_ had more larval nitrogenous reserves at emergence than did anautogenous _C. pipiens fatigans_. After production of the first egg batch, females of the two subspecies did not differ in nitrogen content. Taking into account differences between the two subspecies in time of yolk deposition for the first egg batch, Briegel concludes that the autogenous females are using larval reserves to manufacture the first egg batch to a greater extent than do anautogenous females. Briegel's evidence supports the predictions presented here, in that females with a lower expected adult nutrient intake have a larger nutrient reserve from larval feeding at emergence. Similar results have been obtained by Twenhofel and Rozeboom (1957) for autogenous female _C. pipiens pipiens_ and anautogenous female _C. pipiens molestus._

**Further Considerations**

The data presented here show that allocation of larval nutrient resources to reproductive reserves at metamorphosis may be predicted from knowledge of overall adult nutrient intake and reproductive output. This suggests an evolutionary interaction between patterns of resource allocation during metamorphosis and nutritional/life histories. This finding has various implications for the reproductive biology of organisms with complex life cycles.

First, the finding demonstrates qualitatively the manner in which adult and juvenile energy/nutrient budgets interact. This may then be used in further studies of the factors affecting allocation of resources to reproduction. Questions of interest include the exact form of the relationship between the adult energy/nutrient budget and the pattern of allocation of larval reserves at metamorphosis, the effect of environmental variation on allocation patterns and the effect of relaxing the assumption made in the present study that larval nutrition and survivorship are invariant across species. Given the findings of the present study, models addressing the above questions may now be constructed and tested.

Second, the data presented here for organisms with complex life cycles tie together elements of the life cycle and nutritional budget, demonstrating some of the constraints within which the organism's reproductive strategy operates. That is, an adjustment in overall adult nutrient intake or reproductive output is accompanied by concomitant change in allocation of larval resources at metamorphosis; the various elements of the reproductive strategy do not change independently in evolutionary time.

In a similar manner, the dependence of resource allocation at metamorphosis on overall adult resource intake and output demonstrates that the degree of sexual dimorphism in size or weight in an organism may not directly reflect the degree of sexual dimorphism in resource allocation patterns. That is, _Dryas julia_ exhibit no sexual dimorphism in pupal weight (Smiley 1978), and yet are sexually dimorphic for wing length, with males larger than females (Boggs 1979), and for _a_ with females allocating more larval resources to reproductive reserves than do males.

Finally, there is some indication from the data that _B_, total body nitrogen at adult eclosion, may also have varied slightly (with _D. julia_ having the most nitrogen and _Heliconius charitonius_ the least) even though larval nutrition and life histories were basically equivalent across species. If there is indeed a physiological mechanism for varying _B_ under basically equivalent conditions, then some of the evolutionary adjustment to differences in adult intake and output of nitrogen may occur through changes in total body nitrogen which reinforce changes in the pattern of resource allocation at metamorphosis.

**SUMMARY**

In organisms with complex life cycles, potential reproductive effort at adult emergence may be defined as the sum of the proportion of the body nutrient content devoted to reserves earmarked for reproduction and the proportion of expected adult nutrient intake to be devoted to reproduction, and is proportional to expenditure in reproduction. For organisms with similar larval nutrition and survivorship, the ratio of reproductive reserves to soma at adult eclosion is predicted to vary inversely with expected adult nutrient intake and directly with expected reproductive output of nutrients. These predictions are supported by...
data from heliconiine butterflies. That is, variation in the ratio of reproductive reserves to soma at adult eclosion among heliconiine species and sexes having relatively equivalent larval survivorship and availability of nutrients correlates with patterns of expected intake of nutrients and output of nutrients in the act of reproduction. In general, changes in the ratio over adult life are then determined by actual nutrient intakes and reproductive outputs.

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LITERATURE CITED


