INSECT NUTRITION:
AN ADAPTATIONIST'S PERSPECTIVE

FRANK SLANSKY JR.*

"I'm hungry," he thought and straightway began to eat the leaf he was born on. And he ate another leaf . . . and another . . . and another. And got bigger . . . and bigger . . . and bigger . . . Until one day he stopped eating and thought, "There must be more to life than just eating and getting bigger. It's getting dull." (Stripe the caterpillar, in Paulus 1972).

"Insect nutrition? Aagh, that's boring stuff! Let's talk about something else." This comment has been attributed to a well-known entomologist who has done considerable pioneering research in insect nutrition. One person's opinion, yes, but I suspect it is commonly held. When viewed from the narrow perspective of the basic nutritional requirements of laboratory colonies feeding on artificial diets, insect nutrition, though supplying essential information for a complete understanding of insect life, is indeed "boring stuff." The insects themselves must also share part of the blame; except for their requirement of a dietary sterol, their nutritional needs differ in only minor ways from those of vertebrates (Dadd 1973).

Insect nutrition was given a strong dose of much needed excitement with the realization that not only are basic nutritional requirements important, but so are the amounts and rates of food eaten, digested, assimilated and converted to tissue growth, and that these can be affected by variation in both basic nutrients and non-nutritional compounds (e.g. allelochemicals) in the food. This area of research has been called "insect dietetics" (Beck 1972, Beck and Reese 1976) and "quantitative nutrition" (Scriber and Slansky 1981) (Fig. 1). When we examine and evaluate the changes in an insect's behavior and regulatory physiology, as it attempts to cope with a variable environment, and when we identify the ecological consequences and evolutionary aspects of such behavior, then "insect nutrition" achieves a greater significance by metamorphosing into "insect nutritional ecology" (Fig. 1).

I shall here identify the kinds of interactions we need to understand to lay a solid foundation for a nutritional ecology of insects, and present some illustrative examples.

THE PARADIGM OF NUTRITIONAL ECOLOGY

Paulus' quote above suggests that feeding and growth are basically passive-flow, inflexible processes, similar perhaps to the diversion of a stream to fill a pond: water or food flows in, and the pond or caterpillar gets larger. This is a common misconception. Feeding and growth are active, dynamic processes with feedback mechanisms and wide ranging ramifications throughout an insect's life (Fig. 2, and below)\(^1\).

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*Frank Slansky Jr. is an assistant professor in the Department of Entomology and Nematology at the University of Florida. His research interest is in the nutritional ecology of larval and adult insects within both basic and applied contexts.

Current address: Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611. Florida Agricultural Experiment Stations Journal Series No. 3478.

\(^1\)Superscripts refer to notes in the Appendix of this paper.
Fig. 1. The metamorphosis of insect nutritional ecology from nutrition and dietetics.

Fig. 2. Interactions of feeding behavior with other key behaviors. See Appendix note 1 for specific examples.
Whatever the historical roots underlying this misconception (emphasis on mean values, pesticides and energy flow studies have had some role)\textsuperscript{5}, it must be stressed that individuals in a population are not identical copies of “passive, open-loop, energy partitioning device(s)” (Hubbell 1971, p. 271; see also Slobodkin 1965, Wellington 1977, and others). In addition to differences among species and populations in appearance, physiology and behavior, there are within population differences in individual performance, and this performance includes active modifications of physiological and behavioral responses to a variable environment.

The basic paradigm for nutritional ecology can thus be stated as follows: Within a particular realm of environmental conditions, there is a set of states (e.g. a particular body size, color, wing loading ratio, proportion of resources allocated to eggs, timing of life cycle events, etc.) which is “optimum” in the sense that it will result in maximal fitness for the individual (see McFarland 1977). We wish to identify how this optimal set of states differs among species and populations, and within populations through time, and the selective forces that bring about these differences (Fig. 3A).

Furthermore, we wish to answer the questions of how, and to what extent, an individual can alter, in response to a changing environment, its physiological and behavioral processes (e.g. consumption rate, metabolism, synthesis of glycerol for freezing tolerance, and extent of movement) to achieve and maintain the optimal set of states. We also wish to identify the ecological consequences (including changes in the timing and amount of reproduction and in probability of survival) of alterations in these processes and of inability to achieve and maintain the optimal set of states (Fig. 3B).

Finally, we wish to identify how the differences in process alteration and in deviation from optimal states, in response to a particular change in the environment, vary among populations and species, and to identify the consequences for fitness of these differences (Fig. 3C). This will help us understand the evolution of different lifestyles\textsuperscript{6}.

This view of nutritional ecology is a useful way to structure and synthesize research on both the basic and applied aspects of behavioral ecology. Because of the primacy of feeding behavior, food allocation and associated processes, and because of their pervasiveness throughout an organism’s life, an understanding of these processes should indicate the significance of variation in most of the other aspects of an organism’s lifestyle. In other words, investigating the underlying nutritional basis to many of the “decisions” an insect might make in its lifetime will help us understand why they are made.

**DECISIONS, DECISIONS, DECISIONS:**

**A DAY IN THE LIFE OF AN INSECT**

The life of an insect is filled with decisions. In the sense used here, an insect “makes a decision” when, after “evaluating” environmental inputs, it responds in some manner (Hubbell 1971, Dawkins and Dawkins 1973, McFarland 1977). The response may be to continue physiological and behavioral processes at their current levels. Or, the responses may be inductive or compensatory. An *inductive* response involves a change from some previously optimal set of states to a new set (e.g. see “Diapause” below); a *compensatory* response involves an attempt to maintain some particular set of states in the face of a changing environment (e.g. see “Feeding” below).
Fig. 3, A-C. The paradigm of nutritional ecology. A. Identification of (1) the differences in the optimal set of states (e.g., body size, color, and wing size, indicated by the three units of each symbol) for an individual of different species (different symbols), different populations, and different generations within a population (indicated by the reduction in size of the third box), and (2) the selective factors (arrows) that bring about these differences. B. Identification of (1) the alterations in an individual's physiological and behavioral homeostatic processes such as increased food consumption (plus sign on left) in response to a deterioration in food quality (minus sign on left) and increased time spent basking on the surface of a leaf (plus sign on right) in response to a drop in ambient temperature (three minus signs on right), in an attempt to achieve and maintain the optimal set of states (indicated by the four boxes at the top), and (2) the ecological consequences (dotted lines) resulting from the process alterations (e.g., increased probability of mortality from increased exposure while feeding and basking) and from inability to achieve a particular state (e.g., reduced fitness because of the lowered fecundity indicated by the reduced size of the rightmost box at bottom). C. Identification of (1) differences between an individual of two species (e.g., a migratory one indicated by the boxes and a non-migratory one indicated by the circles) when confronted with a change in environment (e.g., a shortening of daylength indicated by the two minus signs at left and right). The larva of the migratory species responds with a moderate increase in food consumption (three plus signs at left) to
In order to understand the evolution of these active responses within their adaptive context, it is important, albeit often difficult, to distinguish them from situations in which the insect responds passively with little choice. For decisions and responses involving metamorphosis, reproduction, migration and diapause, the underlying neurohormonal integration and physiological feedback mechanisms are reasonably well understood (Chen 1971, DeWilde and DeLoof 1973b, Chippendale 1977, Rankin 1978, Gilbert et al. 1980). This is in contrast to the poorly understood cause/effect interactions relating feeding, metabolism and growth to each other and to other behaviors (Keister and Buck 1974, Barton Browne 1975, Steele 1976, Kammer and Heinrich 1978, Bernays and Simpson 1981, Scriber and Slansky 1981). I shall now discuss some of the many decisions, and physiological and behavioral responses that an insect may make, to demonstrate their underlying nutritional aspects and their consequences throughout the insect's life.

**Egg Hatch**

The timing of egg hatch can be critical to the survival of larvae that feed on young leaf tissue. If an egg hatches too early before budburst the larva may starve to death; if it hatches too late the leaves may have aged sufficiently to render them a poor quality food (Fenoy 1976, Gilbert 1980, Schneider 1980). Furthermore, the energetic cost of embryonic development and maintenance may be considerable, such that delay in egg hatch may cause premature utilization of energy reserves destined for the larval stage. Species that overwinter in the egg or early larval stages may have greater egg size and/or caloric content than related species that overwinter as mature larvae or pupae (Purrington and Nielsen 1977, Anderson 1978, see also Capinera 1979).

**Feeding**

While the underlying nutritional aspects of feeding behavior are obvious, the subtleties of the feeding responses are important to understand because of their significance throughout an insect's life (Fig. 2). The feeding responses of phytophagous insects are strongly influenced by olfactory and gustatory stimuli resulting from both nutritional and non-nutritional (especially allelochemical) compounds in the food. The response to allelochemicals, including both feeding stimulants and deterrents, seems generally to be the primary determinant in the insect's decision of whether or not to feed on a particular plant (for reviews see Chapman 1974, Beck and Reese 1976, Kogan 1977, Nethier 1980).

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*achieve the new state of increased wing size facilitating migratory flight by the adult (increased size of rightmost lower box), whereas the larva of the nonmigratory species responds with an even greater increase in food consumption (five plus signs at right) to achieve its new state of increased lipid storage (increased size of middle circle) to fuel metabolism in the diapausing pupa. Ecological consequences (dotted lines) are as discussed in B. Information on these optimal sets of states, responses and consequences depicted in A-C allows us to better understand the evolution of different lifestyles.*
Given an acceptable food, further decisions of how fast, of how often and of how much to eat are required. Growth rate (including both rate of development and final weight at pupation) has significant impact on fitness. Therefore individuals of a particular species are expected to exhibit a certain feeding rate which will result in an optimal growth rate. The observed feeding rate will probably be less than the physiological maximal rate because of certain costs associated with feeding. That insects are not operating at their maximal feeding rate is indicated by the increase in food consumption frequently observed in response to a deterioration in food quality (Table 1). The degree to which different species exhibit this compensatory response may be related to their lifestyle. For further discussion of feeding strategies (i.e. decisions and responses) see Hassell and Southwood (1978), Mattson (1980), and Sizer and Slansky (1981).

**Pupation**

The ultimate goal of a larva is to produce a reproductively competitive adult. Therefore, it is perhaps not surprising that the decision to pupate, or molt to adult in hemimetabolous insects, often depends on the attainment of some minimal body weight (which is below its optimum) (Gilpin and McClelland 1979, Nijhout 1979, Grabstein and Sizer 1981, and references in Sizer and Slansky 1981). If a larva is subjected to poor food quality (which slows its growth rate) it seems to evaluate the potential costs of prolonged development (see Appendix note 11) versus the potential costs of reduced adult size. When growth is slowed before the larva has achieved the minimal weight, the choice is probably made—the potential costs of prolonged development are going to be less than those of producing an adult too small to be reproductively competent. However, above the minimal weight the larva may make a choice that balances the potential costs of prolonged development and those of producing an adult whose size and performance are somewhat reduced. The percentage of optimal weight at which the minimal weight is evolutionarily adjusted varies between species and is probably related to their particular lifestyle.

**Diapause**

In climates where year round activity is not possible, insects may become dormant (i.e. diapause) to cope with the unfavorable season, or they may migrate to an area with a favorable climate (see papers in Dingle 1978, and section below). When diapause is facultative, the decision to do so is made after evaluating certain environmental cues. Most frequently these are changes in photoperiod and temperature (Hoffman 1978, Hoy 1978, Beck 1980, Makaki 1980, Taylor 1980), although changes in food quality may also be involved.

Diapause occurs in all life stages but within a species it typically occurs in only one stage. In phytophagous insects the pattern of seasonal change in plant quality associated with different plant growth-forms may be a major environmental factor influencing the evolution of which life stage over-winters. Whatever the overwintering stage, it frequently contains a greater percentage of lipid reserves and/or is larger than non-diapausing individuals (Lang 1963, Downer and Matthews 1976, Calow and Jennings 1977, Purring-
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18. In species that exhibit facultative migration, the decision to initiate migratory flight is made by the adult after evaluating environmental cues such as photoperiod, temperature and food. This process is similar to the decision-making for entry into diapause (DeWilde and DeLoof 1973a, 1973b, Johnson 1976, Rankin 1978) but changes in food quality and quantity appear to play a much greater role in influencing an adult’s decision to initiate flight than they do in influencing a larva’s decision to diapause. For example, in some insects mated females choose to begin laying eggs and inhibit flight in the presence of adequate food; a lack of, or poor quality food inhibits their oviposition and stimulates flight (Rankin 1978, Sölbrec and Pehrson 1979, Slansky 1980b). Furthermore, although only a few species have been studied, food quality and other factors affecting larval performance may also have a significant effect on adult movement (Mittler and Sutherland 1969, Wellington and Maelzer 1967, Leonard 1971, Sanders and Lucuik 1975).

Active flight is a costly process, but whether migratory individuals stock up on fuel reserves prior to flight is less clearly understood than is the frequently seen increased lipid storage prior to diapause (Nayar and Sauerman 1969, Sölbrec 1972, and references therein, Downer and Matthews 1976, Slansky 1980c). In many species there are obvious differences in wing and body size between migrant and nonmigrant individuals in a population (Harrison 1980). This certainly suggests differences in the amount of food consumed by larvae and the way it is allocated to building the adult, as well as differences in adult feeding and fecundity (Waldbauer 1988, Raccach and Tahori 1971, Dixon 1972, Rose 1972, Harrison 1980, Ono and Nakasuji 1980). The negative effects on fecundity of fuel utilization during flight seem to be more severe for species that utilize carbohydrate for fuel (e.g., most Diptera) than for those that utilize lipid (e.g., Homoptera and Hemiptera) (references in Slansky 1980c).

Egg Production

In making a choice of oviposition site, a female may evaluate a number of features of the food (e.g. plant size, leaf shape, color, odor, taste and presence of other eggs; DeWilde and DeLoof 1973a, Labeyrie 1978b, Rauscher 1978, 1979, Williams and Gilbert 1981). In species exhibiting a semelparous
<table>
<thead>
<tr>
<th>Species (Reference)</th>
<th>Reduction in Nutrient Concentration</th>
<th>Alteration in Rate of Food Consumption (Dry Weight/Day)</th>
<th>Effect on Rate of Growth (Dry Weight/Day)</th>
</tr>
</thead>
</table>
| *Blattella germanica*  
German Cockroach (Gordon 1972) | Diet diluted from 13% yeast(y), 88% sugar (s) to 6% y, 19% s, 75% cellulose | 234% increase<sup>a</sup> | 33% increase<sup>a</sup> |
| *Hyalephora cecropia*  
Cecropia Moth (Scriber 1977) | 30% decrease in leaf water and 47% decrease in relative humidity | 17% decrease | 59% decrease |
| *Hyles euphorbiae*  
Euphorb Spimx Moth (House 1969) | 50% dilution of total nutrients in diet with water | 22% decrease | 5% decrease |
| *Locusta migratoria*  
Migrant Locust (Dadd 1969) | 104% increase in cellulose in diet | 57% increase | 10% decrease |
| *Melanoplus sanguinipes*  
Migrant Grasshopper (McGinnis and Kasting 1967) | 88% dilution of diet with cellulose 94% dilution of diet with cellulose | 586% increase 498% increase | 9% decrease 62% decrease |
| *Periplanea americana*  
American Cockroach (Bignell 1978) | 70% dilution of dextrin in diet with cellulose | 64% increase | 28% decrease<sup>a</sup> |
| *Phaedon cockleariae*  
Mustard Leaf Beetle (Taylor and Bardner 1968) | 41% decrease in leaf protein; turnip (4 vs 8 week old plants) 37% decrease in leaf protein; radish (4 vs 8 week old plants) | 28% increase | 29% decrease |

<sup>a</sup> Florida Entomologist 65 (1) March, 1982
<table>
<thead>
<tr>
<th>Species</th>
<th>Reduction in Nutrient Concentration</th>
<th>Alteration in Rate of Food Consumption (Dry Weight/Day)</th>
<th>Effect on Rate of Growth (Dry Weight/Day)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pieris rapae</em></td>
<td>56% decrease in % leaf nitrogen; 13 crucifer species</td>
<td>44% increase</td>
<td>25% decrease</td>
</tr>
<tr>
<td>Imported Cabbageworm</td>
<td>75% decrease in % leaf nitrogen; high vs. low fertilized collards</td>
<td>79% increase</td>
<td>26% decrease</td>
</tr>
<tr>
<td>(Slansky and Feeny 1977)</td>
<td>(Slansky 1974a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>33% decrease in % leaf nitrogen; collards (1 vs 5 month old plants)</td>
<td>28% increase</td>
<td>4% decrease</td>
</tr>
<tr>
<td><em>Plutella xylostella</em></td>
<td>Turnip (see <em>P. cochleariae</em>)</td>
<td>126% increase</td>
<td>15% increase</td>
</tr>
<tr>
<td>Diamondback Moth</td>
<td>Radish (see <em>P. cochleariae</em>)</td>
<td>67% increase</td>
<td>31% decrease</td>
</tr>
<tr>
<td>(Taylor and Bardner 1968)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Schistocerca gregaria</em></td>
<td>21% increase in cellulose in diet</td>
<td>208% increase</td>
<td>36% increase</td>
</tr>
<tr>
<td>Desert Locust</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>(Dadd 1960)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*a* Relative rate = dry weight/unit fresh body weight/day.

*b* Fresh consumption rate.

*c* Adult females.

*d* This is a decrease in the number of oothecae produced/unit time.
TABLE 2. **Inductive Process and State Alteration by Last Instar Larvae of the Imported Cabbage Worm, Pieris rapae, as They Prepare to Enter Pupal Diapause in Response to Short Photoperiod (8L:16D), Compared to Larvae Reared in a Non-Diapause Inducing Photoperiod (16L:8D) (Slansky, Unpublished Data)**.

<table>
<thead>
<tr>
<th>Process or State Altered</th>
<th>Magnitude and Direction of Alteration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time in instar (days)</td>
<td>17% increase</td>
</tr>
<tr>
<td>Consumption rate (dry mg/day)</td>
<td>16% Increase</td>
</tr>
<tr>
<td>Food consumed (dry mg)</td>
<td>29% increase</td>
</tr>
<tr>
<td>Growth rate (dry mg/day)</td>
<td>15% decrease</td>
</tr>
<tr>
<td>Weight Gained (dry mg)</td>
<td>7% decrease</td>
</tr>
<tr>
<td>Relative metabolite rate</td>
<td>33% increase</td>
</tr>
<tr>
<td>(dry mg metabolized/dry mg body wt./day)</td>
<td>40% increase</td>
</tr>
<tr>
<td>Pupal lipid content (mg/pupa)</td>
<td></td>
</tr>
</tbody>
</table>

reproductive strategy (Calow 1973), extensive egg production occurs very soon after the adult ecloses, and there is probably little evaluation of environmental cues by the adult prior to oviposition. In such species, poor food quality and other factors causing a reduction in the amount of larval growth (and thus smaller adult size), frequently have a significant negative impact on adult fecundity (Wellington and Maelzer 1967, Leuck and Perkins 1972, Yamada and Umeya 1972, Blau 1978, Wagner and Leonard 1979, Barfield et al. 1980, Barbosa et al. 1981, Moseardi et al. 1981).

At the other extreme are species exhibiting an iteroparous reproductive strategy (Calow 1973). These species manifest repeated reproduction throughout a relatively long-lived adult stage, and food consumption by the adult is important to normal egg production. Decisions are made regarding when to lay, how many, and sometimes even what kind of eggs to lay. Such decisions have great impact on the female’s fitness (Smith and Fretwell 1974, Smith 1976, Istock 1978, Taylor 1980a, Boggs 1981).

In species that feed on a protein source in the adult stage, suggesting that feeding is required not only for adult maintenance but also to supply the energy and nutrients for provisioning the eggs, egg production tends to be closely linked to food consumption through a neurohormonal feedback system (DeWilde and DeLoof 1973a, 1973b, Stoffolano 1974, Regis 1979, Solbreck and Pehrson 1979, Wise 1979, Slansky 1980a, 1980b). Thus a reduction in the quality or quantity of food for the adult female frequently results in a delay in the onset, and a reduction in the rate, of egg production (i.e. process alteration), with the result of prolonging the female’s life and maintaining the size and hatchability of the eggs she does lay (i.e. maintenance of an optimal state) (Table 3, Warren 1924, Engelmann 1970, Calow 1973, Labeyrie 1978a). A further adaptive feature of the female’s choice to halt or reduce egg production under poor food conditions is that she does not waste reproductive effort producing offspring with a low probability of survival (Slansky 1980b).

In nectar-feeders and other insects that utilize a carbohydrate food source, the role of adult food in influencing egg production is not as clear. For only a few of these species is it known whether the food merely supplies...
TABLE 3. MAINTENANCE OF EGG QUALITY (i.e., EGG WEIGHT, % HATCH AND LENGTH OF LIFE OF STARVED NYMPHS) AND CLUTCH SIZE VIA A REDUCTION IN THE RATE AND/OR DURATION OF EGG PRODUCTION BY FEMALES OF 3 SPECIES OF MILKWEED BUGS (Oncopeltus) WHEN FACED WITH FOOD LIMITATION OR STARVATION (F. Slansky Jr., 1980a, and unpublished data). For discussion see Appendix note 25.

<table>
<thead>
<tr>
<th>Food Ration</th>
<th>Egg Production</th>
<th>Egg Quality</th>
<th>Nymphal Life</th>
<th>Clutch Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rate (eggs/wk)</td>
<td>Duration (weeks)</td>
<td>Fresh Weight (mg)</td>
<td>Hatch (%)</td>
</tr>
<tr>
<td><strong>Food Limitation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>O. fesciatus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100% (ad lib.)</td>
<td>138</td>
<td>10</td>
<td>0.39</td>
<td>87(^c)</td>
</tr>
<tr>
<td>50%</td>
<td>74</td>
<td>10</td>
<td>0.34</td>
<td>100(^c)</td>
</tr>
<tr>
<td>25%</td>
<td>34</td>
<td>4</td>
<td>0.35</td>
<td>100(^c)</td>
</tr>
<tr>
<td><strong>O. conquisfer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100% (ad lib.)</td>
<td>88 ± 7(^e)</td>
<td>7.8 ± 2.5</td>
<td>0.23 ± 0.01</td>
<td>55 ± 9(^d)</td>
</tr>
<tr>
<td>50%</td>
<td>34 ± 4</td>
<td>11.2 ± 6.9</td>
<td>0.22 ± 0.01</td>
<td>72 ± 8(^4),</td>
</tr>
<tr>
<td><strong>Starvation</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>O. fesciatus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100% (ad lib.)</td>
<td>188 ± 14</td>
<td>7.0 ± 0.9</td>
<td>0.24 ± 0.01</td>
<td>72 ± 5(^4)</td>
</tr>
<tr>
<td>Starved</td>
<td>73 ± 3</td>
<td>1.2 ± 0.2</td>
<td>0.24 ± 0.01</td>
<td>60 ± 10(^d)</td>
</tr>
<tr>
<td><strong>O. longirostris</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100% (ad lib.)</td>
<td>164 ± 13</td>
<td>12.3 ± 1.7</td>
<td>0.29 ± 0.01</td>
<td>61 ± 6(^4),</td>
</tr>
<tr>
<td>Starved</td>
<td>96 ± 24</td>
<td>1.3 ± 6.3</td>
<td>0.30 ± 0.01</td>
<td>78 ± 5(^4)</td>
</tr>
</tbody>
</table>

\(^a\) Individual newly hatched nymphs were starved with water available until death.
\(^b\) From Slansky 1980b.
\(^c\) Calculated as the percentage of egg clutches in which some eggs hatched. Percentage egg hatch within each clutch was not determined (see footnote \(c\)).
\(^d\) Percentage of egg hatch within each clutch.
\(^e\) All \(\pm\) values are standard errors.
\(^f\) Adults fully fed for seven days after eclosion and then starved with water available until death. Adults starved from eclosion produced no eggs.
\(^g\) Data from seven of eight females; one female never laid eggs.
\(^h\) Data for all females; two females laid only shrivelled eggs which never hatched.
\(^i\) Data for six of eight females; two females never laid eggs.
\(^j\) Data for four of five females; one female laid only shrivelled eggs which never hatched.
water, or if it also serves as an energy source. If the latter, the question remains as to whether the energy is required solely for adult maintenance (i.e., eggs are provisioned from energy and nutrients stored during the larval stage) or to provision eggs as well. Baker and Baker (1975) found considerable variation in sugar and amino acid contents of nectar of different plant species, but there is a lack of data on the impact of this variation on egg production (Shorey 1963, Van Handel 1965, Finch and Coaker 1969, Hines et al. 1979, Penemore 1979).

CONCLUSIONS

The decisions, discussed above, that an insect may make in its lifetime, and many others not discussed (e.g., mate attraction, mate choice, parental investment and nest building) all involve some underlying nutritional component. They include compensatory responses to achieve and maintain the optimal set of states of developmental time, weight gain (body size) and fecundity, in the face of a nutritionally and otherwise variable environment, and inducory responses, changes in optimal states in response to environmental cues. These responses may include changes in amounts, rates and timing of feeding behavior, metabolism, enzyme synthesis, resource allocation, flight behavior and other physiological and behavioral processes.

There are consequences for fitness, because of effects on survival and reproduction, resulting from these responses, and from the inability to achieve and maintain the optimal set of states. Thus, differences among populations and species in the kinds and magnitudes of these responses and optimal states are expected to have evolved as adaptations to different lifestyles. Herein lies the importance of the contribution of nutritional ecology to questions of a basic nature. By understanding the nutritional responses and consequences that occur throughout an organism's life we will achieve an understanding of the ecology and evolution of different lifestyles expressed by species that are migratory or non-migratory, specialized or generalized feeders, herb or tree feeders, parasitic or predatory, and so on.

The fact that this basic information also has applied relevance to the development of integrated pest management strategies has only recently been recognized (Barfield and Stimac 1980, Lovins and Wilson 1980). For example, it is essential that we know the factors influencing the feeding, growth, reproduction, movement and survival of pest insects. Only then can we refine and couple models of pest population dynamics with models of crop plant growth to produce models with greater precision and greater powers of prediction of pest population size and crop plant damage (Hammond et al. 1979, Barfield and Stimac 1980, 1981, Garner and Lynch 1981, Stimac, this Symposium). Such information may also allow us to effectively manipulate the crop environment (such as through chemical fertilization and growing of resistant plant varieties) to disrupt the normal performance of the pest (Louck and Perkins 1972, Jones 1976, Meisner et al. 1977, Norris and Kogan 1980, Tingey and Singh 1980). Thus, structuring and synthesizing research on insect pests within the paradigm of nutritional ecology will yield much useful information of broad relevance. Indeed, just as Stripe the caterpillar found excitement in the prospect of metamorphosing into a butterfly, so too can we find excitement in the unfolding wings of insect nutritional ecology!
**Summary**

Feeding is an active, dynamic process with numerous feedback interactions and consequences throughout an insect's life, affecting and being affected by survival, growth, reproduction and movement. An insect must make a number of decisions during its life, including when to hatch from the egg; what, when and how much to eat; how much and what kinds of nutrients to store prior to pupation; whether and when to diapause and/or migrate; and when, how many, and sometimes even what kinds of eggs to lay. These and other decisions all have an underlying nutritional basis. Thus the paradigm of nutritional ecology that is presented involves viewing insect nutrition within the contexts of behavior, ecology and evolution. It is based on the premise that within a particular realm of environmental conditions, there is an optimal set of states (e.g. a particular body size, color, wing loading ratio, proportion of resources allocated to egg production, and phenology) for the individuals in a population which yield their highest fitness. Research in nutritional ecology involves identifying (1) how and to what extent an individual can alter, in response to a changing environment, various physiological and behavioral processes (e.g. consumption rate, metabolism, excretion, and movement) in order to achieve and maintain the optimal set of states; (2) the consequences for fitness (including changes in the timing and amount of reproduction and in probability of survival) both of the alterations in these processes and of the inability to achieve the optimal set of states; and (3) how the optimal set of states, and (1) and (2) above, differ among species, populations and within a population through time. Nutritional ecology is a useful way to structure and synthesize research on both the basic and applied aspects of insect behavior, and it allows us to achieve a better understanding of the evolution of different lifestyles.

**Appendix**

1 The amount, rate and quality of food consumed by larvae influences their growth rate, developmental time and final body weight (reviewed in Seribor and Slansky 1981). Larval survival may also be affected (Barney and Rock 1975, Hatchett et al. 1976, McWilliams and Beland 1977, Garner and Lynch 1981) although the actual causes are seldom determined. These could include: (1) a direct toxic effect brought about by an increase in the concentration of an allelochemical in the food or by a metabolic impairment due to poor nutrient quality (Gordon 1961, Meisner et al. 1977); (2) mortality due to starvation if essential feeding stimulants are not present in sufficient concentrations, and/or if feeding deterrents and inhibitors are present (for reviews see Chapman 1974, Beck and Reese 1976); (3) increased susceptibility to biotic mortality agents through prolonged development, greater exposure while feeding, and differential attractiveness of different plants to predators and parasitoids (Slansky and Feeny 1977, Price et al. 1980, Vinson and Ivantsch 1980a). Movement in the larval stage can also be affected by food quality (Capinera and Barbosa 1976). A factor affecting growth may feed back to affect feeding. For example, parasitoids frequently alter their host's development, with concomitant changes in the host's feeding behavior (Slansky 1978; Vinson and Ivantsch 1980b).

The amount, rate and quality of food consumed by adults insects influences their fecundity, movement and survival (Shorey 1968, Ellis et al. 1966, Kishaba et al. 1967, Dingle 1968, DeWilde et al. 1969, Finch and

Reproduction is intimately linked with adult feeding behavior (DeWilde and DeLoof 1978, 1978b, Slansky 1980a) and survival (Calow 1978, Slansky 1980a, 1980b). The occurrence and amount of movement (flight) may have an effect on subsequent timing and extent of egg production (Slansky 1980c and references therein).

Reproductive performance may have significant, though often subtle, influences on subsequent larval performance. For example, early-laid eggs of the gypsy moth, Lymantria dispar, are larger and contain more yolk than late-laid eggs (Capinera et al. 1977). Larvae hatching from larger eggs exhibit a greater tendency to disperse (Capinera and Barbosa 1976) whereas larvae from the smaller eggs may exhibit prolonged development and produce larger, more fecund adults (Barbosa and Capinera 1978).

Wellington (1977) discusses how our fetish for mean values seems to have done much to distract us from studying insects as variable individuals, and he suggests we “put the insect back into ‘insect ecology’”. Also, much valuable research effort was diverted from studying basic insect biology when we became stuck on the “pesticide treadmill” (van den Bosch 1978). With current interest in integrated pest management programs, it has become strikingly apparent how little we know about the basic biology of many of our insect pests (Barfield and Stimac 1980). Furthermore, although the concept of energy flow through trophic levels has done much to expand our understanding of the structure and dynamics of ecosystems (Odum 1969), it also seems to have diverted our interest from the behavioral ecology and ecological functioning of individual organisms (Hubbell 1971). The role of organism regulation was not denied (Odum 1962), but for the most part individuals were viewed as passive energy-partitioners and -transducers, hidden away in the “black boxes” of ecosystem energy flow diagrams. In addition, although it was recognized that some organisms could have a greater impact on nutrient cycling than on energy flow (Odum 1962), the possibility that nutrient utilization could, in fact, be a primary determinant of energy utilization seems to have been overlooked. Data indicating the primary significance of nutrient utilization are now available for many species of insects (Slansky and Feeny 1977, McNeill and Southwood 1978) and other animals (Mattson 1980), and plants (Chapin 1980).

Some attributes of different lifestyles: migratory vs. non-migratory, specialized vs. generalized feeding, sap vs. foliage feeding, and aposematic vs. crys
tic coloration.

Two examples to clarify this point: although insects do maintain a certain degree of compensatory ability in relation to a change in temperature, the response of slower growth in a cooler temperature is probably a passive response forced on the insect because of its inability to fully compensate for the reduced temperature (Clarke 1967, Hochachka and Somero 1973, Casey 1977, Block and Young 1978). This should not be confused with the much different question of the evolution of growth rates (Auerbach and Strong 1981, Scriber and Slansky 1981).

The response of an insect to a potentially toxic allelochemical in its food provides another example. Slansky and Feeny (1977) found that larvae of the cabbageworm, Pieris rapae, feeding on three species of crucifers consumed food and grew at rates much lower than expected in comparison to
larvae feeding on a number of other crucifers. Variation in leaf water and nitrogen did not explain these observations. These reduced rates were attributed to unique allelochemicals presumably present in the three species but not in the other crucifers. The problem arises in attempting to interpret these responses. Did the larvae actively and adaptively respond to the presence of potential toxins by reducing their consumption rate in order to reduce their intake of these toxins and perhaps to not overload their detoxication system, with the result of a reduced growth rate? Or, did the consumption of these toxins metabolically interfere with and therefore slow growth rate, with the reduced consumption rate being merely a passive result? Slansky and Feeny (1977) did not resolve this issue, but Blau et al. (1978) seem to have found an experimental and statistical protocol by which to distinguish "toxic" effects on growth from those of a reduced consumption rate. The actual "active choice" nature and physiological mechanisms of many insect "decisions" remain to be determined.

Unfortunately but understandably, we do not have, for any population of insects, enough data to answer more than a few of the questions posed by the paradigm of nutritional ecology. It is therefore necessary to piece together data from different species which answer certain of these questions to indicate the kinds of decisions that these organisms might make, and the kinds of consequences that might result. Many of the examples presented here deal with phytophagous (plant eating) insects, because I am more familiar with these through my own research, and because more studies falling within the paradigm of nutritional ecology seem to have been done with these—in contrast to carnivorous and detritivorous insects. However, the concept of decisions and consequences also applies to insects in these latter groups as well, but the specifics will of course vary with the type of food (e.g. eating a plant leaf versus another insect), mode of feeding (e.g. a sedentary larva vs. an active, hunting predator), and other aspects of the particular organism's lifestyle.

The food quality (for phytophagous insects) of the leaves of many plants, and especially of grasses and trees, frequently exhibits a rapid deterioration as the leaves age. Changes that contribute to this deterioration include increased leaf toughness, decreased water and protein contents, and increased allelochemical content (Feeny 1976, Scriber and Slansky 1981). In fact, this rapid deterioration in food quality of many grass and tree leaves may have been a selective agent leading to the evolution of the egg and early larval stages as the overwintering stages, as frequently seen in grass and tree feeding species (Slansky 1974b; see "Diapause" section and Appendix note 17).

Gilbert and Schneiderman (1961) found a 50% drop in lipid content between egg and early larva in the euc topology moth (see also Richards 1959).

Eggs with reduced amounts of yolk have lower viability and produce less vigorous larvae (Wellington and Maelzer 1967) exhibiting prolonged development (Capinera et al. 1977, Barbosa and Capinera 1978) and suffering greater mortality losses (Iwao and Wellington 1970). Although the eggs in these cases had reduced yolk because they were among the late-laid eggs of these female moths, delayed hatching of fully-yolked eggs, resulting in premature utilization of energy reserves, would probably have a similar effect (Richards 1959).

Evolutionary changes in egg size and energy content would in turn have consequences for adult size, energy and nutrient reserves, total fecundity, etc.

Other decisions for some insects include choosing a particular mixture of foods (Waldbauer and Bhattacharya 1973, Greenstone 1979) and choosing food with particular allelochemicals that are sequestered by the insect (Duffey
The physiological control of feeding has recently been reviewed by Bernays and Simpson (1981).

If a larva decides to feed faster during a feeding bout and/or more often (less time between feeding bouts) in order to increase feeding rate, its ability to digest and assimilate food may decrease (e.g., because of a more rapid passage of food through its gut). As long as the relative increase in feeding rate exceeds the relative decrease in assimilation efficiency, the assimilation rate (i.e., feeding rate x assimilation efficiency) will increase, and, all else equal, growth rate will increase. However, beyond a point, for example, where digestive enzyme production can no longer be increased, then assimilation efficiency and rate will decrease. This decrease, coupled with a probable increase in metabolic cost associated with feeding, digesting and assimilating the food, will result in a decrease in growth rate with a further increase in feeding rate (Smith 1976, Calow 1977, Scriber and Slansky 1981). A further cost of an increased feeding rate may be an increased exposure to biotic mortality agents. For example, a female parasitoid may be attracted to the odors released by fresh leaf damage at the feeding site of a potential host larva (Sato 1979, see also Price 1978, Slansky and Feeny 1977, Windsor 1978).

A larva on a food that has deteriorated in nutritional quality may suffer a reduced growth rate either because it decides not to feed faster or because it does not have the ability to feed faster. Potential costs of the resulting lengthened development include prolonged exposure to mortality agents and a delay in the timing of various aspects of its life cycle (i.e., phenology). For example, prolonged development may subject the larva to even further deterioration in food quality as the leaves age, and it may prevent the larva from pupating and achieving cold-hardiness before the first killing frost. For further discussion of the significance of timing in the life histories of insects, see Taylor (1980a).

Herrboldt et al. (1963) suggested that the several-week-longer developmental time of larvae of certain moth species on Scots pine results from their feeding less often during the day because their mode of protection against enemies lies in their cryptic coloration and posture, in contrast to the more frequent daytime feeding and more rapid development of the aposematically colored larvae of certain other species (see also Heinrich 1979).

The value of the minimal weight at pupation for a particular species has probably been adjusted by natural selection in relation to the smallest weight that will supply the energy and nutrient reserves necessary to allow metamorphosis to a reproductively competent adult.


In species such as Drosophila melanogaster that exploit an ephemeral and frequently crowded food source, rapid development to a minimal weight that is a low percentage of the optimal weight, would seem to have a large selective advantage over a longer developmental time to a greater minimal weight (Sang 1956, Robertson 1965, Collins 1977). On the other hand, in the banded woollybear, Pyrrharctia isabella, which is univoltine and overwinters as a diapausing pupa, a too-rapid development to pupation may risk pupal desiccation and/or untimely utilization of metabolic reserves (Goettel and Philogene 1978, and other references in Scriber and Slansky 1981). In such species we might expect, in addition to a finely-tuned regulation of growth in relation to environmental cues such as photoperiod, a minimal body weight
that is closer to the optimum.

10The incidence of diapause may be increased in larvae feeding on poor quality food (e.g. senescing or desiccated foliage), probably because the resulting slower growth subjects the larvae to a greater number of diapause-inducing photoperiod cycles, rather than because of a direct effect of a photoperiod-induced change in plant quality (Danilevskii et al. 1970, Saunders 1976, but see Morris 1967, DeWilde et al. 1969). On the other hand, induction of diapause in parasitoids and hyperparasitoids seems to be more directly related to the qualitative condition of their host (Fisher 1971, McNeil and Rabb 1973).

11The food quality of the leaves of many trees and grasses often is suitable for only a few weeks in the spring and early summer, in contrast to that of many herbaceous plants in which nutritionally suitable leaves are available for much of the growing season (Slansky 1974b, Scriber and Slansky 1981). Because of this, I suggest that, in insect species whose larvae feed on tree and grass leaves, there is selection to limit the number of generations and to time the appearance of their larvae for development early in the growing season when the food quality is adequate. On the other hand, species feeding on herbaceous plants are probably not under such selection and would be expected to overwinter in the “more hardy” pupal stage as well as exhibit more generations per growing season (Slansky 1974b, Masaki 1975).

Therefore I believe it is advantageous for tree and grass feeding species to overwinter as adults that can quickly lay eggs, or as eggs because the eggs can rapidly hatch into larvae and begin feeding. From the literature, I found that of eighty-six species of butterflies in the temperate United States, (1) about 85% of those species over-wintering in the adult or egg stage feed on trees or grasses, (2) only about 45% of those species overwintering in the pupal stage feed on trees or grasses, and (3) these species tend to have fewer generations per growing season in contrast to those feeding on herbaceous plants (Slansky 1974h). These data support the above hypothesis and would indicate a further underlying nutritional basis to life history patterns.

12In fact, reproductive diapause and migratory flight frequently co-occur (Rankin 1978).

13Such inhibition of flight sometimes includes histolysis of the flight muscles (McCambridge and Mata 1969, Rankin 1978, Sobrerek and Fehrson 1979).

14Metabolic rates during flight may be 50 to 100 times greater than during rest (Kammer and Heinrich 1978).

15In milkweed bugs (Oncopeltus fasciatus), as much as five hours of tethered flight/day for six consecutive days has little negative effect on a female's fecundity or length of life, even when starved during the six days. I could detect no compensatory increase in feeding rate after flight, suggesting that either the metabolic costs of tethered flight are not significant, and/or the documented high rate of pre-flight feeding and associated lipid storage are more than adequate to fuel relatively long duration flights (Slansky 1980c).

16The related question of whether similar sized adults produced from larvae on different quality foods behave differently has received little attention (Barbosa and Capinera 1978, Wellington 1977) except within the context of “quality control” of laboratory reared insects (Chambers 1977).

17In response to variation in food quality and quantity, some females may decide to produce different kinds of offspring (i.e. an inductive response). For example, many Hymenoptera and perhaps some aphids can choose which sex each offspring will be (Gilbert 1980, Torchio and Tepedino 1980 and
references therein) and many aphids can vary the proportion of nymphs destined to become alate (versus apterous) adults (Mittler and Sutherland 1969, Harrison 1980).

24This decision frequently involves the breakdown and absorption of eggs within the female (Bell and Bohn 1975).

25From Table 3 we see that under conditions of food limitation (i.e. the amount of milkweed seeds fed to these bugs was reduced 50% below the ad lib. level), adult females of both O. fasciatus and O. cingulifer reduced their rate of egg production. Thus the duration of egg production was either maintained (O. fasciatus) or extended (O. cingulifer). Egg quality was not reduced, as indicated by the values of fresh egg weight, percentage egg hatch, and length of life of newly eclosed, starved nymphs, which were all similar to those from fully fed females. Clutch size was also maintained at a normal value. For O. fasciatus on a 25% ration, egg quality and clutch size were also maintained but the duration of egg laying was reduced. The importance of maintaining egg quality is obvious, and there is indication that clutch size is also relevant to survival of these gregarious, aposematically colored insects (Slansky 1980b).

Under conditions of total starvation after eclosion, these bugs never oviposit. However, after seven days of feeding (the conditions for the starved bugs in Table 3), they do lay some eggs. It is evident that under these conditions of starvation, egg quality for both O. fasciatus and O. longirostris is again maintained, although clutch size is reduced to about one half that of fully fed females. Thus in these species of Oenopeltinae, maintenance of egg quality seems to rate the highest priority, followed by clutch size and then rate and duration of egg laying.

26One important criterion in mate choice frequently is body size, probably as an indicator of the mate’s “vigor” and/or ability to make an optimal nutritional contribution to the production of eggs (Leopold 1976, papers in Blum and Blum 1979, Boggs and Gilbert 1979, Mullins and Keil 1980). For thorough discussions of decisions involving nest building and occupancy, see Brockmann and Dawkins (1979) and Brockmann (1980).

27Pesticides are frequently a component of pest management programs and thus we need to know the factors influencing their efficacy, which may vary as a function of the amount of food consumed by the insect pest, the insect’s nutritional status (e.g. lipid content) and the host plant fed on (Gordon 1961, Raccah and Tahori 1971, Kea et al. 1978, Berry et al. 1980).

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