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Ecology of Nectar and Pollen Feeding in Lepidoptera

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The author thanks D. Murphy, F. Slansky Jr., and especially W. Watt for comments on the manuscript; K. Brown and L. Gilbert for providing copies of unpublished manuscripts; and W. Watt and D. Murphy for allowing me to cite unpublished data.
12.1 INTRODUCTION

An animal's feeding habits form one cornerstone of its ecology, determining the input into its resource budget. Variation in resource input among species may result in differences in reproductive strategy, longevity, morphology, behavior, and population structure. Resource input and utilization, then, provide one unifying view of an animal's overall ecology (Pianka, 1976; Slansky, 1982a,b).

This chapter examines the effects of adult nectar–pollen feeding in one group, the Lepidoptera, on the ecology of these insects. Nectar feeding is common in Lepidoptera (Norris, 1934; Gilbert and Singer, 1975). Among butterflies, many members of the Pieridae, Lycaenidae, Papilionidae, and Hesperiidae are known to feed on nectar. Within the Nymphalidae, Danainae and Ithoninae are nectar feeders, whereas Charaxinae are not. Within the Nymphalinae, the Heliconiini and Argynnini are known nectar feeders, whereas the Apaturini and nymphalini often do not feed on nectar. Among moths, the Sphinxidae consume nectar, whereas the Lymantriidae and Bombycidae do not feed. Several other moth groups most likely feed on nectar.

Pollen feeding, via steeping pollen in regurgitated fluid and re imbibing the fluid, supplements nectar feeding and is restricted to species of Heliconius (Gilbert, 1972). There is one report of pollen feeding in Parides and Battus ( DeVries, 1979), but this behavior is probably not usual in these genera. Pollen feeding by Micropterygidae with chewing mouthparts has also been reported (Faegri and Van der Pijl, 1979; Thien et al., 1985).

Both nectar and pollen feeding by adults interact with other nutrient sources. In addition to nutrients stored by larvae, adult nutrient sources include dung, carrion and mud puddles as sources of sodium (Arms et al., 1974; Adler and Pearson, 1982), rotten plants as sources of pyrrolizidine alkaloids (e.g., Edgar et al., 1973; Brown, 1984), bird droppings (Drummond, 1976; Ray and Andrews, 1980), sap, rotten fruit, and blood (Banziger, 1981). These latter three food sources are usually alternatives to nectar; the other adult food sources often supplement nectar feeding. Little is known of the nutritional ecology of species feeding on alternatives to nectar and pollen; hence the emphasis of this chapter is on the ecology of species that feed on nectar and pollen.

In what follows, characteristics of nectar and pollen are examined and related to the mechanics and physiology associated with feeding in adult Lepidoptera. Adaptive strategies and ecological consequences of nectar–pollen feeding are next considered, including foraging and life history strategies, competition for nectar/pollen, and the impact of nectar–pollen feeding on population structure. Last, the effects of variation in nectar or pollen supply on lepidopteran biology are considered.

12.2 CHARACTERISTICS OF NECTAR AND POLLEN

12.2.1 Nectar

Plants visited by butterflies and nonhovering moths tend to produce similar nectars that are distinct from nectars of plants visited by hovering moths. The difference in nectar characteristics is related to differences between the two groups in energy requirements (Watt et al., 1974; see Section 12.3.3). In general, butterfly and nonhovering moth nectars have a higher ratio of mono saccharides (glucose + fructose) to disaccharides (sucrose) than do hovering moth nectars (Baker and Baker, 1982, 1983b). Amino acid content is also different: butterfly and nonhovering moth nectars tend to contain more amino acids than hovering moth nectars. However, the total amount of amino acids ingested by hovering moths may still be high, because total nectar production is higher in these plants (Baker and Baker, 1975; Cruden et al., 1983). One to 22 amino acids occur in any one nectar, with most nectars containing two to four amino acids (Baker and Baker, 1983a). The most common nectar amino acids are histidine and glycine (Watt et al., 1974; Baker and Baker, 1975). Thus, one species' nectar generally will not provide a full complement of essential amino acids for a nectarivore.

Lipids occur in a few butterfly nectars and in a much larger proportion of hovering moth nectars (Baker and Baker, 1975). One function of nectar lipids is to reduce evaporation by forming a monolayer on the nectar surface (Corbet et al., 1979).

Antioxidants (often ascorbic acid) are present in about half of the butterfly nectars, but only in one in five to one eighth of the moth nectars examined. Alkaloids, phenolics, glycosides, nonprotein amino acids, and other potential toxins also sometimes occur in nectar (Baker and Baker, 1975, 1983a). Nectar pH varies among species and through the day within a single flower (Corbet et al., 1979). Often, pH lies between 5 and 8, although values as low as 3 and as high as 10 have been reported (Baker and Baker, 1983a).

Sugar concentration in nectar is usually measured with a refractometer, and the data are interpreted as mg sucrose equivalents. Fresh nectar sugar concentrations generally range between 15 and 35% w/v (e.g., Watt et al., 1974; Corbet et al., 1979; Baker and Baker, 1983a; May, 1985a). However, even small amounts of other compounds in nectar will alter the reading (Inouye et al., 1980), such that sugar concentration may be less than indicated.

Nectar concentrations are altered by environmental and biotic conditions. High temperature, wind, and low humidity lead to evaporation of water from nectar, concentrating it. Rain can dilute nectar. Soil and water nutrient conditions can also affect nectar concentration (Shuel, 1957). Nectar concentration varies with altitude in some species, with plants at elevations above 2400 m producing less concentrated nectars than plants below 2400 m
(Cruden et al., 1983). This may be due to differences in abundance of low- and high-energy demand pollinators at these altitudes (Watt et al., 1974).

Nectar production rates vary within and among plants, changing with time of day, genetic differences, age, nutritional status of the plant, location of flower on the plant, and other factors (Shuel, 1957; Percival, 1965; Cruden et al., 1983; Pleasants and Chaplin, 1983). Production of nectar usually starts before onset of pollinator activity and continues until a critical volume is produced. Production then ceases until the nectar is removed (Cruden et al., 1983).

12.2.2 Pollen

*Heliconius* butterflies collect pollen on the proboscis shortly after anther dehiscence and agitate it up to several hours in a fluid they exude. The fluid contains no proteases (Gilbert, 1972) and is not regurgitated nectar (Boggs, unpublished data). The pollen begins to germinate in this fluid, releasing free amino acids (Boggs, unpublished data), proteins, nucleotides, and flavonoids (Stanley and Linskens, 1974). So far as is known, no butterfly toxins are present in the pollen exudate. The fluid is then imbibed, and the pollen is sloughed off the proboscis.

Plants from which the butterflies obtain pollen are successional species (Gilbert, 1972; Boggs et al., 1981; Murawski and Gilbert, 1986). In areas with dry and wet seasons, there are corresponding seasonal differences in pollen collected by butterflies at a single site (Boggs et al., 1981). *Heliconius* individuals act as pollinators rather than pollen thieves in greenhouses (Boggs, unpublished data); the situation in the field is more complex owing to the presence of other floral visitors, and *Heliconius* may be a pollinator in only some habitats (D. Murawski, personal communication).

Within the Micropterigidae, adult *Sabatina* eat pollen using grinding mandibles (Thien et al., 1985). For the tree *Zygogynum*, all pollen is collected from a given flower; however, enough sticks to the moths to allow effective pollination of female-phase flowers. The flowers are used as mating sites, and large numbers of moths congregate at each flower.

12.3 MECHANICS AND PHYSIOLOGY OF NECTAR/POLLEN FEEDING

12.3.1 Mechanics of Feeding

Lepidopteran proboscides consist of two cylinders enclosing a food canal through which liquid is drawn. Nectar is sucked up the food canal by action of two sets of cibarial dilator muscles, and the fluid empties into the bulbular cibarial cavity (Snodgrass, 1935).

Flow rates in butterfly proboscides have been modeled to determine the range of nectar concentrations and nectar extraction times energetically usable by butterflies. Kingsolver and Daniel (1979) provided the first model, which considered physical dimensions of the proboscis, nectar viscosity and density, insect metabolic rate, and energy content of sugar. They assumed that the fluid is Newtonian, that flow through the food canal is laminar, that the change in potential energy can be ignored, that capillary action is not relevant to the nectar feeding process, that the butterfly and nectar are isothermal, and that the pressure drop produced by the cibarial pump is constant for all nectar concentrations. Resulting simulations show that nectar concentrations yielding the highest energy reward per unit time are independent of the range of metabolic rates and physical dimensions of the proboscis found in butterflies, although optimal flow rates do depend on proboscis dimensions. They suggest that the primary mechanistic limitation to feeding is the limiting pressure drop between the proximal and distal ends of the proboscis associated with ambient air pressure.

May (1985b) and Pivnick and McNeil (1985) found that Kingsolver and Daniel's (1979) assumption of constant pressure drop produced by the cibarial pump with varying nectar concentration does not hold empirically in at least four species from four different families. Instead, pressure drop increases to a maximal value with increasing nectar concentration. Incorporation of this observation into the model changes the estimated nectar concentration yielding the greatest energy reward per unit time, which is now found to be about 35–40%. This optimum is independent of temperature within the range likely to be encountered in the field (Pivnick and McNeil, 1985), although rate of feeding was higher at 35 than at 25°C.

Feeding by *Agraulis* and *Phoebis* occurs in pulses (May, 1985b) rather than as a steady flow, as assumed by these models. Interestingly, a model for pulsed feeding by hummingbirds yields nectar concentrations of 35–40% for optimal energy reward per unit time (Kingsolver and Daniel, 1983).

The optimal nectar concentrations according to these models are somewhat above concentrations often encountered by Lepidoptera in nature (Section 12.2.1). However, rate of energy intake may not be the only important factor. For example, Lepidoptera at high altitudes may also be concerned with water balance and hence select nectars less concentrated than predicted from energy considerations alone (Watt et al., 1974).

Pollen-feeding *Heliconius* individuals have modified proboscides. Papillae on the proboscis tip function as a pollen brush; many other species not feeding on pollen lack such papillae (Gilbert, 1972). Further, *Heliconius* has large mechanoreceptor hairs near the head that may yield information on pollen load size. Such hairs are less developed in species not feeding on pollen.

Proboscis length is often related to corolla tube length of flower species visited by Lepidoptera, such that Lepidoptera with longer proboscides can exploit flowers with deeper corolla tubes (Gilbert and Singer, 1975). For example, *Perichares philotes dolores* has a body length of 22 mm but a proboscis length of 43 mm, equal to the length of the corolla tube of the
orchid from which it feeds (Emmel, 1971). A deep corolla tube has been invoked as an adaptation protecting the flower against nectar robbers, which do not pollinate the flower, while allowing pollinators access to the nectar (e.g., Barrows, 1976).

12.3.2 Perceptual Mechanisms

Lepidoptera use vision and olfaction to varying degrees to locate flowers. All species examined have color vision and the ability to perceive ultraviolet light (e.g., Goldsmith and Bernard, 1974). Further, color discrimination in dim light may be important for night-flying moths. For example, the quality of discrimination in dim light is much better for *Deilephila* spp. than for humans (Schlectron, 1979).

Some lepidopteran species clearly have the ability to find flowers using color alone, as they will feed spontaneously from sugar-soaked sponges surrounded by colored papers. These species show innate preferences for particular colors. For example, *Heliconius erato* prefers orange (Crane, 1955), *H. charitonius* prefers oranges or blues (Swihart and Swihart, 1970), and *Papilio demoleus* and *P. machaon* prefer violets and blues (Ilse and Vaidya, 1956). Further, *H. charitonius* can discriminate among various close color shades but apparently not among shades of gray (Swihart, 1971).

*Heliconius charitonius* can be conditioned to nectar at feeders with non-preferred colors (Swihart and Swihart, 1970; Swihart, 1971), suggesting that color is used in flower search images. This species also distinguishes between feeders with a single color and those with a different-colored center, showing that color patterns can be used in search images (Swihart, 1971). Such patterns include "guides" that presumably help the insect locate nectar within the flower (Kevan, 1978). The ability to use search images in finding flowers almost certainly occurs in other Lepidoptera as well (e.g., *Colias* spp.; Watt et al., 1974).

A number of Lepidoptera cannot find flowers by color alone but also use odor (e.g., *Plutia gamma* (Schremmer, 1941) and *Cucullia umbratica* (Brantjes, 1976)). Other species (especially small nocturnal moths) apparently use only olfaction to locate flowers (Brantjes, 1978).

12.3.3 Flight Physiology

Flight is metabolically expensive (Kammer and Heinrich, 1978). Insects have adapted to cope with this expense. Three areas of adaptation related to adult feeding habits include thermoregulation, hovering versus landing at flowers, and compounds used as flight fuel.

Many Lepidoptera can only fly within a limited range of body temperatures (Watt, 1968; Tsuji et al., 1986). Thus, they often must warm up before flight and must thermoregulate during flight (Casey, 1980, 1981). Warm-up may occur either by passive solar basking (e.g., Watt, 1968 for *Colias*) or by muscular shivering (e.g., Kammer, 1970, for hawkmoths). Muscular shivering is much more metabolically expensive than basking, although basking may increase the risk of predation (Gameo and Watt, unpublished data; Urbina and Watt, unpublished data) and limit the time available for flight during the day (Kingsolver, 1983; Kingsolver and Watt, 1983). Energy budgets of species that bask, shiver, or use a mixture of the two (e.g., *Sphagia moriphobia*, personal observation) have not yet been compared. However, species that shiver should have either an energetically richer adult diet or a greater nectar intake than species that bask only.

When inflorescences have a high nectar reward and are loosely clumped, hovering may yield a higher net rate of energy intake than landing at the flower, in spite of the higher energy cost of hovering (Heinrich, 1975; Kammer and Heinrich, 1978). Further, Lepidoptera foraging at night or in adverse weather conditions may cool upon landing on a flower, such that warm-up through shivering is necessary before takeoff. In these cases, hovering might be cheaper in terms of energy and/or time.

The class of compound used as flight fuel depends on whether the species feeds as an adult and whether long-distance flight occurs. Species not feeding as adults use lipid as flight fuel (Kammer and Heinrich, 1978). Species feeding as adults use either carbohydrate only or a combination of lipid and carbohydrate. Carbohydrate alone is used by species that make only short flights. In these cases, nectar sugars may be used directly in glycolysis supporting flight (Bottos and Watt, unpublished data; see Section 12.3.4) or may be stored as trehalose or glycogen until needed. Species feeding as adults and migrating use carbohydrate as an initial short-term flight fuel and lipid to sustain prolonged flight. In this case, nectar sugars may be either used directly to support flight or stored as lipid until needed (Brown and Chippendale, 1974).

Genetic variation in ability to metabolize nectar sugars to support flight occurs among individuals in at least some species. For example, variation at the phosphoglucone isomerase locus in *Colias* results in differences in rate of sugar processing and hence differing flight capabilities (Watt, 1977, 1983; Watt et al., 1983).

Effects on flight physiology of nectar constituents other than sugar are known. However, there is some evidence that coadjustment among nectar constituents may occur in plants. For example, large quantities of nectar must be imbied by hovering moths to obtain adequate sugar to support costly hovering flight. To become more attractive to hovering moths, plants cannot simply evolve nectar with a greater sugar concentration because of constraints on the ability of the foraging insect to imbibe concentrated solutions (Heinrich, 1975; Kingsolver and Daniel, 1979; Baker and Baker, 1983a; May, 1985b; Pivnick and McNeil, 1985). Instead, plants whose nectar is used by hovering moths have apparently evolved a low amino acid concentration to keep the overall amount of amino acids taken in by moths below a toxic level.
12.3.4 Interaction with Other Resources

Use of nutrients derived from adult feeding and other sources interact, resulting in adjustments to the overall resource budget of the organism. Thus, differences in adult feeding habits should be correlated with differences in allocation of nutrients obtained in other stages in the life cycle. For example, adult feeding habits are correlated with the allocation of larval-derived resources to reproduction as opposed to soma during metamorphosis (Boggs, 1981a). *Heliconius cydno, H. charitonius,* and *Dryas julia* will all feed on the same larval host plant. The two *Heliconius* species have a richer adult diet (pollen plus nectar as opposed to nectar only) and allocate a smaller proportion of larval resources to reproductive structures and fat body than does *D. julia*. Similarly, May (1985a) found an inverse correlation between lipid content at adult eclosion and relative energy intake by adults of *Phoebis sennae* and *Agraulis minucula*, demonstrating that the relationship between adult diet and allocation of larval nutrients during metamorphosis can be seen even in unrelated species with unrelated larval host plants.

Nothing is known concerning shifts in allocation of adult resources within a species in response to poor larval nutritional experience. Four noctuid moths, whose adult feeding habits are unknown, alter allocation of larval resources to produce adults with proportionately more wing area to body mass in response to poor larval nutrition (Angelo and Slansky, 1984). With the resultant lower wing loading, such individuals may have lower energy costs associated with foraging and may be able to obtain proportionately more adult resources to replace missing larval resources. The extent to which such compensation can occur is unknown.

Allocation of adult nutrients to reproduction, maintenance, and other functions depends on physiological demand and on the variety and quantity of compounds in the adult diet as well as on the allocation of larval resources. Data on the allocation patterns of adult nutrients are sketchy, although initial radiotracer studies indicate that nectar- or pollen-derived amino acids are used in both soma and reproduction (Gilbert, 1972; Rothchild, 1974; Boggs and Gilbert, 1979) and sugars are used in flight metabolism (Watt and Boggs, unpublished data).

Several predictions concerning allocation of adult resources can be made. First, adult resources should be metabolized preferentially to larval reserves, if the adult resources can be used directly, because of energetic savings resulting from avoidance of costs of metabolic conversions required for storage. Preliminary data for *Colias eurytheme* support this prediction. Glucose fed to adults is processed directly through glycolysis rather than first being transformed into glycogen, if flight occurs immediately after feeding (Boggs and Watt, unpublished data). Second, if adult food contains an incomplete spectrum of nutrients needed by the insect for a particular function, then those nutrients will be useless unless supplemented by larval reserves. In such a case, once larval reserves are exhausted, adult resources become irrelevant to continued functioning of the insect. Such a relationship may result in the decline in egg laying seen in nectar-feeding Lepidoptera, even under laboratory conditions where nutrient expenditure in flight is minimal and food is provided ad lib (Boggs, 1986a). Third, adult resources may be stored in species facing predictable fluctuations in resource availability. For example, *P. sennae*, which undergoes reproductive diapause, increases body lipid content when nectar is available (May, 1985a). Finally, allocation of adult resources to reproduction may depend on the physiological state of the ovaries or male accessory glands. There is currently no evidence that feeding habits of nectar/pollen feeding Lepidoptera change within an individual in relation to reproduction, but preliminary data indicate that allocation of nectar resources varies with the stage in the ovarian cycle in Lepidoptera laying eggs in batches (D. Murphy, personal communication).

Nutrients derived from adult nectar or pollen feeding may interact with nutrients from other sources. Male (or in some species, female) Lepidoptera feed both on nectar and other resources such as mud puddles, dung, carrion, and rotting plants. Further, females receive nutrients from the male through the spermatophore and accessory-gland fluids (Goss, 1977; Boggs and Gilbert, 1979; Boggs, 1981b; Boggs and Watt, 1981). In many cases these adult sources provide complementary nutrients. Mud puddling provides sodium, not otherwise abundant in the lepidopteran diet (Arms et al., 1974). Feeding on rotting plants provides pyrrolizidine alkaloids that protect thiohmiine butterflies from predators (Brown, 1984). Further, these alkaloids are transferred from the male to the female at mating, and they are used to protect the female and her eggs as well (Doussard et al., 1984; Brown, 1985). Nutrients passed to the female by the male could reduce the need of the female to forage herself, allowing her more time to learn the location of adult resources or increasing her longevity by lowering the risk of predation associated with feeding. No data addressing these hypotheses exist.

12.4 STRATEGIES AND CONSEQUENCES OF NECTAR/POLLEN FEEDING

12.4.1 Foraging Strategies

Much of the literature on adult foraging behavior of Lepidoptera addresses the subject from the point of view of the plant. However, a few workers have examined lepidopteran behavior from the standpoint of optimal foraging (e.g., Levin, 1978) and made predictions regarding flight distances and constancy of flower choice.

Many Lepidoptera show a high degree of fidelity to one or a few preferred flower species (Watt et al., 1974; Schemske, 1976; Kay, 1978; Murphy, 1984; May, 1985a). The degree of fidelity may vary from species to species; for example, *P. sennae* switches flower species less frequently within a foraging
bou than does A. vanillae in Florida (May, 1985a). Butterflies and hawk- 
moths may also discriminate between different flower color morphs within a 

Flight distances among flowers are not normally distributed. Lepidoptera 
show an excess of both short- and long-distance moves, with an average 
distance between sequential nectar visits generally of less than 10 m (Levin 
and Kerster, 1968, 1974; Linhart and Mendenhall, 1977; Levin, 1978; 
Schmitt, 1980; Webb and Bawa, 1983). A few species trap-line among plants 
that are more widely spaced (e.g., Ehrlich and Gilbert, 1973).

Foraging efficiency may depend on flower density as well as nectar avail-
ability. Both P. sennae and A. vanillae increase foraging rate and decrease 
flight time with increasing flower density. However, flower species available 
at high densities have relatively small nectar rewards (May, 1985a).

These behaviors have implications for the population structure of the 
plants that Lepidoptera pollinate. First, constancy improves the efficiency 
of pollination, which was found to be low in the only study examining it 
(0.5% of Phlox pollen grains were calculated to reach a receptive stigma; 
Levin and Berube, 1972). Second, short average distances moved between 
flower visits limit the neighborhood size of the plants, allowing local differ-
entiation (Schmitt, 1980).

12.4.2 Life History Strategies

Life history elements include longevity, number and size of offspring, and 
timing of the production of offspring. Nectar and pollen feeding affect all of 
these elements to varying degrees.

Longevity in Lepidoptera normally feeding as adults is strongly depend-
dent on nectar or pollen feeding. Water alone increased longevity in Euphy-
dryas editha (Murphy et al., 1983) and Epeisata spp. (Norris, 1934). Adding 
sugar to the water (to mimic the carbohydrate component of nectar) further 
increased longevity in E. editha and Epeisata spp. and also increased lon-
gevity in Piersis rapae (Minnich, 1924). Longevity increased with increasing 
amounts of sugar available from the adult diet in A. vanillae (May, 1985a). 
However, addition of amino acids in concentrations similar to those of nectar 
had no further effect on longevity in E. editha, indicating that the effect of 
nectar feeding on longevity in this species is due only to carbohydrates 
and water.

Daily survival rates in several temperate-zone butterflies in the field de-
pend on nectar availability, decreasing in years with little rainfall and hence 
lowered flower availability (Scott, 1973b; Watt et al., 1979). However, one 
temperate-zone species, Speyeria mormonia, shows a sexual dimorphism in 
control of survival rates. While male daily survival rate is correlated with 
summer rainfall, female daily survival rate is not; instead, it is correlated 
with microhabitat. These results suggest that female longevity is not depen-
dent on nectar and/or that local variation in factors such as predation plays a 
more dominant role in determining survival rates (Boggs, 1986b).

Pollen feeding has a strong effect on longevity in Heliconius. With pollen 
feeding, butterflies live up to 8 months, as opposed to 3 weeks without pollen 
(Gilbert, 1972; Dunlap-Pianka et al., 1977). Butterflies deprived of pollen 
may show normal longevity patterns if pollen is provided later in life.

Nectar and pollen feeding may also affect longevity indirectly through 
resultant unpalatability or exposure to predation. Nahrstedt and Davis 
(1983) showed that Heliconius adults synthesize cyanogenic glucosides from 
valine and isoleucine, which are obtainable from pollen by these butterflies. 
Thus, unpalatability may be increased as a result of normal adult feeding 
(L. E. Gilbert, personal communication). Predation on Lepidoptera at 
flowers is often seen, but contribution of such predation to mortality rates 
has not been measured.

Adult feeding can affect the size or number of offspring produced by a 
female. Water alone increased fecundity over that of nonfed females in 
Epeisata cautella, E. elutella, and E. kuhniella. The effect was less pron-
ungounced in the last species, perhaps because it contains more mature eggs in 
the ovaries at eclosion than the other two species. Addition of sugar to the 
diet yielded no further increase in fecundity (Norris, 1934). Inclusion of 
sugar in the diet increases fecundity in C. eurytheme (Stern and Smith, 1960). Sugar consumption increases number of eggs in only later egg batches in 
Euphydryas editha (Murphy et al., 1983), because this species ecloses 
with the first one or two egg batches already mature (Labine, 1968). Egg 
weight in later egg batches in this species increases if amino acids are 
included in the diet, whereas sugar has no such effect. Increasing sugar avail-
ability in the adult diet increases the number of chorionated eggs (indepen-
dent of age effects) in A. vanillae. The effect is nonlinear, with less 
proportionate increases in egg production at higher energy availability levels 
(May, 1985a). All these experiments were done under confined laboratory 
conditions. If females are allowed opportunities to fly normally, the results 
may be more striking, as extra demands would be made on available res-
ources.

In species normally feeding, lack of nectar affects both the rate of egg 
maturation and the rate of drawdown of the fat body (Stern and Smith, 1960; 
Rothschild, 1974; Murphy et al., 1983; May, 1985a). For example, in C. 
eurytheme, the first eggs mature later if the female is not allowed access to 
food. Further, in Colias spp., E. editha, and A. vanillae, the fat body is 
reduced at a faster rate if females are not allowed to feed. These results, 
combined with radiotracer data showing that adult resources are used in egg 
production (Gilbert, 1972; Rothschild, 1974; Boggs and Watt, 1981), suggest 
that adult feeding delays or reduces use of larval-derived nutrients and may 
thus lead to the observed increase in fecundity in fed versus nonfed females.

The effects of differences in amount of nectar feeding among females
within a species on longevity, fecundity, or egg weight in the wild have not been examined.

Pollene feeding dramatically affects egg production in *Heliconius* species (Gilbert, 1972; Dunlap-Pianka et al., 1977; Dunlap-Pianka, 1979). Oogenesis is continuous in this genus if adults are given continued access to pollen. Thus, the number of eggs that could be laid is in principle unlimited. This behavior contrasts with other described Lepidoptera, which eclose with a fixed number of oocytes in the ovaries. Withholding pollen from *Heliconius* leads to a decrease in egg production, which is sometimes reversed once access to pollen is restored. No species so far examined shows a correlation between egg weight and amount of pollen processed by a female.

Adult feeding habits, combined with the importance of adult nutrients in egg production, are correlated with age-specific fecundity among species (Chew and Robbins, 1984; Boggs, 1986a). Species with little or no adult feeding show a rapid decline in age-specific fecundity with age. Species with richer adult feeding sources used more in egg production show a longer plateau of age-specific fecundity with age, until in the *Heliconius* (with reproduction strongly dependent on a rich adult food source), a drop in daily egg number does not occur.

In general, egg production in species with greater dependence on adult resources for egg production might also be buffered against fluctuations in amount of resources gathered in the larval stage—as long as body size does not constrain ovary size (e.g., *Heliconius charitonius*; Dunlap-Pianka, 1979) or ability to gather adult resources.

Adult feeding habits also interact with reproductive diapause. In many cases, reproductive diapause coincides with periods of nutritional stress (e.g., *Danaus plexippus*: Brower et al., 1977; *Libytheana* and *Kricogonia*: Gilbert, 1985). Decreasing nutritional demands by not reproducing is one method of dealing with such stress.

Resorption of eggs due to nutritional stress has not been found in Lepidoptera (Bell and Bohm, 1975). This may be due to insufficient study. Alternatively, because many Lepidoptera eclose with a fixed number of oocytes in the ovaries, they may have evolved the capacity to simply slow down or stop the vitellogenic cycle in the face of nutritional stress, because resorbed eggs would be irreplaceable.

The effects of adult feeding on male reproduction, through ability to form a suitable spermatoaphore, to transfer sperm, or to display proper courtship, have generally been ignored, and no data are available for nectar-feeding species. The absolute effect of pollen feeding in *Heliconius* on these parameters is likewise unknown. However, there is no correlation between relative amount of pollen collected and number of matings by male *H. cydno* in a free-flying greenhouse population. A negative correlation has been observed for *H. charitonius* under similar conditions, because mating and pollen collecting occupy the same time period in this species (Boggs, 1979).

### 12.4.3 Intra- and Interspecific Competition

Partitioning of nectar and pollen resources occurs both within and among species of Lepidoptera. *Heliconius* species vary in quantity and type of pollen collected in the field and in competitive ability to collect different types of pollen under greenhouse conditions (Boggs et al., 1981). These differences generally reflect differences in habitat utilized by adults (Boggs et al., 1981).

Three species of *Pieris* show substantial overlap in nectar plant species used (Ohsaki, 1979). *Pieris melete*, the most common of the three, exploits the broadest set of nectar sources. Nectar sources visited by all three species have the widest distributions and longest flowering periods of all potential nectar sources. However, frequency of use of each nectar source differs among butterfly species and is not solely determined by the insects' microhabitat preference.

In a more extreme case, Clench (1967) argued that temporal differences in the adult flight of a group of hesperine butterflies are caused by avoidance of overlap of use of nectar resources. However, he did not explore other mechanisms potentially determining timing of adult flight, nor did he examine quantitatively the use of nectar by the different hesperine species.

Intraspecific variation in quantity of nectar or pollen gathered also presumably occurs, although this has only been documented for pollen feeding. All *Heliconius* species are sexually dimorphic in the amount of pollen collected, with females collecting more than males (Gilbert, 1972; Boggs et al., 1981). Though females may be heavier than males, wing lengths are not dimorphic, and the sexual dimorphism in pollen collection probably results from higher metabolic demands on females associated with egg production and flight. The amount of pollen collected also increases with age within each sex (Boggs et al., 1981). The form of the increase varies among species and may also be affected by the amount of competition for pollen (Boggs, unpublished data).

The deme structure of some *Heliconius* may be influenced by intraspecific competition for pollen. Recruitment to a deme may occur only if flowers within the home range are not saturated by visitors, such that a new butterfly finds nectar and/or pollen on the first few visits (Gilbert, 1984).

### 12.4.4 Population Structure

Distribution of nectar sources in space and time plays a crucial role in the location and dispersal of butterfly (and probably moth) populations. Where the distribution of nectar plants does not overlap that of larval host plants or adult mating areas, the area occupied by a butterfly population is extended to include the nectar plants, and dispersal radii are increased. For example, *Leptidea sinapis* in central Sweden oviposits in open meadows but nectars on plants growing in adjacent woodland (Wiklund, 1971). Some Theclini
form male mating aggregations on hilltops but must fly downvalley in search of nectar and mud puddles, extending the habitat used by adults (Scott, 1973a). Nectar plants for *E. editha* at Del Puerto Canyon in California are distributed independently of larval plants, especially late in the season. As a result, adults occupy a greater area than larvae and disperse farther than butterflies in populations with sympatric nectar and larval host plants (Gilbert and Singer, 1973).

Alternatively, nectar plants may be found in the same places as larval host plants. This occurs for *E. editha* on Jasper Ridge in California. As a result, the distribution of adult butterflies is almost the same as that of larvae, dispersal radii are low, and the butterflies are separated into small, patchily distributed populations corresponding to plant patches (Gilbert and Singer, 1973). If individuals from Del Puerto Canyon are transplanted to Jasper Ridge, they continue to show a high dispersal radius. Although the results may be confounded by differences in phylogeny between the two sites, dispersal may be at least partly genetically controlled in this species.

Another possible pattern involves adult nectar hosts distributed in a small area within a sea of suitable larval hosts, such as occurs for an *Euphydryas chalcedona* population near Echo Lake, California (Murphy, 1983). Males are found primarily in the vicinity of adult nectar sources throughout the flight season, whereas females are widely distributed early in the season and found closer to adult nectar resources at the end of the season. Murphy (1983) postulates that the female pattern is due to an increasing dependence on nectar resources with age. A similar situation has been documented for *Heodes virgaureae* in southern Sweden, where the presence of butterflies is correlated with nectar plants in warm, sheltered microhabitats; larval host plants are more equally distributed in the area (Dowues, 1975).

Distribution of pollen (and nectar) resources also affects the distribution of adult *Heliconius*, because these butterflies establish home ranges around a set of adult host plants (Turner, 1971; Ehrlich and Gilbert, 1973; Gilbert, 1975; Waller and Gilbert, 1982). A number of *Heliconius* species, including *H. charitonius*, *H. erato*, and *H. sara*, also roost communally (Poulton, 1931; Benson, 1972; Turner, 1975; Young, 1978; Waller and Gilbert, 1982). Such roosts may result from newly emergent adults following older adults to nectar/pollen resources and to the roost (Gilbert, 1975, Waller and Gilbert, 1982).

A number of lepidopteran species contain both migratory and nonmigratory forms. Differences in nectar usage among individuals of the two forms have not been explored. Given the costs of flight, however, migratory forms could be more dependent on adult food, unless the net costs are reduced by lack of reproduction or altered body form (Slansky and Scriber, 1985).

Distribution of nectar resources also affects the distribution of offspring in space. For example, in *E. chalcedona* the number of larvae found decreases sharply as distance from the nectar sources increases in the population near Echo Lake (Murphy, 1983). In a Jasper Ridge population of a different subspecies, females lay more eggs on less suitable host plants where the distribution of those plants overlaps the distribution of nectar host plants (Murphy et al., 1984).

On a larger scale, feeding versus nonfeeding by adult moths is related to clustering of eggs (Hebert, 1983). Nonfeeding species are more likely to lay eggs in clusters of eight or more than are feeding species. Hebert (1983) argues that this may reflect an advantage to reduced flight in nonfeeding species, such that more larval reserves can be allocated to egg production.

### 12.4.5 Impact of Variation in Nectar/Pollen Supply

Essentially nothing is known about effects of variation in nectar or pollen supply on the ecology of Lepidoptera. The only partial exception is the effect on population numbers of variation in nectar supply due to weather fluctuations (Scott, 1973b; Watt et al., 1979; Brown and Ehrlich, 1980; Ehrlich et al., 1980). For example, wet years on Jasper Ridge, California, result in bursts in the population size of *E. editha*, because of increased nectar feeding by females increasing their fecundity, a longer prediapause larval period that increases survival rates of later eggs, and decreased dispersal by the larger adult population in the succeeding year (Ehrlich and Murphy, 1981; Murphy et al., 1983). Such population bursts may be a key factor in reducing the likelihood of extinction of these small populations, whose numbers are controlled by density-independent factors such as rainfall.

Areas relating to variation in nectar or pollen supply that need addressing include the effects of predictable or unpredictable environmental variation on allocation of both larval and adult resources, on life history strategies, and on metabolic adaptations, all in both physiological and evolutionary time. Are there adaptations (such as shifts in egg number or size, in flight propensity, in foraging strategy) to fluctuations in resource availability? Further, are there behavioral responses, such as migration, that mitigate the effects of environmental variation? Are there genetic variants predisposed to survive decreases or to take advantage of increases in nectar or pollen supply? One such variant in *Colias* may be the "alba" polymorphism, in which white females have more larval reserves as adults than do yellow females (Graham et al., 1980).

### 12.5 CONCLUSIONS

A good start has been made in understanding the interaction of pollen and nectar feeding with the ecology of Lepidoptera. Several generalizations are possible concerning the mechanisms and physiology underlying nectar or pollen feeding strategies. First, usable nectar concentrations and intake rates are constrained by the physical properties of the proboscis and nectar. Second, food location is accomplished in different species by differing mixtures
of vision and olfaction. Use of search images is possible in some species, enhancing feeding efficiency and flower constancy. Third, adult feeding habits may be correlated with thermoregulatory strategy, hovering versus landing at flowers, and flight fuel metabolites utilized. Finally, selection minimizing energy waste should coadjust metabolic use of nectar- or pollen-derived nutrients with allocation and use of other adult and larval-derived nutrients.

Further generalizations are possible concerning the effects of nectar or pollen feeding on foraging and life history strategies. First, lepidopteran foraging strategies are usually characterized by short average flight distances between flowers and constancy of flower choice. Second, adult longevity and offspring number and size are affected by adult feeding, probably through the interaction of adult and larval nutrients. If larval-derived nutrients can be conserved by primary use of adult resources, then adult longevity is increased, and decreases in daily fecundity and offspring size can be delayed. Third, little is known of the effects of competition for adult food other than that it can occur. Finally, the abundance and distribution of nectar plants influences the size and distribution of adult Lepidoptera populations and hence the number and distribution of eggs.

Information is still sketchy in a number of areas. Little is known concerning the interaction of adult feeding with metabolism and resource allocation. Almost no work has been done on the effects of adult feeding on male life history strategies. Few attempts have been made to integrate ecological strategies with their underlying mechanistic constraints. Finally, essentially nothing is known concerning effects of variation in nectar or pollen supply or concerning variation in the insects’ use of food when food availability is constant. Understanding variation in nectar–pollen availability and quality and insect responses to this variation are prerequisites to the analysis of the evolution of nectar/pollen feeding habits and associated biology in the Lepidoptera.

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