FORAGING SELECTIVITY IN ADULT BUTTERFLIES:
MORPHOLOGICAL, ECOLOGICAL, AND PHYSIOLOGICAL
FACTORS AFFECTING FLOWER CHOICE

By
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I studied flower selection by adult butterflies of two species, Agraulis vanillae (Nymphalidae) and Phoebis sennae (Pieridae), from several perspectives. First, I critically evaluated recent theoretical models of the feeding mechanics of butterflies. These models predicted that butterflies should select flowers with nectars of 20-25% sugar concentration, which provide the greatest rate of energy intake. I measured nectar uptake rates of these butterflies and empirically determined that the greatest rate of energy intake is at nectars from 35-40% sugar. Second, I quantified the energy rewards of the flowers visited by these butterflies and showed that energy intake rate while foraging is associated with corolla length and nectar volume, but not with nectar concentration. The two

butterflies differ significantly in flower selection. Phoebis sennae selects flowers that are more energetically rewarding, because a) it has a longer proboscis and can exploit long-corolla flowers from which Agraulis is excluded, and b) it discriminates more often between low- and high-reward flowers. Differences in discrimination (specialization) may be due to differences in vagility and time-allocation patterns between the two species. As predicted by recent theory, Phoebis sennae, which acquires more energy than Agraulis as an adult, emerges from the pupa with small fat stores and rapidly builds fat reserves by profitable adult foraging. Agraulis vanillae individuals emerge from the pupae with larger fat stores and do not add to them during life, but instead gradually depletes these lipids acquired through larval foraging. Increased energy intake of adult Agraulis vanillae is associated with increased fecundity, lower mortality, and a lower rate of fat depletion, but the benefits associated with increasing energy intake may diminish at higher energy intake levels.

CHAPTER I GENERAL INTRODUCTION AND PLAN OF THIS STUDY

All animals are to some extent selective in their choice of food items. Thus, no animal feeds on all potentially nutritive items that it encounters while foraging. In large part this selectivity is due to morphological and biochemical constraints that are the result of evolutionary adaptation towards feeding on some particular type of food. Thus, herbivorous insects do not pursue and consume other insects, peregrine falcons do not browse foliage, and so on. But even within the range of food items that are potentially consumable by a given species, some food items are usually preferred over others. In the last twenty years a large body of literature has developed dealing with the subject of food choice by animals, and has attempted to derive generalizations that will explain and predict observed patterns of prey choice in a variety of animals. This literature is collectively referred to under the general term optimal foraging theory and will be discussed in some detail below.

Whereas some authors have pursued a theoretical approach to the topic of prey choice, other researchers have attempted to apply this theory to observed feeding behavior of real organisms in both laboratory and field contexts. Feeding habits and food selection of a variety of organisms have been studied. There has been relatively little work on the feeding behavior of holometabolous insects, which are somewhat distinct in their feeding strategy. Whereas vertebrates

and a great many invertebrates do not radically change their food habits over the lifespan of an individual, holometabolous insects may have two completely distinct feeding strategies during the life of an individual. Feeding occurs during the larval stage and may be the predominant activity engaged in by this stage. In addition, feeding may or may not occur during the adult stage, and the nature of the food that is taken is usually quite dissimilar from that of the larva.

Insects of the order Lepidoptera are holometabolous. The primary function of the larval stage is acquisition of nutrients to be used in forming the adult insect and provisioning it with reproductive reserves. These nutrients are obtained through feeding on vegetation in the majority of species. The main function of the adult stage is reproduction, and feeding during the adult stage is highly variable both in extent and in the nature of the food taken. Generally, feeding by the adult is primarily to obtain energy, since the insect is fully grown upon emergence and tissue repair does not occur (Opler and Krizek 1984). The importance of adult feeding in butterflies has been largely ignored (Gilbert and Singer 1975), but is certainly interrelated in a complex fashion with larval feeding behavior. The interrelationships between larval and adult feeding have only recently begun to be addressed in the ecological literature (Boggs 1981).

Because of the complexity of feeding behaviors during the life of a holometabolous insect, feeding behavior of either the larval or adult stage of these insects may be subject to different constraints or selective pressures than in animals with more homogeneous feeding habits. In this study I examine flower choice by adults of

two species of butterflies. Specifically, I have 1) revised the predictions of mechanical models of butterfly feeding that predict selectivity of flowers based on nectar concentration, 2) examined energetics of foraging and selection of nectar sources actually chosen by foraging butterflies, and 3) considered the bases for the observed foraging choices. 4) I have examined differences in the lipid storage patterns of two butterfly species and the relationship between lipid dynamics and foraging energetics. Finally, 5) I show effects of energy intake of adults on fitness components such as longevity and fecundity. In this introductory chapter, I selectively review the literature on several topics pertinent to the studies outlined above. First, I consider some of the literature on optimal foraging. My work asks the general question: what factors affect flower choice in foraging butterflies? Therefore, I will concentrate on that segment of the literature dealing with the selection of food items by foragers (as opposed to patch choice, time allocation, etc.). Next, I review some pertinent studies concerning foraging behavior of other nectarivores, concentrating on factors that are thought to influence food choice in these animals. I then discuss the applicability of this information to foraging butterflies. Finally I review several studies dealing with the effects of adult diet on fitness, the ultimate criterion by which any animal's foraging decisions are evaluated.

Optimal Foraging Theory -- A Selective Review

The first formal treatments of prey choice (which stimulated the development of what has come to be known as optimal foraging theory) were those of Emlen (1966) and MacArthur and Pianka (1966). These papers were followed by numerous others summarized in Schoener (1971)

and Pyke et al. (1977). All of this work is based on the following argument. Given that most behavior, including foraging, shows some heritable variation, there is then a range of possible foraging strategies within a population or species. If these strategies differ in their efficiency, then natural selection should favor those genotypes and individuals whose foraging behavior is most efficient. This assumes that differences in foraging efficiency (however it is defined) will result in differences in fitness, and that the rate of behavioral change is greater than the rate at which the position or strategy conferring the maximum fitness changes. Thus evolution of the behavior is capable of tracking environmental changes which might shift the optimal foraging strategy. In support of the first of these assumptions, Schoener (1971) points out that it is well known that increased food intake increases the growth rate in many organisms. He proposes several mechanisms whereby increased growth rate may increase reproductive fitness. Still, there are few data linking differences in feeding behavior to differences in fitness.

The feeding models considered in Schoener (1971) and Pyke et al. (1977) center on four types of foraging choices that may affect food intake and thus fitness: a) the types of food to eat (optimal diet), b) the area in which to feed (optimal patch choice), c) how much time to spend in an individual patch, and d) speed and direction of movement while foraging. Pyke (1984) has updated these reviews and has considered several new classes of foraging models. I will limit my review to selection of food items.

As pointed out by Schoener (1971), modeling any aspect of foraging involves first choosing an appropriate currency (energy, nutrients, nitrogen) to maximize, constructing cost-benefit functions for that currency, and then solving for the optimum. In the original foraging models of Schoener (1971), Charnov (1976), and in most subsequent work, the chosen currency has been energy. Each potential food item has an associated caloric reward, and this energy reward is discounted by the energy costs associated with finding, capturing, and consuming the item. An optimal forager ranks items for inclusion in the diet on the basis of the energy/time ratio, and selects the diet by successively adding lower ranking items until such addition causes the net rate of energy intake/time to drop. The set of all available food items that do not cause this net energy/time rate to drop constitutes the optimal diet. This model yields several predictions regarding the inclusion of food types in the diet, such as a) the inclusion or exclusion of a food item is independent of the abundance of that type of food, but dependent on the abundance of higher ranking items; b) as the abundance of preferred food items increases, selectivity should increase, i.e., the number of types of food taken decreases; c) a given food item should always be either eaten or rejected. In fact, some bee species have been shown to violate prediction c and exhibit partial preferences (Waddington and Holden 1979, for example). These insects do not always accept or reject a given type of food item (flower type in this case). Such partial preferences have led several authors to speculate on the causes of partial preferences and other types of diet selection that are more varied than those predicted by these original formulations.

Pulliam (1975) and Westoby (1978) have both considered factors leading to diverse diets. Pulliam (1975) showed that nutrient constraints may cause an optimal predator to show partial preferences, and Westoby (1978) listed several factors that may cause an animal to choose a diverse diet. These include situations in which taking several types of food reduces search time, cases where the optimal diet cannot be deduced from past experience (i.e., sampling is required), and cases where different foods are the best sources of different required nutrients. Heinrich (1976a) and Waddington and Holden (1979) have also emphasized the importance of sampling to organisms that must monitor resources that vary over time. The inclusion of nutritive qualities other than energy content may be critical to building realistic foraging models for some organisms. For example, Belovsky (1981) has modeled food selection by a generalist herbivore, the moose, and has shown that food selection can be explained reasonably well by consideration of protein and ash content of browse plant species (which are highly correlated with digestibility), size of the food items, and relative abundance.

Another factor that may lead to broader diets than those predicted by early models is the amount of time available to the animal for foraging. Lucas (1983) points out that these early models generally assume that infinitiely long periods of time are available for foraging. In fact in many animals, foraging periods may be terminated by biotic factors, such as presence of a predator or conspecifics, as well as abiotic factors such as tidal cycles. Lucas has integrated the effects of limited foraging time into energy-maximization models of foraging. His models make two

interesting predictions: 1) as the length of the foraging bout decreases, the optimal forager should become less selective and include lower-quality prey items in the diet; 2) variability in prey distributions can produce situations where partial prey preference (i.e., not always either rejecting or taking an encountered prey item) will result in a greater rate of energy intake than either a pure specialist (always take only one prey type) or a generalist (always take more than one prey type) strategy. Thus, the nature of the time constraints under which a given animal operates may be important to prey selectivity decisions.

Another source of variability in diet selection may be differences in the variability of nutritive rewards offered by different food types. Caraco (1980), Real (1980a, 1980b, 1981) and Real et al. (1982) have emphasized the importance of variability in the current energy balance of the individual forager as well as variation in food quality within a food type in producing diversified diet selection. Their premise is that some animals may be selected not to maximize energy intake as suggested by the family of models reviewed by Schoener (1971) and Pyke et al. (1977), but to reduce the uncertainty associated with obtaining some critical level of energy intake. Thus, they might choose food types with low variability in reward over those that on average are more rewarding but also more variable. Caraco (1980) reasoned that an organism that can incur an energy deficit and survive may prefer high-variability items if they offer a higher mean reward. Such animals are "gambling" that they will encounter some high-reward items and reap the consequent energy benefit. Such animals are termed risk-prone foragers.

Other animals that cannot afford to incur a negative energy balance may opt for a more conservative risk-averse strategy and choose low-variability items even though they may be associated with a lower mean reward. Experimental tests of these hypotheses have lent some support. Caraco et al. (1980) showed that white-eyed juncos (Junco phaeonotus) exhibit risk-averse foraging when on a positive energy budget whereas starved birds switched to risk-prone foraging. They interpreted these results as indicating that the birds are willing to gamble on higher net rewards when those rewards are required to balance the energy budget. Birds that are experiencing no difficulty in balancing their energy budget are less likely to risk foraging on high-variability items. Real (1981) conducted feeding experiments with bumblebees and wasps and found risk-averse foraging in both types of insects; i.e., both showed preference for low-variability rewards. Real et al. (1982) found that, in foraging bumblebees, a food type with high reward variability required a greater mean energy reward than an invariant food type before the bees would visit it with equal frequency. The magnitude of the bees' risk-aversion was directly related to the degree of variability in the variable reward food item. At high reward levels, however, the degree of risk aversion declined, suggesting that finely-tuned foraging responses are more likely when energy may be limiting.

In addition to these factors that may modify the predictions of simple models of foraging, Mitchell (1981) has offered several cautions concerning simple energy maximization models of foraging. Whether the rate of energy intake or foraging efficiency actually affects fitness is not always clear. Some species select foods that

are most efficiently assimilated, whereas others select foods that are not. In some blowflies the threshold levels of sugar receptors to sugar solutions are highly variable, which is unexpected if energy content of the diet is directly related to fitness. Some sugar receptors are also stimulated by various amino acids, suggesting that there may be selection for dietary diversification in order to provide nutrients for reasons other than their caloric content. Real (1980a) has argued that even in species where energy content of the diet is related to fitness, there may be diminishing fitness returns at higher energy intake levels.

The foraging models discussed above thus make two basic assumptions that are rarely tested. First, they usually assume that animals will forage so as to maximize the rate of energy intake. As will be pointed out below, this assumption is more reasonable for some types of animals than others. Second, they assume that maximizing energy intake will maximize the achieved fitness. As pointed out by Real (1980a, 1980b, 1981), Caraco (1980), and others, factors other than energy content, such as variability in energy content, may be important to maximizing the probability of survival and therefore may form the basis of foraging choices. In the following sections, I will review some of the evidence for energy-maximizing behavior and food choice in nectarivorous animals and the effects of foraging choices on fitness.

Foraging Behavior of Nectarivores

Despite the untested assumptions of energy-maximization foraging models discussed above, Pyke (1981a) has emphasized that nectar-feeding animals are ideal test subjects for energy-based

foraging models. First, factors other than energy content affecting foraging decisions, such as non-energy nutrient content and risk of predation while foraging, can often be ignored with these animals. Nectar often contains little other than sugar and water, and is virtually the only source of energy for some nectarivores such as bumblebees. The survival, growth, and reproduction of these organisms are thus directly related to energy intake. Additionally, nectarivores are often quite visible while foraging, allowing easy quantification of food choice. Energy content of individual flowers can be measured. It is possible for researchers to construct time-energy budgets for foraging animals and reasonably estimate energetic costs and benefits encountered while foraging. It is therefore not surprising that much research has focused on foraging behavior and energetics of nectarivorous animals of diverse taxa.

Two nectarivore groups that have been thoroughly studied are nectar-feeding birds (Nectariniidae, Meliphagidae, Trochilidae) and various species of bees (Apoidea). The birds and their floral resources have been studied from the viewpoint of community organization and resource partitioning (Feinsinger 1976, 1978; Kodric-Brown et al. 1984; Wolf et al. 1976), morphology and flight energetics (Feinsinger et al. 1979), and energetics and behavioral ecology of the foraging process itself (Gill and Wolf 1977; Hainsworth 1978, 1981; Hainsworth and Wolf 1972a, 1972b, 1976; Kingsolver and Daniel 1983; Montgomerie 1984; Montgomerie et al. 1984; Pyke 1978, 1981a, 1981b; Pyke and Waser 1981; Wolf and Hainsworth 1971; Wolf et al. 1976). While it has generally not been

possible to test rigorous optimal foraging models under the complex and variable conditions encountered in the field, these studies have all emphasized the importance of energetic considerations in foraging selectivity. Numerous studies (Gill and Wolf 1977; Pyke 1978, 1981a, 1981b) have shown that hummingbird and sunbird movement patterns while foraging are non-random and serve to minimize the probability of the birds revisiting flowers and to maximize the probability of their visiting the most rewarding flowers. Metabolic rates of perching and hovering hummingbirds have been measured in the laboratory, and the energetic costs of the components of foraging have been estimated. By combining these data with time budgets recorded in the field, fairly accurate energy budgets have been constructed for several hummingbird-flower systems. This work has generally supported the contention that the birds are behaving so as to maximize the rate of energy gain (Hainsworth 1978). Because of their rapid rate of flower visitation, energy requirements of these birds may be obtained by their foraging during as little as 10 to 35% of each active hour (Hainsworth and Wolf 1972b; Wolf et al. 1976). The effect of the current energy status of the individual bird on its foraging behavior has been emphasized by Hainsworth (1981). He has demonstrated that the rate of energy gain by foraging hummingbirds increases with decreasing energy reserves, and that sensitivity of the birds to differences in nectar concentration (which in part determines energy content) is most pronounced in low-concentration, energy limited nectars.

One of the primary factors affecting energy content of nectar is sugar concentration. The relationship between nectar characteristics

and their effect on the rate of energy intake has also been studied in some detail (Hainsworth and Wolf 1976; Heyneman 1983; Kingsolver and Daniel 1983; Montgomerie 1984; Montgomerie et al. 1984; Pyke and Waser 1981). Theoretical models of hummingbird feeding mechanics of hummingbirds indicate that the net rate of energy intake will be maximized at nectar concentrations between 25 and 40% sucrose (Heyneman 1983; Kingsolver and Daniel 1983), due to constraints on nectar uptake rates produced by the high viscosity of concentrated nectars. Other studies discount the effects of viscosity on uptake rate and suggest that increasing sugar concentrations will increase the net rate of energy intake (Hainsworth and Wolf 1976; Pyke and Waser 1981; Montgomerie et al. 1984; Montgomerie 1984). The studies of Montgomerie (1984) and Montgomerie et al. (1984) demonstrate the sensitivity of hummingbirds to nectar characteristics while foraging under artificial conditions. These authors show that the birds' foraging decisions are consistent with maximization of the rate of energy intake or a closely related quantity, net energy per volume consumed. But nectarivorous birds differ in several important respects from nectarivorous insects. Foraging hummingbirds are homeothermic, which increases energy demands by increasing the rate of energy expenditure. Nectarivorous insects are able to vary body temperature and thus reduce metabolic rates at certain times to reduce overall energetic demands (Heinrich 1979b). The smaller body size of insects further reduces energy demands, allowing them to exploit nectar resources that would not support larger homeothermic nectarivores. Nectar quantities produced by insect-visited flowers are sometimes minute (Heinrich 1975; Watt et al. 1974).

The best studied nectarivorous insects are the hymenopterans, particularly within the family Apidae. Various studies have emphasized the effect of dispersion of floral resources on movement patterns of bees (Waddington 1980; Waddington and Heinrich 1981; Zimmerman 1979), competition for and differential strategies of exploitation of floral resources used by more than one species (Heinrich 1976b; Hubbell and Johnson 1978; Morse 1981; Inouye 1978, 1980; Johnson and Hubbell 1975; Schaffer et al. 1979), and selectivity of nectar resources in relation to nectar reward characteristics (Ginsberg 1983; Heinrich 1979a; Heithaus 1979; Pleasants 1981; Real et al. 1982; Real 1981; Roubik and Buchmann 1984; Waddington et al. 1981; Waddington and Holden 1979; Wells et al. 1981). The importance of some of these factors to flower selection in nectarivorous insects is considered next.

Among the more important factors affecting the choice of flowers by bees are dispersion of the resource, nectar volume, and concentration and variation thereof, evolved foraging strategy of the species (social vs. solitary, aggressive vs. passive), and length of the mouthparts in relation to flower structure. For stingless bees, the ability to find, recruit to, and defend floral resources varies among species, and different species select their floral resources accordingly. For example, two species of Trigona foraging at Cassia biflora separate on the basis of plant clump size, with the larger aggressive species foraging at large clumps and displacing the smaller species to isolated plants (Johnson and Hubbell 1975). In a study of several Trigona species, Hubbell and Johnson (1978) found that solitary foragers were the first to find new

resources, but were later displaced by larger, more aggressive group foragers. Schaffer et al. (1979) studied foraging of three genera of temperate bees (Apis, Bombus and Xylocopa) on Agave schlottii, which varied in nectar productivity along a density gradient. The solitary species (Xylocopa) exploited the lowest density sites, and the two social species required denser floral arrays before foraging was initiated. These authors suggest that the cost of provisioning the colony prevents the social species from foraging at the low productivity sites.

The importance of nectar productivity and availability to floral choice has also been studied in the field by Heinrich (1975, 1976a, 1979a, 1979b and references therein), Roubik and Buchmann (1984), and Pleasants (1981) and in laboratory situations by Real (1981), Real et al. (1982), Waddington (1980), Waddington and Holden (1979) and Waddington et al. (1981). Heinrich's extensive work with Bombus spp. has shown that individual bees learn to forage efficiently by specializing on a single flower species that provides them with the greatest energy reward. However, some sampling of less rewarding flowers is maintained by the bees in order for them to monitor changing floral resources. Pleasants (1981) also found that Bombus chooses nectar sources on the basis of nectar productivity and relative reward values. However, Corbet (1978) and Corbet et al. (1979) found that the frequency of bee visits to several species of flowers did not correspond to periods of maximum nectar availability. Roubik and Buchmann (1984) emphasize the importance of nectar concentration to flower selectivity by Apis mellifera and suggest that nectar of 45-60% sugar concentration maximizes the rate of energy

intake. They caution, however, that the net rate of energy intake is seldom due to concentration alone.

Another important factor influencing floral selectivity in wild bees is mouthpart length. Bees and flowers vary in the length of their tongues and corollas, respectively. Several studies have shown that long-tongued bees prefer long-corolla flowers and short-tongued bees prefer open flowers (Heinrich 1976b; Inouye 1978, 1980; Ranta and Lundberg 1980). Because they are inaccessible to short-tongued visitors, flowers with long tubular corollas or structures requiring strength to manipulate often accumulate greater nectar rewards than open flowers, and are preferred by the long-tongued bees, which can exploit them. Although Inouye (1980) found that longer-tongued bees were generally more rapid in their manipulation of the same flowers than short-tongued bees, Ranta and Lundberg (1980) suggested that intermediate tongue lengths were most effective. Short tongues may be more efficient at exploiting densely packed flowers with short corollas, such as composites (Inouye 1980).

Foraging selectivity of bees and wasps at artificial flower arrays is generally consistent with predictions of energy maximization models. Bees consistently learn to discriminate among flowers varying in reward value (Waddington 1980; Waddington and Heinrich 1981; Waddington et al. 1981; Waddington and Holden 1979). To this component of selectivity, Real (1981) has added the effect of variability in nectar rewards as a factor influencing choice, and has shown selectivity by bees and wasps for nectar sources with lower variability in volume and thus lower variability in energy content (Real et al. 1982).

The foraging behavior and energetics of insect nectarivores other than bees has been largely ignored. In particular, the feeding behavior of adult lepidopterans is described in the literature only anecdotally, although Schmitt (1980) has demonstrated that bees and butterflies foraging at the same resource differ in behavior. Butterflies foraging at Senecio (Asteraceae) tend to visit fewer flowers per plant and fly longer distances between plants than do bees. She suggested that the butterflies might be foraging suboptimally, but pointed out several differences between bee and butterfly biology that could cause the observed differences. These included the non-social nature of butterflies, the fact that foraging butterflies may be simultaneously searching for mates or oviposition sites while foraging, and the non-aggressive characteristics of lepidopterans. Thus we might expect floral selectivity of butterflies to be subject to different constraints than those of bees. In the next section I will review the available information regarding the choice of foods by adult lepidopterans.

Adult Foraging in Lepidopterans

Gilbert and Singer (1975) pointed out that the importance of resources to adult butterflies is highly diverse but poorly understood. Moth species of several families (Oestriidae, Gastrophilidae, Saturniidae) emerge from the pupae as adults with degenerate mouthparts and subsist completely on lipid resources stored as larvae (Domroese and Gilbert 1964; Heinrich 1975; House 1974). At the other extreme are groups such as sphingids, which due to their high wing-loading and hovering flight have metabolic

expenditures while foraging comparable to those of hummingbirds, and are consequently highly dependent on adult resources (Heinrich 1975). Some butterflies, such as some tropical Heliconius species, may live for up to six months and are highly dependent on pollen sources for maximal egg production (Gilbert 1972). Several authors anecdotally mention that adult resources may be a limiting factor to several butterfly species (Heliconius charitonius, Cook et al. 1976; H. ethilla, Ehrlich and Gilbert 1973; Chlosyne lacinia, Neck 1977) but no evidence is presented. Clench (1967) showed that population sizes of eleven hesperiine species were highly correlated with abundance of major nectar sources, and that the phenologies of ecologically similar skipper species were staggered. This suggests competition for limiting nectar resources. He concluded that most "typical" butterfly species may be limited by nectar resources. Murphy (1983) demonstrated that oviposition by Euphydryas editha is highly dependent on the proximity of suitable nectar sources to the larval host plants. Scott (1973) documented extensive flights by males of four species of lycaenids in search of nectar. Gilbert (1976) described an African lycaenid, Megalopalpus zymna, that feeds on larval lycaenid secretions (honeydew) and is morphologically adapted to mimic an ant in order to elicit honeydew production and avoid aggression by ants tending the larvae. Emmel (1971) reported an apparently mutualistic symbiosis between an Ecuadorian skipper (Perichares philietes) and a Maxillaria orchid. The orchid has a long, convoluted corolla that prevents access to the nectar by most insects. The skipper has apparently morphologically adapted to this orchid and was not observed visiting

other flower species. These studies suggest that in some butterflies there is strong selection for profitable or efficient adult foraging.

Butterflies as a group feed on a wide variety of substances. Various species have been reported feeding on floral nectar, pollen, honeydew, frog hopper secretions, rotting fruit, urine, perspiration, dung and carrion (Gilbert and Singer 1975). Within a species, however, food habits are more restricted. Opler and Krizek (1984) point out that many forest-dwelling butterflies do not visit flowers. Certain groups of butterflies tend to be associated with particular food types. Danaine butterflies tend to be flower feeders, ithomiines feed on nectar and bird droppings, charaxines feed on dung and rotting plants, and among the nymphalines, the Heliconiini and Argynnini tend to be nectar feeders whereas the Apaturini and Nymphalini are generally not flower visitors, but may feed on sap or rotting fruits (Gilbert and Singer 1975).

The nutrients obtained from these diverse food sources are also varied. Arms et al. (1974) identified sodium as the stimulus eliciting "puddling" behavior in Papilio glaucus. This is a common behavior in several butterfly families in which congregations of butterflies gather to suck on wet sand or soil. Curiously, these gatherings are usually composed entirely of young males (Adler 1982; Adler and Pearson 1982). The behavior seems to be due to the high sodium requirements of males for spermatophore production (Adler and Pearson 1982). Watt et al. (1974) studied nectar sources of several montane Colias species and concluded that water balance may be a major function of nectaring. Amino acids may be obtained by butterflies feeding at dung, carrion, etc., and are certainly one of the main

sources of nutrition of pollen-feeding Heliconius butterflies.

Gilbert (1972) has shown that amino acids released from pollen after soaking in nectar are rapidly incorporated into eggs and significantly increase fecundity.

Although as a group butterflies feed on a variety of food types, the main source of nutrition for many species is floral nectar. Nectar composition in relation to pollinator type has been extensively studied by Baker and Baker (1983 and references therein). Although a variety of compounds has been detected in nectar, such as amino acids, proteins, lipids, ascorbic acid, and alkaloids (Baker and Baker 1975), the main component of most nectars is a variety of mono- and disaccharide sugars (Heinrich 1975; Baker and Baker 1983). Most nectars, regardless of pollinator type, contain some fructose, glucose and sucrose, although their relative proportions vary (Baker and Baker 1983). Butterfly visited flowers tend to contain about 25% sugar (weight/weight) (Heinrich 1975; Watt et al. 1974; Pyke and Waser 1981), and can be divided into two groups. Butterflies visit short-corolla, open flowers that are also exploited by other insects (termed bee-butterfly flowers by the Bakers), and these flowers tend to be hexose-rich (glucose, fructose). Most composites (Asteraceae) fall into this category. Shields (1972) found that the plant family most commonly used by butterflies for nectar is the Asteraceae. The second type of butterfly-visited flower, comprising long-corolla tubular flowers, is characteristic of the "butterfly pollination syndrome" (Faegri and van der Pijl 1979) and tends to be sucrose-rich (Baker and Baker 1983). Watt et al. (1974) suggest that hexoses may be cheaper for the plant to manufacture, but point out that Colias

butterflies have the enzymatic capability of converting hexoses to sucrose and vice-versa. Butterflies are therefore presumed to be able to use the sugars found in most floral nectars.

The amount of nectar produced by a flower is closely related to the metabolic needs of the pollinator (Heinrich and Raven 1972; Heinrich 1975). Because of the low energy demands of butterflies, nectar availability of butterfly flowers tends to be low relative to other pollinator types (Watt et al. 1974; Opler 1980). In fact, no published data exist concerning standing crops of butterfly nectar, the amount actually available to the forager. Both Watt et al. (1974) and Opler (1980) bagged flowers to prevent insect visitation and measured accumulated nectar after 24 hours. Opler found a maximum availability of 0.93ul/ flower (of eight butterfly visited plant species), and Watt et al. found between 0.4 and 5.6ul/ flower among 16 species of flowers visited by Colias species. Opler found a maximum nectar availability of 9.7 ul in large-bee pollinated flowers. Butterflies can forage at low-reward flowers because their energetic costs while foraging are relatively low. They do not thermoregulate by endothermy as bees do, but rather use solar energy to maintain high body temperatures (Clench 1966; Heinrich 1974; Rawlins 1980). Energetic cost of flight in butterflies is probably relatively low due to their low wing-loading and ability to use wind currents for gliding (Heinrich 1975; Casey 1981).

The selectivity and use of nectar resources by butterflies have not been quantitatively studied. Numerous studies suggest that butterflies feed on a limited subset of available floral resources (Boggs et al. 1981; Neck 1977; Wiklund and Åhrberg 1978; Opler and

Krizek 1984; Watt et al. 1974; Levin and Berube 1972; Ohsaki 1979; Richman and Edwards 1976; Wiklund 1977), although these are mainly qualitative observations and do not attempt to determine the factors influencing selectivity. Foraging studies of Heliconius charitonius at artificial flowers have shown that these butterflies learn to discriminate by color among flowers differing in nectar reward (Swihart and Swihart 1970; Swihart 1971), and Vaidya (1969) showed that Papilio demoleus prefers larger artificial flowers to smaller ones and that a fused corolla is preferable to separate petals. Root and Kareiva (1984) compared the behavior of ovipositing versus nectaring Pieris rapae and showed that distinctly different behaviors were used, with nectar foraging involving more turning in order to keep the butterfly within a restricted area. They did not quantify selectivity between available nectar sources. Wasserman and Mitter (1978) suggested that lepidopterans that are generalist feeders as larvae tend to be larger than specialists, but they do not extend their discussion to adult feeding habits. Butterflies as a group are apparently more generalized and opportunistic in their feeding habits than most other nectarivores (Gilbert and Singer 1975; Opler and Krizek 1984; Clench 1966).

One factor that has been related to adult resource use in butterflies is the relationship between proboscis length and flower morphology. Opler and Krizek (1984) report on visitation patterns of a northern Virginia butterfly community and show a positive correlation between proboscis length and mean corolla tube length of flower species visited. They also point out that the ratio of proboscis length to forewing length (an indicator of body size) is

indicative of feeding habits of individual species. Non-flower visitors have ratios of 0.3:1.0 or less, flower visiting butterflies generally fall between 0.3 and 0.5:1.0, and skippers have ratios greater than 0.45:1.0. The benefits of having such a long proboscis have not been quantified. Other factors they feel are important in determining flower choice are flower abundance (the most abundant species is usually preferred) and flower color (white, blue, pink or purple are preferred).

Nectar characteristics may also be important to floral selectivity. From a theoretical standpoint, Kingsolver and Daniel (1979) and Heyneman (1983) have constructed theoretical models that predict that butterflies should prefer flowers with nectar concentrations of 20-25% sucrose, as these nectars should provide the maximal rate of energy intake during feeding. Both papers are based on simulation models and lack empirical support, but reach the same conclusions independently. The models are based on the physics of fluid flow through a tube-like conduit, such as a butterfly proboscis. In such a system, the rate of energy intake is determined by the volumetric rate of consumption as well as the energy content per volume, which depends on sugar concentration. Since the viscosity of sugar solutions (which limits volume uptake rate) increases exponentially with increasing concentration while energy content increases linearly, the result is a decline in uptake rates at higher sugar concentrations that outweighs the effects of increased energy content. The maximal rate of energy intake thus occurs at moderate concentrations. Neither model addresses factors other than nectar

concentration, but, if realistic, these models may have important implications regarding floral selectivity in butterflies.

From the above discussion, it seems clear that adult butterflies are quite variable in their dietary needs. The volumes and concentrations of nectar sources used by butterflies suggest that energy intake of these insects may be quite small relative to that of other nectarivores. Yet there are suggestions, based on both qualitative observations and theory, that some butterflies may be selective in their choice of flowers. Is there any evidence that adult resources or selectivity of such significantly influences fitness? This question is considered below.

Effects of Adult Foraging on Fitness

The voluminous literature on animal foraging in the past decade has dealt almost entirely with the immediate behavior and proximate consequences associated with foraging decisions. Yet an underlying assumption of all optimal foraging models is that an increase in foraging efficiency (or rate of energy gain, or whatever quantity is being studied) will result in increased fitness (Schoener 1971; Mitchell 1981; Pyke et al. 1977). This assumption is rarely tested, and for some organisms there is virtually no information regarding the relationship between foraging efficiency and survival, fecundity, longevity, or any other factor affecting fitness. Some authors of bee studies have asserted that nectar is by far the most important source of energy to the colony, so that increasing the energy supply will increase the growth and reproductive success of the colony (Heinrich 1979; Pyke 1981a). No data or corroborating studies are cited.

For a number of organisms there are data on the relationship between adult dietary intake and factors affecting fitness. In many holometabolous insects, the feeding habits of adults are completely different from those of the larvae. Even though the larva is usually considered the main feeding stage of the insect's life cycle, dietary intake during the adult stage can also be crucial to fully realizing potential longevity and fecundity. Smith (1965) compared the effects of a water diet and a diet of dried, powdered aphids to adult coccinellid beetles of 13 species. The water diet increased longevity over starved insects, but protein in the diet further increased longevity and was required for egg production in some species. Finch and Coaker (1969) studied the effects of various carbohydrates on the survival and fecundity of the cabbage root fly, Eroischia brassicae. In contrast to most dipterans, which must feed on both carbohydrates and protein before egg laying, E. brassicae needs only carbohydrates before laying the first egg batch. Protein is required for later clutches. These authors showed that water alone doubled the longevity of female flies but stimulated virtually no egg production. The effects of different sugars were quite variable. Pentoses and hexoses (except for glucose and fructose) resulted in poor fecundity, while glucose and fructose increased fecundity by a factor of more than 25. Sucrose produced the greatest fecundity increases. Interestingly, 0.1M sucrose solutions promoted greater longevity than 0.5M solutions. They also tested the effects of a variety of wild nectars normally fed on by the flies and found fecundity was increased in most cases.

For lepidopterans, the picture is more complex. As mentioned earlier, some species do not feed as adults, and their resources for

adult activities and reproduction come solely from reserves stored by the larvae. Thus, in Hyalophora cecropia, females contain about 9% lipid (of fresh weight) on the second day after eclosion, while males contain about 33%. These lipid stores fall throughout the lives of the adults. The greater lipid content of males is attributed to the greater metabolic expenditures of these insects incurred as a result of searching for the sedentary females. Interestingly, these insects use only lipids as flight fuel and cannot use glucose added directly to the muscle (Domroese and Gilbert 1964). Similarly, in Galleria melonella (Pyralidae), adults do not feed, and energy for adult activities is derived from stored lipids (as indicated by respiratory quotients between 0.75-0.77). Females use about 51% of their eclosion energy for metabolic costs and 17% for reproduction (Carefoot 1973).

Even in species that do feed as adults, the foods ingested by the larvae and the amount of stored reserves carried over to the adult stage can markedly affect fitness (Beckwith 1970; Fenemore 1977; Slansky 1982 and references therein) as well as adult morphometrics and behavior (Angelo and Slansky 1984). The effects of adult feeding on fitness seem to be quite variable though. Fecundity and longevity differences caused by variation in adult diet have been best studied in several pest moth species, which show a variety of patterns. For example, the European corn borer (Ostrinia nubilalis: Pyralidae) does not need even water in the diet to realize some egg production (Raina and Bell 1978). In soybean loopers (Pseudoplusia includens: Noctuidae) the inclusion of sugar in the diet increases fecundity over starved and water-fed moths. Similarly, in cabbage loopers (Trichoplusia ni: Noctuidae) the number of eggs laid is directly

related to the sugar concentration on which the adults are fed (Raina and Bell 1978). In the pink bollworm (Pectinophora gossypiella: Gelechiidae) the number of eggs laid is increased by sucrose or honey in the diet, but viability of these eggs is no greater than those produced by starved or water-fed moths. The same effects were seen in the cotton leafperforator (Bucculatrix thurberiella: Lyonetiidae) (Benschoter and Leal 1976), where fecundity increases to a maximum with 40% sucrose solutions. In the potato tuber moth (Pthorimaea operculella: Gelechiidae), however, fecundity is higher on a 5% sucrose diet than on more concentrated diets (El-Sherif et al. 1979). In studies of the same species, Fenemore (1977, 1979) found that water feeding alone doubled the fecundity over that of starved moths, but that sucrose did not further increase egg production. Labeyrie (1957) found however that honey caused a tripling of fecundity over that of starved moths, leading Fenemore (1979) to conclude that honey contains important nutrients other than sucrose.

Among the butterflies, effects of adult feeding on fitness are not as well known as in moths. Stern and Smith (1960) studied the factors affecting egg production in Colias philodice eurytheme (Pieridae) and found that egg production is supported in part by fat stored during the larval stage. However, the presence of sugar in the diet decreases the rate at which the fat body is depleted and increases the number of eggs laid. Water alone tripled the fecundity of females as compared to starved individuals. Starved individuals usually lived no more than 6 days compared to a normal lifespan of 24-30 days. The presence of sucrose in the diet causes another tripling of egg production over that of water-fed females. Gilbert

(1972) showed that Heliconius butterflies rapidly incorporate amino acids from pollen-feeding into eggs, and that pollen-feeding significantly increases egg production over nectar-feeding alone. Brower (in press) has shown that migrating monarchs build up lipid stores while in the southern U.S. Tuskes and Brower (1978) suggest that the amount of stored lipid possessed by an individual monarch arriving on the overwintering grounds is an important factor determining the probability of surviving the winter as well as the distance to which that butterfly can remigrate the following spring.

The most detailed study of the importance of adult resources to fitness is that of Murphy et al. (1983) on the nymphalid Euphydryas editha. They fed female butterflies on six different diets and measured weight change, survival and fecundity. The diets included starvation, water only, 20% sucrose, water and 0.004M amino acids, and 20% sucrose plus 0.004M or 0.02M amino acids. The most significant increases in fecundity and longevity were due to sugar in the diet. Weight declined most rapidly in the water-fed group, less quickly in the water/amino acid diet, and least quickly in the sucrose and sucrose/amino acid treatments. Fed females lived longer than unfed ones, and the maximum longevity was seen in the sucrose diets. The sucrose diets increased fecundity, but only in later egg masses. Amino acids did not increase fecundity, but did increase the weight of later eggs, which directly affects hatchability. They found no effect of increasing amino acid concentration above that normally found in floral nectar. They concluded that since early egg masses contribute more to fitness than later ones (because larval foodplant quality

declines in the latter part of the season and many caterpillars die), adult feeding increases fitness only in wet years when later egg masses have a chance of surviving. Murphy and his colleagues also speculated that populations without nectar sources may be at a higher risk of extinction in dry years.

It thus seems clear that adult diet can have significant effects on fitness. Furthermore, adult dietary requirements may depend to a large degree on the amount of stored resources provided by the larval stage. Boggs (1981) has discussed this interdependence between larval and adult feeding requirements in holometabolous insects. She reasoned that the potential reproductive effort of an insect depends on the proportion of larval resources allocated to reproductive reserves plus the overall proportion of adult-acquired nutrients to be allocated to reproduction. This leads to the prediction that resource allocation during metamorphosis should be adjusted relative to the expected adult nutrient intake. Boggs tested this prediction using three species of heliconiine butterflies (H. cydno, H. charitonius and Dryas julia). She examined nitrogen budgets of these animals and estimated the proportion of nitrogen earmarked for reproduction as the ratio of abdominal N to total body N. This proportion is independent of body size as predicted. The three species differ in the extent of pollen-feeding exhibited as adults (D. julia does not feed on pollen). As predicted, the greater the amount of pollen-feeding as an adult, the lower was the proportion of reproductive nitrogen to total nitrogen in the newly emerged adult. D. julia stores the largest amount of reproductive nitrogen from larval feeding and this stored nitrogen declines most rapidly in this non-pollen feeding species.

Boggs concluded that an adjustment in overall adult nutrient intake is accompanied by a concomitant change in allocation of larval reserves at metamorphosis. This hypothesis has not been tested with nutrients other than nitrogen. Most butterflies do not feed on pollen (Gilbert 1972), however, and the major adult dietary component is sugar from floral nectar. We should thus see a similar relationship between expected adult energy intake and larval energy reserves stored (as lipid) for adult activities.

General Approach of This Study

Clearly, foraging behavior of adult insects is affected by a large number of factors that determine the extent of adult feeding and the choice of food items. I have reviewed models and data regarding energetic considerations in food choice, including mechanical constraints as well as parameters of the reward itself (such as nectar concentration and volume) that affect the rate of energy intake. The dispersion of food items may also affect the rate of energy intake while foraging. Also, the selection of nectar resources by the adult insect can be based upon morphological properties (proboscis length and corolla tube length), and on the patterns of nutrient storage by larval stages. Finally, to understand fully the foraging decisions made by a species requires some knowledge of the effects of the chosen food items or nutrients contained therein on fitness parameters. Below I review the purpose and plan of each of the following sections with regard to the above considerations.

Chapter II addresses the theoretical modes of Kingsolver and Daniel (1979,1983) and Heyneman (1983). These models are based on the mechanics of fluid flow through nectarivore mouthparts and predict

that certain nectar concentrations (20-25% for butterflies) will maximize the net rate of energy intake of the feeding animal and should therefore be preferred by the foraging insect. I present data, heretofore lacking, that address the applicability of these models to butterflies. These data were collected from two common butterfly species (described in detail below). The same species, Agraulis vanillae and Phoebis sennae, are considered in subsequent chapters as well.

Chapter III pertains to the nectar sources used by these two species and the characteristics thereof. Combining data on energetic rewards offered by these nectar sources with time budget data on foraging behavior, I construct energy budgets to estimate foraging profits offered by the various flower species. I use these estimates to determine which floral characteristics (nectar volume, concentration, corolla length, floral density) most significantly affect the energetic profits obtained by the butterflies. Data are also considered that deal with the effect of differing morphologies (proboscis length) on flower visitation. Using observations on the two species foraging in the same floral arrays, I demonstrate that these species do differ in foraging selectivity. Finally, data from a mark-recapture study of Agraulis are considered with respect to the effects of mobility on flower selectivity.

In Chapter IV, I compare the stored larval resources (lipids) of the two species in light of the observed differences in flower selectivity and foraging energetics described in Chapter II, in order to test Boggs' (1981) hypothesis of larval reserve-adult feeding interdependence. I also examine the change in lipid stores over the

adult lifespans of the two species, and relate differences in fat storage and depletion to foraging behavior.

Chapter V considers the effects of sugar components of nectar on various components of fitness such as fat storage, longevity and egg production. I describe in this section feeding experiments designed to determine the effect of varying the level of energy intake of adult Agraulis vanillae on these factors. Data are also presented which address the effect of larval feeding success on adult fecundity.

Finally, I present a general discussion in Chapter VI of the entire set of studies and summarize the major conclusions.

Biology of the Study Species

The gulf fritillary, Agraulis vanillae nigrrior (Nymphalidae: Heliconiinae) ranges from the southern U.S. through central America to Argentina. In the Alachua Co., Florida, area it is a common inhabitant of open areas, such as old fields, roadsides and pastures (Opler and Krizek 1984). Breeding populations are restricted to the vicinity of the larval food plant, Passiflora incarnata (Arbogast 1965), which is commonly found in a variety of disturbed habitats. Eggs are laid singly on older leaves, and the period between oviposition and eclosion as an adult lasts 22-28 days. Breeding in the Alachua Co. area is continuous from April-May to November. Adults live 14-21 days, and only adults overwinter (Opler and Krizek 1984). This species apparently does not overwinter in Alachua Co. (Arbogast 1965), and is presumed to recolonize northern Florida each spring from overwintering populations in southern Florida. Extensive southward migrations occur from September

to November, and a less distinct remigration occurs in April-May (Walker 1979). Details of the migration are unknown.

The cloudless sulphur, Phoebis sennae eubule (Pieridae), is also a common inhabitant of open habitats in Florida. It ranges from the southern U.S. (with occasional incursions farther north) through central America to Argentina (Opler and Krizek 1984). The adults are most commonly found in the vicinity of the larval host plants (Cassia obtusifolia and C. fasciculata), but are apparently not as restricted to local concentrations of the food plant as in Agraulis. Although there is a large southward migration from September-November (Walker 1979), some individuals overwinter in the Alachua Co. area and can be seen flying in small numbers on warm days throughout the winter. Only adults of this species overwinter also (Opler and Krizek 1984). Though adults can be seen throughout the year, sizable numbers are not usually seen until August-September when the Cassia foodplants mature. Population sizes near the food plants tend to be smaller than those of Agraulis populations around Passiflora. Howe (1975) noted that wide fluctuations in populations are characteristic of Phoebis species. Although the longevity of adults is unknown, it is apparently greater than that of Agraulis, because overwintering Phoebis adults are in reproductive diapause and presumably survive to remigrate in the spring (Opler and Krizek 1984).

Both species are often abundant in the north Florida area. Both frequent open habitats, making observation practical. Finally, both are avid flower visitors and floral nectar is apparently the major component of the adult diet. They are thus ideally suited for comparative studies of many aspects of adult foraging.

CHAPTER II
NECTAR UPTAKE RATES OF AGRAULIS VANILLAE
AND PHOEBIS SENNAE: EFFECT ON OPTIMAL
NECTAR CONCENTRATIONS

Introduction

Ecologists in recent years have devoted much attention to the foraging behavior of animals, particularly addressing the problem of dietary optimization (Schoener 1971; Pyke et al. 1977). Many theoretical studies have yielded predictions about foraging time allocation, prey selectivity, habitat utilization, and other behavioral decisions regarding foraging behavior, whereas other recent models have considered mechanical aspects of the feeding structure in an attempt to identify physical optima regarding food choice. In particular, the models of Kingsolver and Daniel (1979,1983) and Heyneman (1983) have addressed the feeding mechanics of nectarivores and have derived predictions regarding optimal nectar concentrations. The Heyneman (1983) model, applicable to nectarivores in general, predicts that nectar of 20-25% sucrose concentration yields a maximal rate of energy intake. Kingsolver and Daniel have applied two different approaches to nectar feeders that result in different predictions depending on the feeding mechanism. One model (Kingsolver and Daniel 1979), designed for suction feeders such as butterflies that feed continuously in a steady-state fashion, also predicts that 20-25% sucrose concentrations maximize the rate of energy intake.

Interestingly, field studies of nectar composition from butterfly-visited flowers have found sugar concentrations to average about 25% (Pyke and Waser 1981; Watt et al. 1974). The second model (Kingsolver and Daniel 1983), which applies to non-steady-state feeders that rely on cyclic filling and emptying of the feeding apparatus (such as the tongue of a hummingbird), predicts that 35-40% sucrose solutions maximize the rate of energy intake. While these models stress the importance of mechanical constraints (especially the effects of viscosity) in determining the optimal nectar concentration, other workers (Pyke and Waser 1981) minimize the effects of these mechanical factors and have argued that energy intake rate should increase with increasing sugar concentration. According to Pyke and Waser (1981), the optimal nectar concentration (for hummingbirds) is around 70% sucrose.

The rate of energy intake is crucial to most optimal foraging models, as it is this quantity that is generally assumed to be optimized while foraging (Pyke, Pulliam and Charnov 1977). The Kingsolver-Daniel (1979) model predicts that a 20-25% sugar concentration provides the maximal rate of energy intake while the butterfly is actually feeding. This optimum occurs because the energy content of nectar increases linearly with increasing sugar concentration, while the viscosity increases exponentially. The exponential increase in viscosity limits the rate of nectar uptake at higher concentrations and causes the rate of energy intake to decline above 20-25% sucrose. The mathematical form of this model is summarized in Table 2-1. In their model simulations, Kingsolver and Daniel (1979) and Heyneman (1983) estimated uptake rates

TABLE 2-1 - A SUMMARY OF THE KINGSOLVER-DANIEL (1979)
FEEDING ENERGETICS MODEL

$$1) E_{diff} = E_{in} - E_{met} - E_{mech}$$

where E_{diff} = net rate of energy intake
 E_{in} = gross rate of energy intake
 E_{met} = metabolic rate of feeding insect
 E_{mech} = mechanical energy required to pump nectar

$$2) E_{in} = QRAS/100$$

where Q = nectar uptake rate
 R = nectar density
 A = energy content of sugar
 S = nectar concentration

$$3) E_{mech} = (P_1 - P_2) Q/E$$

where E = muscle efficiency
 other terms as above or as in equation 4

$$4) P_1 - P_2 = 32V_1uL(1+C+C^2)/3D_1^2C^3 - rV_1^2(1-1/C^4)/2$$

where $P_1 - P_2$ = pressure drop generated by sucking insect
 V_1 = nectar velocity at distal end of proboscis
 L = proboscis length
 u = nectar viscosity
 r = nectar density
 D_1 = proboscis diameter at distal end
 C = constant obtained by dividing proximal diameter
 of proboscis channel by distal diameter

by assuming that the nectarivores exert a constant pressure drop at all nectar concentrations. The pressure drop is the change in pressure between the proximal and distal ends of the proboscis (due to frictional losses and change in diameter of the feeding channel), and this quantity along with nectar viscosity and the morphology of the proboscis determine the nectar uptake rate. The assumption of constant pressure drop predicts that uptake rates decline curvilinearly with increasing sugar concentration. They estimated the net energy intake rate from predicted uptake rates of the feeding animal. The uptake rates are critical to the rate of energy intake, since uptake rate (volume/time) multiplied by energy content of the nectar (energy/volume) determines the energy intake rate. As mentioned by Kingsolver and Daniel (1979), the mechanical cost of pumping the nectar (E_{mech}) should be negligible. Since metabolic rate of feeding insects is assumed to be independent of nectar concentration and thus does not affect the optimal concentration, it will be ignored here. My purpose is to examine the relationship between nectar concentration and nectar uptake rates. This relationship, which is crucial to estimating energy intake rates, requires empirical support. Specifically, I present data that test the pressure drop assumption and uptake rate predictions of both the Kingsolver-Daniel (1979) and Heyneman (1983) models. The actual nature of the concentration-uptake relationship necessitates modifications of the predictions of these models concerning both the sucrose concentration of the "optimal" nectar as well as the evolutionary importance of such an optimum with regard to natural selection for food choice in these nectar feeders.

Methods and Materials

I captured adult Agraulis vanillae (Nymphalidae) and Phoebis sennae (Pieridae) while they were feeding at nectar sources at field sites on Paynes's Prairie State Preserve, Alachua Co., Fla. I maintained them in the laboratory by keeping each individual in a glassine envelope in a plastic box at room temperature. The boxes were kept at high humidity to prevent dessication. Each butterfly was kept for five days, during which time it was allowed to feed once a day and its nectar uptake rates measured. Each butterfly was fed with solutions of 10,20,30,40 and 50% sucrose concentration (weight/weight). The five concentrations were presented to each individual butterfly on consecutive days in a random order, so that during captivity each butterfly was fed once at each concentration. I released all butterflies at the end of the five-day test period.

I measured the insects' nectar uptake rates of by inducing the butterflies to feed from 100ul microcapillary tubes (Drummond microcaps) that had been filled with sucrose solution of known concentration. The microcap was mounted on a small balsa platform alongside a millimeter scale (see Appendix). I placed the butterfly on a perch in front of the platform and induced it to feed by uncoiling its proboscis manually and touching the tip to the nectar inside the microcap. The rate at which the rear meniscus of the nectar column moved along the millimeter scale was timed with a stopwatch. I made three to five measurements for each butterfly during a feeding bout and averaged these figures to obtain one uptake rate per butterfly at each concentration. As both species maintain body temperatures in the field that are 6-8° C above ambient

temperature (see Chapter III); and since nectar uptake rate of these poikilothermic insects is most likely related to body temperature, the entire procedure was performed inside a styrofoam chamber that was heated to 28° C. Before each butterfly was tested it was allowed to warm up to flight temperature in the chamber. The procedure is described in the Appendix and in May (in press).

Because the amount of nectar imbibed by butterflies was not controlled, the actual caloric value of each butterfly's daily meal varied. (This depended on the uptake rate of that individual, the nectar concentration that was tested on that particular day, and feeding duration, which varied depending on how quickly the required measurements could be made.) To determine whether or not this variation in energy intake affected the uptake rates, I measured uptake rates of two groups of butterflies receiving diets of the same sucrose concentration but different caloric content over a five-day period. One group received 12.9 ul of 30% sucrose nectar per day, or 0.21 Joules/day (this corresponded to 15 mm on the scale) and the other received 34.5 ul per day, or 0.57 Joules/day (40 mm on the scale). The low-energy group consisted of 4 male and 2 female Agraulis vanillae, and the high-energy group consisted of 2 male and 3 female Agraulis vanillae. The daily energy contents of the diets for the two groups encompassed the range of energy contents of the diets received by the butterflies used in the main uptake rate measurements. This design also allowed me to test for effects of age (over a five-day time span) on uptake rate.

I measured proboscis lengths by excising the proboscides at the bases, mounting them on clear glass slides with transparent tape, and measuring them with a millimeter scale. Proximal and distal diameters of the internal feeding channel of each proboscis were measured by scanning electron microscopy.

Results

Proboscis measurements are presented in Table 2-2. The length of the proboscis and the proximal and distal diameters of the feeding channel are parameters of the Kingsolver-Daniel (1979) model. These measurements were taken without regard to sex. Internal diameters of the feeding channels do not differ greatly between the two species, but Phoebis sennae has a proboscis that is a full centimeter longer than that of Agraulis vanillae. According to Kingsolver and Daniel (1979) this should result in lower nectar uptake rates and therefore lower energy intake rates for Phoebis. The ratio of proximal diameter to distal diameter of the feeding channel, C , is slightly larger in Phoebis, indicating that the feeding channel of Phoebis is more sharply tapered than that of Agraulis. The uptake rates of both species differ considerably from those predicted by the models, particularly at low sucrose concentrations (Figures 2-1 and 2-2). The predicted curves were obtained using the equations of Kingsolver and Daniel (1979) and the proboscis dimensions of Agraulis and Phoebis by assuming a constant pressure drop of one bar. Two-way ANOVAs indicate that there are significant effects of both sex and concentration on volume uptake rates for both species (Table 3-2). All regressions of uptake

TABLE 2-2 - PROBOSCIS DIMENSIONS OF AGRAULIS VANILLAE AND PHOEBIS SENNAE. [mean $\pm$ 1 standard deviation (n)]

	SPECIES	
	Agraulis	Phoebis
Length (cm)	1.92 $\pm$ 0.18 (18)	2.95 $\pm$ 0.22 (9)
Proximal diameter (um)	79.5 $\pm$ 3.31 (4)	86.5 $\pm$ 3.44 (2)
Distal diameter (um)	59.7 $\pm$ 2.20 (4)	55.4 $\pm$ 27.1 (2)
C ^a	1.33 $\pm$ 0.09 (4)	1.56 $\pm$ 0.01 (2)

^a C = proximal diameter/distal diameter

TABLE 2-3 - RESULTS OF TWO-WAY ANOVAS OF NECTAR UPTAKE RATES VS. CONCENTRATION AND SEX. Uptake rates as a function of concentration are presented in Figures 2-1 and 2-2. Analyses of variance indicate that both sex and nectar concentration significantly affect uptake rate.

A. Agraulis vanillae

Two-way analysis of variance

Source	DF	MS	F	P
Sex	1	0.152	25.27	< 0.0001
Nectar conc	4	0.752	124.78	< 0.0001
Interaction	4	0.009	1.45	> 0.21

B. Phoebis sennae

Two-way Analysis of Variance

Source	DF	MS	F	P
Sex	1	0.076	6.67	< 0.011
Nectar conc.	4	0.927	81.71	< 0.0001
Interaction	4	0.007	0.61	> 0.65

Figure 2-1 - Predicted and observed nectar uptake rates (mean $\pm$ one standard error on either side of the mean, in $\mu\text{l/s}$) as a function of nectar sucrose concentration (weight/weight) in *Agraulis vanillae*. Given are means $\pm$ one standard error. Predicted curve based on Kingsolver and Daniel (1979) assuming a pressure drop of one bar at all concentrations.

Figure 2-2 - Predicted and observed nectar uptake rates (mean $\pm$ one standard error on either side of the mean, in ul/s) as a function of nectar sucrose concentration in *Phoebis sennae*. Given are means $\pm$ one standard error. Predicted curve based on Kingsolver and Daniel (1979) assuming a pressure drop of one bar at all concentrations.

rate on nectar concentration are highly significant (Agraulis males: $n = 116$, $F = 418.1$, $p < 0.0001$; Agraulis females: $n = 101$, $F = 158.7$, $p < 0.0001$; Phoebis males: $n = 108$, $F = 183.0$, $p < 0.0001$; Phoebis females: $n = 66$, $F = 150.2$, $p < 0.0001$). There were no significant differences in uptake rates between the two groups receiving different amounts of energy in the diet (Table 2-4); i.e., uptake rates are independent of energy intake within the range of diets used in this study. In addition, the two-way ANOVA indicates that there is no effect of day number on uptake rate over the five-day course of the experiment. I therefore conclude that failure to control rigidly daily energy intake did not affect the uptake rate measurements presented in Figures 2-1 and 2-2.

Using the measured uptake rates and proboscis dimensions for each species, I calculated the rates of energy intake, E_{in} (uptake rate multiplied by energy content of the nectar); E_{mech} , the mechanical energy required to pump the nectar; E_{diff} , the net rate of energy intake; and $P_1 - P_2$, the pressure drop produced at each concentration (Table 2-5). (Viscosity data are from Weast [1974].) These data show that a) the butterflies do not produce a constant pressure drop at all nectar concentrations, but instead increase pressure drop with increasing sucrose concentration of the nectar; b) that this pressure drop exceeds 1 bar (as calculated by equation 1 in Table 2-1) at higher concentrations; and c) that the optimal sucrose concentration, i.e., that concentration providing the maximum rate of energy intake, is from

TABLE 2-4 - UPTAKE RATE VS. DAILY ENERGY CONTENT OF DIET. [mean $\pm$ one standard deviation (n)]

Day #	Daily Energy Intake	
	0.57 Joules/day	0.21 Joules/day
	Uptake Rates (in $\mu\text{l/s}$)	
1	0.409 $\pm$ 0.050 (6)	0.418 $\pm$ 0.095 (5)
2	0.443 $\pm$ 0.040 (6)	0.447 $\pm$ 0.114 (5)
3	0.406 $\pm$ 0.064 (6)	0.434 $\pm$ 0.097 (5)
4	0.436 $\pm$ 0.064 (6)	0.436 $\pm$ 0.091 (5)
5	0.405 $\pm$ 0.139 (6)	0.415 $\pm$ 0.116 (5)

Two-way analysis of variance

Source	DF	MS	F	P
Energy content	1	0.0015	0.18	> 0.67
Day number	4	0.0018	0.22	> 0.92
Interaction	4	0.0010	0.11	> 0.97

TABLE 2-5 - FEEDING ENERGETICS OF AGRAULIS AND PHOEBIS. See text for details of calculations.

	E_{in}	E_{mech}	E_{diff}	$P_1 - P_2$	
%sucrose	Gross rate of energy intake (Watts)	Mechanical energy (Watts)	Net rate of energy intake (Watts)		Pressure drop (Bars)
<u>Phoebis sennae</u> - males					
10	1.1084	0.000151	1.0182		0.474
20	1.8712	0.000171	1.8710		0.609
30	2.6398	0.000228	2.6396		0.901
40	2.6525	0.000230	2.6523		1.257
50	1.4299	0.000177	1.4297		1.746
<u>Phoebis sennae</u> - females					
10	0.9956	0.000144	0.9955		0.463
20	1.8012	0.000159	1.8011		0.586
30	2.2441	0.000165	2.2439		0.766
40	2.1699	0.000153	2.1668		1.027
50	1.8556	0.000165	1.8554		1.686
<u>Agraulis vanillae</u> - males					
10	0.9480	0.000125	0.9479		0.422
20	1.6481	0.000127	1.6480		0.513
30	1.9109	0.000114	1.9108		0.623
40	2.1017	0.000138	2.1016		0.952
50	1.7791	0.000145	1.7790		1.546
<u>Agraulis vanillae</u> - females					
10	0.8112	0.000092	0.8111		0.361
20	1.3418	0.000084	1.3417		0.417
30	1.7599	0.000097	1.7598		0.574
40	1.7575	0.000097	1.7574		0.796
50	1.4106	0.000091	1.4105		1.225

35-40% rather than 20-25%. The calculations of pressure drop are based on an assumption of steady state flow (for other assumptions see Kingsolver and Daniel [1979]). Observations of feeding butterflies indicate that the flow is not steady state. The butterflies seem to vary pressure drop while feeding because the nectar being removed from the microcapillary tubes moves in pulses. The pressure drop calculations should therefore be taken as rough approximations.

The observed rates of energy intake differ from those predicted by Kingsolver and Daniel (1979) (Figs. 2-3 and 2-4). These predicted curves were derived from the actual proboscis dimensions given in Table 2-2 and the model of Kingsolver and Daniel (1979), assuming a constant pressure drop of 1 bar. This assumption predicts a higher rate of energy intake at all sucrose concentrations for Agraulis than for Phoebis. Since Phoebis has a longer and slightly narrower proboscis, the Kingsolver and Daniel (1979) model predicts lower uptake rates and consequently lower rates of energy intake for this species. In fact, Phoebis has a higher rate of energy intake at any nectar concentration (Table 2-5) because of the greater pressure drops generated and the greater uptake rates produced (Figures 2-1 and 2-2). Table 2-5 illustrates two additional points: a) pressure drops increase with increasing nectar concentration, and b) males have greater rates of energy intake due to the higher uptake rates. Higher uptake rates in males are presumed to be the result of greater pressure drops produced by males. Alternatively, sexual dimorphism in proboscis dimensions might cause this difference. Regardless of the basis for the difference between males and females, the assumption of constant pressure drop that is central to the

Figure 2-3 - Predicted and observed rates of energy intake (watts) of feeding butterflies as a function of sucrose concentration in *Agraulis vanillae*. Predicted curve based on Kingsolver and Daniel (1979) assuming a pressure drop of one bar at all concentrations. See text for details.

Figure 2-4 - Predicted and observed rates of energy intake (watts) of feeding butterflies as a function of sucrose concentration in Phoebis sennae. Predicted curve based on Kingsolver and Daniel (1979) assuming a pressure drop of one bar at all concentrations. See text for details.

theoretical models is not upheld, and consequently the optimal sucrose concentration is shifted upward. In addition, the ecological significance of this optimum is likely to be less important than suggested by the model simulations, as the relative increase in energy intake rate around the optimum sucrose concentration is not as great as the models predicted. That is, the empirically determined graph of energy intake vs. sucrose concentration is not as sharply peaked as the original simulations suggested.

Examination of the data in Table 2-5 shows that E_{mech} is negligible with respect to the energy content of the nectar, and the major factor influencing the net rate of energy intake is simply the volume uptake rate.

Discussion

The data presented here suggest that modification of the original theoretical models is in order, and they raise new questions about the energetics of feeding butterflies. Contrary to the assumption of the Kingsolver and Daniel (1979) and Heyneman (1983) models, neither species exerts a constant pressure drop at all nectar concentrations. Instead, both butterflies increase suction pressure with increasing nectar concentration. This is enigmatic, as they could greatly increase the rate of energy intake at lower nectar concentrations by exerting the pressure drops that they produce at higher nectar concentrations. The fact that they do not produce greater suction at lower nectar concentrations suggests that there may be some physical limit on the rate at which the feeding apparatus can accept nectar. Producing a high pressure drop with a low concentration nectar might exceed this limit. Alternatively, if the insects are under little or

no selection pressure to maximize energetic efficiency of foraging or minimize feeding time, there may be no advantage to producing higher uptake rates.

If these species are under selection to maximize the rate of energy intake, then the data here suggest that they should selectively forage at flowers with 35-40% sucrose nectars, as these nectars provide the greatest energetic return per unit time. The intensity of selection to forage at the "optimal" nectar concentration, however, is probably weaker than suggested by the Kingsolver-Daniel (1979) and Heyneman (1983) models since the increase in energy intake realized by feeding at the "optimal" concentration is not as great as predicted by their simulations. Surprisingly, the nature of this empirically determined optimum and the shape of the energy intake vs. concentration curve are similar to those predicted by Kingsolver and Daniel (1983) for discontinuous feeders such as hummingbirds. While measuring the uptake rates of both species I observed pulsing of the nectar in the microcapillary tube as the butterflies were feeding, suggesting that butterfly feeding may be a discontinuous process. If so, then the Kingsolver and Daniel (1983) model may more accurately describe the energetics of feeding in these insects than does the earlier model for suction feeders. This latter model is based on a feeding structure that relies on capillary flow of nectar to fill the apparatus rather than suction, however, so it is not directly applicable to butterflies without modification.

Particularly curious is the male-female dichotomy in uptake rates. Males have higher nectar uptake rates, resulting in greater rates of energy intake at any given nectar concentration. Females of

Agraulis vanillae are significantly larger than males, so one might expect the females to be able to generate greater suction pressure and thus greater uptake rates. (Males and females of Phoebis sennae do not differ in size.) As a proximate mechanism, sexual dimorphism in proboscis morphology could also cause differences in uptake rates and energy intake rates. However, since females of Agraulis vanillae are larger in body size, they would be expected to have larger proboscides, and thus produce greater uptake rates than males exerting a similar pressure drop. Females must bear the energetic expense of egg production, suggesting at an ultimate level that selection for maximizing the energy intake rate might be greater than in males. However, neither of these alternatives is suggested by the data. Males may be under greater selective pressure to maximize foraging efficiency and/or minimize foraging time because of the energetic and time expense associated with finding females and courting them. Stanton (1982) and Kingsolver (1983) showed that males of some Colias species spend a greater amount of time in flight and make longer flights than females. Males of the two species described here seemed to spend a greater amount of time in vigorous flight around nectar sources, chasing both females and other males. A female may be as easily found by a male when she is feeding as when she is in flight, and therefore there may be weak selection for females to minimize feeding time. Searching for mates by males may require active searching while in flight, which imposes obvious time and energy constraints on foraging.

One important caution concerning these models should be mentioned. The models discussed here make the implicit assumption

that nectar concentration is the major factor affecting the rate of energy intake by a foraging butterfly. Several other unrelated factors may also affect the rate of energy intake while these butterflies are foraging. If they were offered unlimited quantities of nectar varying only in concentration, with foraging involving no more than imbibing nectar, then 35-40% sucrose nectars would provide the greatest rate of energy intake. Butterflies foraging at real flowers, however, spend only a small fraction of foraging time actually extracting nectar. Most foraging time is spent in transit between flowers or in handling time (Chapter III). Heyneman (1983) incorporates the effect of transit costs into her model and suggests that increasing travel costs will raise the optimal nectar concentration. In addition, since the butterfly's rate of energy intake while foraging is dependent in part on the number of flowers visited per unit time, a nectar source that occurs in dense concentrations but is of a nonoptimal concentration could be more profitable than a nectar source that is of the optimal concentration but occurs at low density. Further, once a butterfly has reached a flower, it must find the nectaries. A long-corolla flower with relatively inaccessible nectar and high handling time can lower the rate of energy intake by decreasing the proportion of foraging time devoted to actually imbibing nectar (Heinrich 1983). Finally, nectar does not occur in unlimited quantities but in small discrete packets, often in minuscule amounts (Watt et al. 1974; Chapter III). If there is great variation in volume among nectar sources, this could nullify the energetic benefits of feeding at the "optimal" nectar concentration. More complex models incorporating the effects of

variation in nectar concentration, nectar volume, flower density and handling time on foraging profitability may be necessary for a full understanding of foraging behavior in these nectarivorous animals. An important question to be addressed in the next chapter, then, is what are the relative values of single-factor approaches (such as the concentration models here) and multi-factor approaches in describing the energetics of foraging in nectarivores?

Summary

Mechanical models of butterfly feeding energetics have predicted that the maximum rates of energy intake of butterflies imbibing nectar occur when sugar concentration of the nectars are between 20 and 25% sucrose. This prediction is based on the assumption that the butterflies exert a constant pressure drop at all nectar concentrations (assumed in the original simulations to be one bar). I measured uptake rates of Agraulis vanillae and Phoebis sennae and found these rates to deviate significantly from those predicted by the models. These butterflies vary the pressure drop produced as a function of nectar concentration; pressure drop is increased with increasing sugar concentration (and therefore viscosity) of the nectar. Calculated pressure drops range from 0.36 to 1.8 bars. One effect of varying pressure drop in this mannner is to produce lower uptake rates at low nectar concentrations than those predicted by the original models. In addition, males of both species produce greater pressure drops and uptake rates than do females. Since energy intake rate is determined by the volume uptake rate (volume imbibed/time) multiplied by the energy content (energy/volume) of the nectar, these butterflies exhibit lower rates of energy intake at low nectar

concentrations (since pressure drop is less than one bar) than predicted by the models. Higher rates of energy intake are exhibited at higher nectar concentrations than predicted, since pressure drop is greater than one bar. The empirically determined energy intake rates show that the optimal nectar concentration (that concentration maximizing the energy intake rate) is between 35 and 40% sucrose rather than 20 and 25%.

CHAPTER III
FLOWER SELECTION AND THE ENERGETICS OF FORAGING IN AGRAULIS VANILLAE
AND PHOEBIS SENNAE

Introduction

The importance of nectar sources to adult butterflies is not well known. Clench (1967) argued that nectar sources were a limiting factor to several species of hesperiines, based on the synchrony of flowering phenologies of several nectar sources and the numbers of adult skippers. Shreeve and Mason (1980), however, found that the number of butterfly species in a woodland habitat was not related to the abundance of nectar sources, and Sharp, Parks and Ehrlich (1974) found little correlation between abundance of nectar sources and numbers of several butterfly species. Sugar in the diet of adults has been shown to increase both fecundity and longevity for Colias (Stern and Smith 1960) and Euphydryas (Murphy et al. 1983) butterflies and for several moth species including Bucculatrix thurberiella (Lyonetiidae) (Benschoter and Leal 1980), Pectinophora gossypiella (Noctuidae) (Raina and Bell 1978), and Phthorimaea operculella (Gelechiidae) (El-Sherif, Gomez, and Hemeida 1979, Fenemore 1979).

If the energy derived from nectar sources is critical to adult butterflies, natural selection should favor foraging behavior that maximizes the energy intake rate while they forage at these resources. I have shown in Chapter II that energy intake is maximized at nectar concentrations of 35-40% sucrose rather than 20-25% as suggested by

Kingsolver and Daniel (1979) and Heyneman (1983). Yet Roubik and Buchmann (1984) caution that foraging success is rarely due to the effects of nectar concentration alone. Other variables affecting foraging success include nectar volume, flower handling times, and flower density (and hence travel costs). Thus it is important to evaluate the relevance of single factor models, such as Kingsolver and Daniel (1979), to modeling phenomena that are known to be affected by a variety of factors, such as the energetics of foraging butterflies. The relationship between variables such as volume, floral density, and handling times and foraging energetics has not been investigated for any butterfly species, and surprisingly little is known about the quantitative characteristics of butterfly nectar sources in general. Watt et al. (1974) investigated nectar resource use by two montane Colias species and found that the butterflies chose nectar sources that tended to be rather dilute in sugar concentration (about 25% sugars) and rich in monosaccharides. Nectar availability was measured, but only after preventing visitation for 24 hours, which provides little information about standing crop actually available to foraging butterflies. Wiklund and Ahrberg (1978) qualitatively described nectar use by Anthocaris butterflies, but did not quantify nectar characteristics. Richman and Edwards (1976) briefly described visitation patterns of four species of migrating butterflies in Florida and showed differential flower selection by these species, but again did not quantify nectar characteristics.

Flower selection and foraging energetics of bees have been thoroughly studied. Heinrich (1979b) has done much work on the foraging energetics of bumblebees and has attempted to estimate

foraging success in terms of energetic profit, but this probably has little relevance to butterflies because of the major differences in the biology of these two groups. Schmitt (1980) compared bee and butterfly foraging at several species of Senecio and demonstrated significant differences in foraging behavior. Butterflies (all foraging species were lumped under the general category of butterflies) tended to visit fewer flowering heads per plant than bumblebees and to fly greater distances between flowers than did bees. She suggested that the butterflies were not foraging optimally in terms of energy intake.

In this section I consider the behavior and energetics of foraging by Agraulis vanillae and Phoebis sennae at the nectar sources most frequently used by these two species at my study sites in order to determine which floral characteristics are most closely related to the energetic gain realized by butterflies foraging at these flowers. By quantifying the nectar available (standing crop volume and sugar concentration), and butterfly foraging behavior (flower visitation rate and amount of time spent perching and in flight), I estimate energy budgets of each species at the major nectar sources. These estimates can then be used to search for ecologically relevant cues to foraging success, including the nectar characteristics themselves (concentration and volume) and floral characteristics. Corolla length has been shown in bees to affect the floral resources available to a given bee species (Inouye 1980; Ranta and Lundberg 1980). By preventing access of short-tongued nectarivores to the nectar, long-corolla flowers may accumulate more nectar; corolla length may therefore be a useful predictor of foraging profitability. Flower

density may also be a predictor of foraging success as flower species that occur in higher densities result in a greater visitation rate (increased energy intake) and reduced traveling distances (reduced energy expenditure).

One goal of this chapter is to address the utility of single-factor (concentration) models of foraging energetics as compared to a multi-factor approach. In addition to seeking correlations between floral and nectar characteristics and foraging success, I compare foraging selectivity in these two butterfly species. Both are commonly found in the same habitats, so foraging decisions made in response to the same resource arrays can be compared. Several questions can be addressed with this sort of comparison. Do these species differ in their foraging behavior at the same resources? Do these differences result in different energetic consequences to the species? What factors might lead to divergent foraging tactics and energetics when the two species are feeding at a common resource?

Methods and Materials

Nectar characteristics

I monitored nectar resource use by both Agraulis vanillae and Phoebis sennae at several sites on Payne's Prairie State Preserve, Alachua County, Florida, between April and October 1982. I defined major nectar sources as all flower species at which feeding was frequent enough and of sufficient duration to permit collection of behavioral data (described below). I did observe visitation at other nectar sources, but only sporadically. For major nectar sources, available nectar volume and sucrose concentration were measured at

three to seven different times for each species. Corolla length and flower density (flowers/m²) were also measured once for each nectar source at a typical patch of flowers. I measured nectar volume with Drummond microcapillary tubes (1 - 5 ul). Most previous studies of nectar characteristics of butterfly visited flowers have not quantified available nectar, but have allowed nectar to accumulate for up to 24 hours (Watt et al. 1974; Opler 1980), as available nectar is often minuscule. Most workers measure nectar by insertion of the capillary tube into the flower corolla; this is impossible in many butterfly flowers because of the small corollas. I measured nectar volumes by removing the flowers from the calyx, and squeezing the corolla tube from the top to expel the nectar as a small droplet from the bottom of the corolla. This droplet can then be picked up with a microcap; this allows measurement of nectar volumes that are undetectable by insertion of the microcap into the corolla. Nectar concentrations were measured by use of an American Optical 10431 temperature-compensated hand refractometer, which measures nectar concentrations in per cent sucrose equivalents. Since both glucose and fructose have refractive indices approximately half that of sucrose, the concentration of nectars that are mixtures of these sugars can be expressed as the equivalent amount of sucrose to give similar refractive properties. A single concentration measurement requires about 0.5 to 1 ul of nectar; since many of the flowers measured contained volumes of a few thousandths of a microliter per flower, this often required the pooling of nectar from as many as 25-100 flowers to obtain a single nectar concentration. Given sucrose concentration and nectar volume, milligrams of sugar per flower can be

calculated (Bolten et al. 1979), and this quantity can be converted to energy per flower, assuming 16.48 joules per mg of sucrose (Heinrich 1975). Inouye et al. (1980) have shown that various non-sugar nectar constituents (such as lipids, amino acids, etc.) can add to the refractive index of nectars, causing overestimation of energy content. However, even at very high concentrations of several of these constituents, Inouye and his colleagues found a maximum error of 3.6% sucrose equivalents. Each of these constituents alone (at high concentrations) caused errors ranging from 0.06 to 0.94% sucrose equivalents. This magnitude of error is acceptable for the approximate energetic estimates derived here.

Foraging behavior and energetics

Foraging behavior of the butterflies at each nectar source was quantified by measuring the visitation rate (flowers visited/s), and the proportion of foraging time spent in flight. This was done using two stopwatches. On one stopwatch, the length of the foraging bout under observation was timed, and on the other, the duration of flight during the bout was recorded. From these data, I calculated the proportion of foraging time spent in flight for each butterfly species at each of the nectar sources. A tally was kept of the number of flowers visited during the observation period to calculate foraging rate. As the butterflies often moved out of sight fairly rapidly, the length of most bouts I measured was about one minute. These data were then used to estimate energy intake and expenditures of the foraging butterflies. Energy intake was calculated as the mean visitation rate multiplied by the mean energy available per flower or

$$E_{in} = \text{flowers/s} \times \text{joules/flower.} \quad (3-1)$$

Energy expenditure was estimated as the proportion of time in flight (T_{fl}) multiplied by the metabolic expense of flight (E_{fl}) plus the proportion of time perched (T_{per}) multiplied by the resting metabolic rate (T_{per}) or

$$E_{cost} = T_{fl} (E_{fl}) + T_{per} (E_{per}). \quad (3-2)$$

Heinrich (1975) suggests that in nectarivorous insects the metabolic costs of walking and feeding are probably close to resting metabolic rates. Metabolic rates were obtained from the literature. Zebe (1954) measured the metabolic rate of Vanessa io (Nymphalidae) at rest and in flight. The resting metabolic rate was measured at 0.32 ccO₂/g/hr at 21.5°C. I have used this figure for both Agraulis and Phoebis, whose average weights are 0.195 g and 0.231 g, respectively. Thoracic and abdominal temperatures of foraging butterflies were measured using a Bailey BAT-12 electronic telethermometer and needle probe. Butterfly temperatures were measured within 10 seconds after the insect was netted. As both species attain thoracic temperatures averaging about 38°C in the field, metabolic costs must be scaled accordingly. Chaplin and Wells (1982) found a Q_{10} of 3.0 for monarch metabolic rates. Using this figure, I calculated resting metabolic rates at 38°C for Agraulis and Phoebis to be 1.53 ccO₂/g/hr. Since butterflies burn mainly fat as fuel (as indicated by an RQ of 0.7) (Zebe 1954), one cc of oxygen oxidizes 0.000497g of fat, which produces 19.75 joules of energy. Thus, the resting energy expenditure of Agraulis is estimated at 0.0016J/sec at 38°C, and that of Phoebis is estimated at 0.0019 J/sec. Using a similar procedure, and starting with Zebe's (1954) measurements of the metabolic cost of flight in Vanessa io, I estimated flight costs in

Agraulis as 0.0573 J/sec and in Phoebis as 0.0679 J/sec. Because Zebe measured flight metabolism of butterflies forced to flap continuously in a metabolic chamber, he probably overestimated the cost of flight compared to foraging butterflies which may glide or use wind currents to reduce energetic expenditure. Thus, foraging costs are probably overestimated, resulting in conservative estimates of foraging profit. Foraging profitability for each nectar source was calculated as energy intake (Equation 3-1) minus metabolic cost of foraging (Equation 3-2) or

$$E_{\text{net}} = E_{\text{in}} - E_{\text{cost}} \quad (3-3).$$

Measuring the energy content of each nectar source species several times throughout the day gives several estimates of foraging profitability for each nectar source species. Foraging rates and percent flight time are assumed to be constant for each nectar source species. Since only nectar volume changed between times of day, and since the time required to extract the nectar is only a small fraction of foraging time, changes in nectar volume should not affect the butterflies' foraging rates or their amount of time spent in flight.

Flower selectivity

I observed both species while they foraged at two patches of flowers of different composition. The first floral array, observed from 7 September to 12 September 1984, occupied approximately 100 m², and included two major nectar species (Hyptis mutabilis and Verbena brasiliensis). The second floral array was observed between 14 September and 26 September 1984, was of approximately 150 m² and included four major nectar species (Hyptis, Verbena, Bidens pilosa,

and Ipomoea trichocarpa). Foraging bouts of individual butterflies were quantified by recording the sequence of flowers (or flower heads for Bidens) visited while in the patch.

Temporal changes in behavior

To determine if diurnal partitioning of foraging and other behaviors occurred, I conducted censuses of all Agraulis vanillae seen along a 220 m transect (described below) at half-hour intervals throughout the morning and early afternoon on eleven days between 10 August and 31 August 1984. The length of the transect was traversed in approximately five minutes, and each butterfly sighted was recorded as exhibiting one of the following behaviors: 1) nectaring, 2) basking or perched, 3) in reproductive flight, or 4) in rapid searching flight. Reproductive flight included several distinct behaviors. Females spend a large proportion of their activity time in a slow, turning flight through the vegetation in search of oviposition sites. Males engage in a similar flight, apparently in search of females. Occasional courtship flights (following, wing fluttering) were also observed and included in this category. The last category included flight behavior quite different from reproductive flight. This flight is more rapid, direct, and usually about 1m above the vegetation. I observed mostly males exhibiting this type of flight.

Movement patterns

The vagility of a species can determine what resources it is exposed to, which could influence flower selectivity. Because the two species studied here were markedly different in this regard, I quantified the extent of movement by individuals within a population. This was possible only for Agraulis vanillae, due to low population

densities and difficulty of capturing sufficient numbers of Phoebis sennae. A mark-recapture study of Agraulis vanillae was carried out between 9 August and 14 September 1984 at a population about 500 m south of the Alachua sink on the north edge of Payne's Prairie. This butterfly population was centered on a population of Passiflora incarnata growing along a network of dikes through the marsh. A 220 m transect was set up along the main dike road, and numbered flags were placed at 10 m intervals along this transect. The entire length of the transect contained both larval host plants (Passiflora) and nectar plants. At one- to three-day intervals, all butterflies captured along this transect were marked using the 1-2-4-7 wing marking method (Ehrlich and Davidson 1960). Before release, the location of capture, behavior prior to capture, sex and wing wear condition of each butterfly were recorded. Wing wear was subjectively assigned to one of the following categories: 1) fresh - no visible wear, 2) young -- < 25% scale loss (visually estimated), little or no fraying of wing margins, 3) 25-50% scale loss, light to moderate fraying of wing margins, and 4) >50% scale loss, heavy fraying of margins. Behaviors were categorized as 1) nectaring, 2) basking or perching, 3) oviposition, mate search or courtship flight, and 4) rapid searching flight. The location, date, time and behavior of any marked butterfly observed or recaptured were recorded.

Results

Phoebis, with a proboscis of nearly 3 cm, can feed at a greater range of floral resources than does Agraulis, resulting in a greater range of flowers to select from and consequently greater energetic rewards during foraging. Table 3-1 presents the proboscis lengths of

TABLE 3-1 -- MEAN PROBOSCIS LENGTH OF AGRAULIS AND PHOEBIS AND FLORAL CHARACTERISTICS OF NECTAR SOURCES. [mean $\pm$ 1 standard deviation (n)]. Comparisons between species were by Mann-Whitney U test.

	<u>Agraulis vanillae</u>	<u>Phoebis sennae</u>	<u>U</u>	<u>p</u>
Proboscis length(cm)	19.2 $\pm$ 1.81 (16)	29.5 $\pm$ 2.20 (9)	0	<.0001
Corolla length (cm)	6.27 $\pm$ 4.13 (7)	14.09 $\pm$ 9.93 (7)	11.5	0.10
Nectar volume (ul)	0.107 $\pm$ 0.192 (36)	0.486 $\pm$ 0.889(31)	314	<.005
Nectar concentration (% sucrose)	24.01 $\pm$ 9.81 (21)	25.90 $\pm$ 9.21 (25)	199.5	0.46
Energy/flower (joules)	0.400 $\pm$ 0.701 (36)	2.884 $\pm$ 5.062(31)	316.5	<.002

the butterflies and floral characteristics of the major nectar sources of the two butterfly species. The differences in foraging selectivity are considered in more detail below. On a gross level, however, resource use by Phoebis results in an average energy reward per visited flower over seven times as great as that of Agraulis. This is due primarily to differences in the mean nectar volume of the flowers visited by the two species. Nectar concentrations of the flowers visited do not differ between the two species. Although the corolla lengths of the two butterflies' nectar sources do not differ statistically (Table 3-1), the difference is biologically significant. Four of the nectar sources visited by Phoebis have corolla lengths over 2 cm long. The nectar in these flowers is inaccessible to Agraulis. As shown below, there is a highly significant correlation between corolla length and energy per flower.

I observed both species foraging at seven or eight major nectar sources. Table 3-2 presents the phenologies of the nectar sources studied. These observations are qualitative only; no attempt was made to collect phenological data. Not all of these species were available at the same site. Cnidioscolus stimulosus was available for only 2-3 weeks at a upland site south of the prairie and was the only nectar source for this Agraulis population for the period during which Cnidioscolus bloomed. Vernonia gigantea bloomed at a site in the NW section of Payne's Prairie and was essentially the only nectar source used by Agraulis and Phoebis foraging in this area. Richardia scabra is a common plant of roadsides and waste areas and I studied it at a fallow agricultural field west of Lake Alice on the University of Florida campus. Interestingly, this low-reward flower was only

TABLE 3-2 -- NECTAR SOURCES AND FLOWERING PHENOLOGY

<u>Species</u>	<u>Blooming period</u>	<u>Peak visitation</u>	<u>Foragers</u>
<u>Cnidoscopus</u> <u>stimulosus</u>	May - September	late May-June	<u>Agraulis</u>
<u>Verbena</u> <u>brasiliensis</u>	April - September	May - September	<u>Agraulis</u>
<u>Sida</u> <u>rhombifolia</u>	May - September	July-August	Both
<u>Bidens</u> <u>pilosa</u>	June -October	September-October	<u>Agraulis</u>
<u>Hyptis</u> <u>mutabilis</u>	mid-June - October	August - October	Both
<u>Vernonia</u> <u>gigantea</u>	August - September	August	Both
<u>Richardia</u> <u>scabra</u>	June-October	September-October	<u>Agraulis</u>
<u>Agalinis</u> <u>purpurea</u>	October	October	<u>Phoebis</u>
<u>Ipomoea</u> <u>trichocarpa</u>	August - October	September-October	<u>Phoebis</u>
<u>I.</u> <u>coccinea</u>	August - October	September-October	<u>Phoebis</u>
<u>I.</u> <u>quamoclit</u>	August - October	September-October	<u>Phoebis</u>

visited by Agraulis where it occurred in large stands away from other nectar sources. Small patches blooming simultaneously with preferred nectar sources at the Alachua sink population were generally ignored. The three Ipomoea species are also common roadside species and I observed them both on Payne's Prairie and in the Gainesville area. Agalinis purpurea was studied in an open field south of Payne's Prairie near Lake Wauberg. I observed all of the other nectar source species on the north side of Payne's Prairie near the Alachua sink, where all are available simultaneously for a period of several weeks from late summer to early fall. Notice that the peak numbers of nectar sources are available in late summer and fall; this corresponds to the peak of butterfly abundance for both species. Flower density seems to peak at this time as well.

The available nectar volumes of the flowers visited by these species span a wide range of variation, and consequently the energetic reward per flower varies widely as well. The flowers selected by Phoebis, however, tend to have greater nectar volumes and therefore energy contents. Table 3-3 presents the nectar availability data broken down by flower species. The nectar availability of each species was measured several times throughout the morning and mid-day when foraging behavior was at a maximum. These measurements were analyzed to give a mean reward averaged throughout the foraging period. The sample sizes referred to in Table 3-3 thus refer to the number of discrete samples taken (i.e., times of day) and the total number of flowers measured (or number of concentration readings taken). As nectar concentration measurements required more nectar than was sometimes available, not all nectar volume measurements

TABLE 3-3 -- NECTAR AVAILABILITY AND ENERGY CONTENT OF MAJOR NECTAR SOURCES OF AGRAULIS AND PHOEBIS. [mean $\pm$ 1 standard deviation, (n;n). First number indicates number of times sampled, second number indicates total number of flowers sampled].

Species	X volume (ul)	X concentration (% sucrose)	X energy/flower (joules)
<u>Richardia</u> <u>scabra</u>	0.0076 $\pm$.0125(5;98)	18.7 $\pm$ 9.8(3;9)	0.015 $\pm$.018 (5)
<u>Verbena</u> <u>brasiliensis</u>	0.0079 $\pm$.0041(7;188)	38.4 $\pm$ 5.8(1;6)	0.058 $\pm$.030 (7)
<u>Bidens</u> <u>pilosa</u>	0.0118 $\pm$.0048(3;68)	40.4 $\pm$ 1.9(1;8)	0.093 $\pm$.038 (3)
<u>Agalinis</u> <u>purpurea</u>	0.0415 $\pm$.0243(4;67)	17.1 $\pm$ 1.1(3;23)	0.123 $\pm$.071 (4)
<u>Vernonia</u> <u>gigantea</u>	0.0387 $\pm$.0337(6;110)	29.5 $\pm$ 14.5(3;18)	0.174 $\pm$.185 (6)
<u>Hyptis</u> <u>mutabilis</u>	0.0832 $\pm$.0499(6;96)	18.7 $\pm$ 8.5(5;18)	0.248 $\pm$.079 (6)
<u>Sida</u> <u>rhombifolia</u>	0.132 $\pm$.039 (4;55)	25.6 $\pm$ 6.6(3;13)	0.568 $\pm$.238 (4)
<u>Ipomoea</u> <u>trichocarpa</u>	0.220 $\pm$ 0.159(3;45)	34.9 $\pm$ 1.4(3;10)	1.488 $\pm$ 1.144 (3)
<u>Cnidoscolus</u> <u>stimulosus</u>	0.494 $\pm$.293(5;81)	19.8 $\pm$ 1.6(4;37)	1.770 $\pm$ 1.126 (5)
<u>Ipomoea</u> <u>coccinea</u>	1.562 $\pm$ 0.235(3;44)	31.1 $\pm$ 1.7(3;21)	9.102 $\pm$ 1.751 (3)
<u>Ipomoea</u> <u>quamoclit</u>	1.853 $\pm$ 1.490(5;70)	28.4 $\pm$ 0.5(3;25)	9.270 $\pm$ 7.85 (5)

were accompanied by a concentration reading at the same time of day. In these cases, energy/flower was calculated using the concentration that was taken closest in time to the volume measurement. For two of the extremely low volume flowers, Verbena brasiliensis and Bidens pilosa, accumulation of enough nectar for a concentration measurement required bagging the flowers and preventing visitation for several hours; thus nectar concentration could not be measured before mid-day, and the concentration obtained at that time was used in conjunction with all volume measurements taken earlier. The result is probably an overestimation of the energy content of these flowers, as the nectar on which I took the concentration measurement was probably more concentrated due to evaporation than the actual available nectar on which the volume measurements were taken (Corbet 1978; Corbet et al. 1979). A common trend in most nectar sources begins with maximum availability in the morning, usually soon after the flowers open or begin secreting nectar. Nectar availability then declines throughout the morning. By noon, the visitation rate by butterflies and a host of other nectarivorous insects is so great that nectar availability at most flowers is kept at a minuscule amount. After about 1300 hours nectar volumes approached zero for most species. Most nectar sources showed very high variances in volume of available nectar. Variation in nectar concentration was most pronounced in open flowers with short corollas (see Table 3-4) and apparently is due to evaporation and concentration of the nectar as the morning progressed. There seems to be less of a tendency for evaporation in flowers with long corollas, such as the Ipomoea spp. and Agalinis purpurea. It became apparent early in the study that Phoebis did not visit

TABLE 3-4 -- DENSITY AND COROLLA LENGTHS OF NECTAR SOURCES [mean $\pm$ 1 standard deviation (n)].

Species	Corolla length (mm)	Density (flrs/m ²)
<u>Richardia</u>	7.03 $\pm$ 0.62 (15)	199.2 $\pm$ 117.7 (15)
<u>Verbena</u>	3.59 $\pm$ 0.28 (21)	1272.0 $\pm$ 936.0 (10)
<u>Bidens</u>	4.56 $\pm$ 0.72 (12)	1312.3 $\pm$ 459.0 (20)
<u>Agalinis</u>	21.91 $\pm$ 2.16 (16)	66.8 $\pm$ 31.8 (20)
<u>Vernonia</u>	10.30 $\pm$ 0.76 (15)	514.1 $\pm$ 401.7 (10)
<u>Hyptis</u>	6.09 $\pm$ 0.33 (16)	527.9 $\pm$ 226.2 (12)
<u>Sida</u>	0(no corolla)	124.0 $\pm$ 58.3 (10)
<u>Ipomoea trichocarpa</u>	20.80 $\pm$ 1.87 (10)	47.7 $\pm$ 17.0 (24)
<u>Cnidoscolus</u>	12.30 $\pm$ 1.27 (28)	72.1 $\pm$ 33.9 (18)
<u>Ipomoea quamoclit</u>	24.93 $\pm$ 0.76 (15)	60.4 $\pm$ 28.6 (15)

low-reward species such as Richardia, Verbena and Bidens. Occasional visits by Phoebis to these flowers were seen, but they were apparently for sampling as no prolonged foraging was seen at these species. Conversely, Agraulis does not feed at the Ipomoea species or at Agalinis, due to morphological exclusion. These flowers are energetically quite rewarding but have corolla tubes so long as to prevent Agraulis from reaching the nectar (see Tables 3-1 and 3-4). When all nectar sources are considered, the range in energy contents of flowers is quite remarkable, and spans several orders of magnitude. The largest part of this variation is due to differences in nectar volume, which ranges between 0.0076 and 1.85 μ l/flower. Nectar concentration shows much less variation, ranging between 17.1 and 40.4% sucrose.

Both species visit flowers that occur at a wide range of densities. In addition, the morphology of visited flowers is variable and includes dish-shaped flowers with no corolla tube (Sida), composites (Bidens, Vernonia), and flowers with long tubular corollas (Ipomoea spp., Agalinis). Table 3-4 presents the floral densities and corolla lengths for each of the nectar sources. The effect of corolla length on nectar rewards has already been mentioned. Low reward flowers such as Bidens and Verbena generally occur in higher densities than the other species, somewhat offsetting the energetic consequences of their low nectar volumes.

The two butterfly species differ significantly in their patterns of exploitation of these floral resources. These differences are most apparent at nectar sources used by both species. Table 3-5 gives percent of time in flight while foraging and foraging rates for both

TABLE 3-5 -- FLIGHT TIME AND FORAGING RATE OF AGRAULIS AND PHOEBIS.
[mean $\pm$ 1 standard deviation (n)].

Nectar species	% of time in flight		Foraging rate (flrs/s)	
	<u>Agraulis</u>	<u>Phoebis</u>	<u>Agraulis</u>	<u>Phoebis</u>
<u>Vernonia</u>	26.8 $\pm$ 18.0(21)	19.5 $\pm$ 11.0(17)	0.541 $\pm$ 0.137(18)	0.475 $\pm$ 0.176(10)
<u>Verbena</u>	20.8 $\pm$ 8.4 (65)	-----	0.493 $\pm$ 0.134(65)	-----
<u>Sida</u>	35.8 $\pm$ 8.8 (25)	23.4 $\pm$ 10.6(19)	0.191 $\pm$ 0.057(29)	0.155 $\pm$ 0.049(22)
<u>Cnidoscolus</u>	21.0 $\pm$ 7.1 (18)	-----	0.339 $\pm$ 0.076(24)	-----
<u>Hyptis</u>	30.9 $\pm$ 10.5(20)	18.1 $\pm$ 7.6(22)	0.318 $\pm$ 0.109(20)	0.321 $\pm$ 0.061(22)
<u>Bidens</u>	15.3 $\pm$ 7.1 (20)	-----	0.680 $\pm$ 0.137(20)	-----
<u>Richardia</u>	22.7 $\pm$ 7.5 (17)	-----	0.618 $\pm$ 0.109(17)	-----
<u>Agalinis</u>	-----	26.3 $\pm$ 9.2 (23)	-----	0.184 $\pm$ 0.036(23)
<u>I. trichocarpa</u>	-----	34.9 $\pm$ 10.4(24)	-----	0.156 $\pm$ 0.029(24)
<u>I. quamoclit</u>	-----	27.6 $\pm$ 6.7 (20)	-----	0.162 $\pm$ 0.052(26)

species at each of the nectar sources. These data were not collected for Ipomoea coccinea. Because its floral morphology and density are quite similar to those of I. quamoclit, density, percent flight, and foraging rate used in calculating the foraging profit for I. coccinea were those measured for I. quamoclit. Phoebis generally spends less time in flight than does Agraulis. The differences in percent flight are significant for two of the three shared nectar sources (Sida: $U = 378$; $p < .0002$; Hyptis: $U = 369.5$; $p < .0002$; Vernonia: $U = 217$, $p = .26$). Phoebis also forages at a slower rate than does Agraulis, but these differences are only significant at one of the three shared nectar sources (Sida: $U = 449$, $p < .05$). This is not due to the time required to extract the nectar since Phoebis has a higher uptake rate than Agraulis (Chapter II). It may reflect a cost of having a longer proboscis, which may not be as efficient at probing short corolla flowers as a short proboscis. This may increase handling time, as has been shown for some bumblebees by Inouye (1980). For both species, less time is spent in flight at the nectar sources with higher densities. Foraging rate is also greatest at these densely packed flowers.

Because of the selection of high-reward flowers by Phoebis and because of this species' more efficient foraging behavior, it generally realizes greater foraging profits does Agraulis. Table 3-6 shows the estimated foraging profits at each of the nectar sources. Some caution need be applied in interpreting these estimates. First, the metabolic costs on which they were based are rough estimates at best. Metabolic costs of flight as measured in butterflies in a metabolic chamber may differ significantly from the the costs of

TABLE 3-6 -- FORAGING PROFITABILITY OF AGRAULIS AND PHOEBIS AT DIFFERENT NECTAR SOURCES. [mean $\pm$ 1 standard deviation (n)].

Nectar source	<u>Agraulis</u> Profit (joules/s)	<u>Phoebis</u> Profit (joules/s)
<u>Richardia</u>	-0.005 $\pm$ 0.011(5)	-----
<u>Verbena</u>	0.016 $\pm$ 0.015(7)	-----
<u>Bidens</u>	0.053 $\pm$ 0.026(3)	-----
<u>Agalinis</u>	-----	0.006 $\pm$ 0.014(4)
<u>Vernonia</u>	0.069 $\pm$ 0.086(6)	0.053 $\pm$ 0.069(6)
<u>Hyptis</u>	0.060 $\pm$ 0.025(6)	0.066 $\pm$ 0.025(6)
<u>Sida</u>	0.087 $\pm$ 0.045(4)	0.071 $\pm$ 0.037(4)
<u>I. trichocarpa</u>	-----	0.207 $\pm$ 0.178(3)
<u>Cnidoscolus</u>	0.587 $\pm$ 0.382(5)	-----
<u>I. coccinea</u>	-----	1.455 $\pm$ 0.287(3)
<u>I. quamoclit</u>	-----	1.675 $\pm$ 1.183(5)

flight in unhampered butterflies in the wild. Second, the energy benefits are based on mean nectar rewards available and not on rewards of individual flowers. Thus meaningful patterns of variation among individual flowers will be obscured. Nonetheless, these estimates should be useful for comparative purposes, because the magnitude of error in estimation should be similar among nectar sources. According to these estimates, Agraulis may occasionally forage at or near an energy deficit (Richardia), but Phoebis never does. There is a wide range of foraging profitability at different nectar sources. Particularly note the difference between Sida and Verbena; Agraulis is commonly observed going from one species to the other during a foraging bout, even though there is nearly a ten-fold difference in energy reward. Two of the Ipomoea species (coccinea and quamoclit) are by far the most rewarding of the flowers visited by either species, and are available to Phoebis for about six weeks during the fall migratory period (Walker 1978).

Using the nectar availability data, the behavioral data, floral characteristics, and energetic profit estimates, I asked the question: Which cues available to the butterflies are most likely to be related to energetic profitability of foraging? Table 3-7 is a correlation matrix of several of the variables presented above. Notice first that energetic reward per flower is most strongly correlated with nectar volume, and both variables are highly significantly correlated with foraging profits of both species. Concentration, on the other hand, shows no meaningful correlation with any of the other variables. Flower density is correlated strongly only with foraging rate, and then much more so in Phoebis than in Agraulis. Combined with the fact

TABLE 3-7 -- CORRELATION MATRIX OF FORAGING ENERGETICS DATA

* indicates correlation significant at .05 level

** indicates correlation significant at .01 level

	Volume	Conc	Density	Corolla	Energy/flower
Energy/flower	0.9949**	0.1052	-0.3698*	0.6216**	-----
<u>Phoebis</u> rate	-0.4343*	0.0989	0.9504**	-0.5279**	-0.4407*
<u>Agraulis</u> rate	-0.4305*	0.3156	0.5214**	0.1945	-0.4271*
<u>Phoebis</u> flight	0.3743	-0.0726	-0.9155**	0.6948**	0.3879
<u>Agraulis</u> flight	-0.0376	-0.4107*	-0.4955*	-0.3065	-0.0340
<u>Phoebis</u> profit	0.9972**	0.2057	-0.3768	0.5756**	-0.9942**
<u>Agraulis</u> profit	0.9745**	-0.1771	-0.3836	0.5080*	0.9844**

that Agraulis generally flies more while foraging, this may indicate that Agraulis is less efficient in its between flower movements than Phoebis. This interpretation is supported by the negative correlations between density and the amount of time spent in flight, which again are more strongly correlated in Phoebis than in Agraulis. Corolla length is correlated well with energy reward and foraging profitability, again more strongly in Phoebis. A longer corolla flower is generally a more rewarding flower, presumably due to its inaccessibility to most foragers, which allows accumulation of greater nectar rewards. Corolla length is negatively correlated with foraging rate in Phoebis but not in Agraulis. This is due to the long-corolla Ipomoea spp., which have high nectar volumes and occur in low densities. This causes the butterflies to spend more time at individual flowers and more time flying between flowers, and thus produces low foraging rates. The lack of a similar correlation in Agraulis is probably because Agraulis visits no long corolla flowers with nectar volumes comparable to those of Ipomoea. The correlation between percent flight time and corolla length in Phoebis is also due mainly to the influence of the Ipomoea spp., which are borne singly and in low density, thus requiring more between extensive flower flights.

As mentioned above, nectar concentration is not clearly correlated with any aspect of foraging success. The Kingsolver and Daniel (1979) model, however, (as modified in Chapter II) predicts a maximum energy intake rate at nectars of 35-40% sucrose concentration. As the maximum nectar concentration in the flowers visited by these two butterflies is just over 40%, we should see a correlation

between nectar concentration and foraging profit or energy intake if nectar concentration is of overriding importance in determining energy intake rate. As seen in Table 3-7 however, none of the correlations between concentration and energy/flower or foraging profit of either species is significant. The variation in other determinants of foraging profit, particularly nectar volume, are more closely related to differences in foraging profit.

The foraging selectivity of the two butterflies at mixed floral arrays differs significantly. In a mixed floral array containing mainly Hyptis and Verbena, Phoebis restricts its visits to the more rewarding species (Hyptis) to a greater degree than does Agraulis (Table 3-8). The two flower species are quite similar in color, size and general appearance, yet Phoebis is still able to discriminate between them. The small number of visits by Phoebis to Verbena flowers may be attributed to either sampling or misidentification by the butterflies, as generally only 1 or 2 flowers of Verbena were visited before the insects returned to Hyptis. Within a foraging bout, Agraulis frequently switches flowers, whereas Phoebis does so much less often. The average foraging bout of Agraulis is about twice as long as that of Phoebis in this floral array. Table 3-9 presents similar data for a mixed patch of Bidens, Ipomoea trichocarpa, Hyptis and Verbena. This patch was observed about one week after the Hyptis-Verbena patch was observed. During this time span, Ipomoea trichocarpa had begun to bloom, and Phoebis completely ceased visiting any other flowers. Notice that Agraulis concentrated its visits on Bidens, the most common flower in the patch. The number of Bidens

TABLE 3-8 -- FORAGING SELECTIVITY AT MIXED FLORAL ARRAY 1 (SEE TEXT).
 [mean $\pm$ 1 standard deviation (number of bouts observed)]. Comparisons
 between species were with Mann-Whitney U test.

	<u>Agraulis</u> (38)	<u>Phoebis</u> (15)	U	p
# <u>Hyptis</u> visited	8.9 $\pm$ 8.3	8.5 $\pm$ 8.1	293.5	0.87
# <u>Verbena</u> visited	13.6 $\pm$ 11.5	1.7 $\pm$ 2.2	478	<.0005
Switches/bout	2.5 $\pm$ 2.6	0.7 $\pm$ 1.2	412	<.010
% <u>Hyptis</u> visited	44.6 $\pm$ 34.2	77.2 $\pm$ 35.3	135.5	<.005
Total flowers/bout	22.7 $\pm$ 13.9	10.3 $\pm$ 8.0	447.5	<.005

TABLE 3-9 -- FORAGING SELECTIVITY AT FLORAL ARRAY 2 (SEE TEXT). [mean $\pm$ 1 standard deviation (number of bouts observed)]. Comparisons between species were with Mann-Whitney U test.

	<u>Agraulis</u> (37)	<u>Phoebis</u> (36)	U	p
# <u>Bidens</u> visited	7.6 $\pm$ 6.9	0.0	1170	<0.0001
# <u>Ipomoea</u> visited	0.0	15.2 $\pm$ 10.7	0	<0.0001
# <u>Hyptis</u> visited	4.1 $\pm$ 8.7	0.0	864	<0.0005
# <u>Verbena</u> visited	0.6 $\pm$ 1.9	0.0	756	0.023
Switches/bout	0.4 $\pm$ 0.9	0.0	792	0.006
% visits to <u>Bidens</u>	70.8 $\pm$ 44.3	0.0	1170	<0.0001
% visits to <u>Ipomoea</u>	0.0	100.0 $\pm$ 0.0	0.0	<0.0001
Total flowers visited	12.4 $\pm$ 8.1	15.2 $\pm$ 10.7	581.5	0.351

visited per bout refers to the number of flower heads visited; as each head may contain 10-40 individual flowers, the actual number of flowers visited per bout is much greater. Thus, even though there was no significant difference in the total number of flowers visited per bout, this is probably misleading as it does not take individual Bidens florets into account. As before, Agraulis switches between flower species within a foraging bout more often than Phoebis, which was completely constant in its flower preference.

Agraulis maintains a body temperature that is $5-7^{\circ}\text{C}$ above ambient temperature (Figure 3-1). This is accomplished primarily by dorsal basking (Clench 1966), both while foraging and when perched. Because the body temperature rises, metabolic expenditure increases through the morning as ambient temperature increases. In addition, nectar availability and energy content per flower generally decrease throughout the day, particularly in the afternoon. If Agraulis is selected to maximize energy intake while foraging, we might expect foraging activity to be restricted to the morning when energetic costs are lowest and nectar rewards are high. Figure 3-2 shows that this is not the case. Although the proportion of individual butterflies observed that are nectaring does decrease from a maximum after 1100 to 1200 hr, a significant amount of nectaring occurs throughout the mid-afternoon. As shown in Table 3-10, the individuals foraging in the afternoon are generally older individuals. (These data were compiled from first capture records of the mark-recapture study. Young individuals were defined as those belonging to age classes 1 and 2, and age classes 3 and 4 were considered older.) Figure 3-2 also shows that there is no distinct partitioning of behaviors to different

Figure 3-1 -- Thoracic and abdominal temperatures of *Agraulis vanillae* as a function of ambient temperature (T_{am}). See p. 62 for details of measurements. Regression equation for abdominal temperature (T_{ab}): $T_{ab} = 0.857 T_{am} + 8.458$ ($r = 0.907$). Regression equation for thoracic temperature (T_t): $T_{th} = 1.018 T_{am} + 5.988$ ($r = 0.890$).

Figure 3-2 - Behaviors exhibited by active *Agraulis vanillae* as a function of time of day. See text for descriptions of behaviors. Figures above bars are numbers of individuals observed during that 1 hour period.

TABLE 3-10 -- AGE OF NECTARING INDIVIDUALS VS. TIME OF DAY. Data analyzed using 2 x 2 contingency χ^2 .

	Time of day	
	0900 -1100	1100 - 1400
Young	61	37
Old	22	27

$$\chi^2 = 3.999$$

$$p = 0.0455$$

times of day. Courtship, mate search and oviposition search occur throughout the morning concurrently with nectaring. None of these activities occurs until the thoracic temperatures of the butterflies reaches approximately 30° C however. Thus, basking is the only behavior observed until about 0900, and the amount of basking behavior then declines throughout the morning. Agraulis divides its time during the morning between nectaring and reproductive behaviors, and it is not unusual to see a female momentarily cease oviposition search to nectar or a male quit nectaring to chase a female. Butterfly activity reaches a peak between about 1100 and 1200 hr, after which time the number of butterflies seen per unit time decreases throughout the afternoon. The frequency of rapid searching flight increases in the afternoon, although the function of this behavior is unknown. It is seen mainly in males. Females apparently retire to the vegetation in the afternoon as relatively few are seen after 1300.

Agraulis vanillae is a fairly sedentary butterfly, and individuals appear to have quite restricted home ranges. Table 3-11 presents average movement distances between capture and recapture of Agraulis, separated by age and sex. There are no significant differences among these categories. These data represent 62 individuals that were recaptured or resighted out of a total of 247 marked (25.1%). Notice that the average amount of movement between captures averaged between 18 and 54 m. These represent inter-capture periods of up to 16 days. Thus this species is apparently quite sedentary, and individuals seem to remain within a restricted area for extended periods. This has two implications to foraging behavior. First, the variety of nectar resources to which they are exposed and

TABLE 3-11 -- AVERAGE DISTANCE MOVED (m) BETWEEN CAPTURES FOR AGRAULIS
[mean $\pm$ 1 standard deviation (n)].

Age	Distance moved (m)	
	Males	Females
1	25.6 $\pm$ 24.9 (32)	54.0 $\pm$ 37.8 (5)
2	34.4 $\pm$ 55.5 (18)	29.7 $\pm$ 21.9 (34)
3	29.3 $\pm$ 31.3 (44)	35.8 $\pm$ 43.6 (12)
4	18.5 $\pm$ 16.9 (39)	25.0 $\pm$ 17.3 (4)

can select among may be quite small relative to a more mobile species. In addition, travel costs must be quite low as very little prolonged flight is required. Total energetic costs may therefore be low relative to a more mobile species.

Discussion

Agraulis vanillae and Phoebis sennae differ significantly in their selection of nectar source plants, both on a seasonal basis and when foraging at the same resource arrays. The effect of these differences is to provide Phoebis with a greater rate of energy intake when considering foraging within a single array of flowers and a greater mean energy reward per flower visited overall. This difference is due primarily to differences in the nectar volumes of flowers visited by the two species and not to sugar concentration differences between the nectars. Nectar volumes, and thus energy contents, of flowers visited by Phoebis are greater than those encountered by Agraulis for two reasons. First, Phoebis avoids low nectar volume flowers such as Bidens pilosa, Richardia scabra and Verbena brasiliensis, which are avidly visited by Agraulis. Second, Phoebis visits several flower species (Ipomoea spp.) with extremely large nectar volumes (relative to other butterfly-visited flowers) that are inaccessible to most other butterflies due to their long corolla tubes. These flowers accumulate greater nectar rewards because insect visitation is restricted to those insects with sufficiently long mouthparts to reach the nectar (Faegri and van der Pijl 1979). There may also be differences in nectar secretion rates, but these were not measured here.

Phoebis sennae selects flowers with greater mean energy rewards, and it is also more energy efficient in its foraging behavior at the three flower species that are visited by both butterflies. Phoebis spends less time in flight at these nectar sources, thus reducing energetic expenditures. Between flower flights are more direct than those of Agraulis. However, the foraging rate is either the same (Hyptis, Vernonia) or slower (Sida) at these shared resources. This may result from increased handling time per flower because of the longer proboscis. However, Inouye (1980) found that, in bumblebees, long-tongued species generally had shorter handling times than short-tongued species at the same flowers. Decreased flight costs (increases foraging profit) and slower foraging rates (decreases foraging profit) offset each other such that the rate of energy intake while foraging at these nectar sources does not differ greatly between the two species.

The rewards offered by the nectar sources of both these species vary greatly, both within a species of flower and among flower species. Nectar volumes range from thousandths of a microliter (many flowers are in fact empty) to several microliters per flower. Nectar concentration shows less variation, although it is still significant. The effect of both of these factors is to produce a remarkable amount of variability in energy availability per flower. The major component of variance in energy content, however, is variation in nectar volume.

If either of these species is selected to maximize the rate of energy intake while foraging, either to maximize the energy available to the animal or to minimize the amount of time spent foraging, as suggested by optimal foraging models (Schoener 1971; Pyke et al.

1977), what cues might be used by these species as predictors of foraging profit? Kingsolver and Daniel (1979) and Heyneman (1983) have predicted that certain nectar concentrations should maximize the rate of energy intake while the butterfly is imbibing nectar. These models as modified in Chapter II predict that nectars of 35-40% sugar concentration will provide the maximal rate of energy intake and should be preferred by the insects. However, these models consider only the rate of energy intake while the insect is actually imbibing nectar. In fact, a very small proportion of total foraging time of butterflies is spent actually extracting the nectar; most of their time is spent flying between flowers and finding the nectar within a given flower. Even in flowers with only thousandths of a microliter of nectar, which requires a small fraction of a second to extract, visit duration at a single flower can be several seconds. The amount of time spent in flight between flowers depends on the floral density and the handling time of a flower is dependent on flower morphology. When these factors are taken into account, the importance of the nectar concentration in determining energy intake is insignificant, as indicated by the lack of correlation between nectar concentration and foraging profit estimates. Therefore I suggest that the single-factor approach to modeling foraging energetics used by Kingsolver and Daniel (1979,1983) and Heyneman (1983) is of little value for these insects. Much meaningful variation in the profitability of foraging caused by a variety of factors other than nectar concentration is ignored by this approach. Viewed in this light, I would not expect these insects to base foraging decisions on nectar concentration.

The density of flowers may affect foraging profit in several ways. High density floral arrays reduce inter-flower flight distances and thus decrease foraging costs. This effect is more evident in Phoebis, again apparently due to their more direct flight between flowers. High density flowers are thus associated with lower foraging costs (lower foraging costs) as well as greater visitation rates, both of which will increase the profitability of foraging. However, high floral density is also correlated with relatively small nectar rewards, thus decreasing profitability. Again the different factors offset each other, so that there is no consistent relationship between floral density and foraging profit. Therefore I would not expect foraging decisions to be made on the basis of density either.

Length of the corolla tube is positively correlated with foraging profit. This is because flowers with long corollas restrict access to nectarivores and thus tend to accumulate larger amounts of nectar. On the other hand, for the flowers visited by Phoebis, increasing corolla length is associated with decreased foraging rates, most likely due to increased handling times (the long corolla takes longer to probe) as well as increased extraction times (high nectar volumes increases time spent actually removing nectar). Overall, however, corolla length is positively correlated with foraging profitability for both butterfly species.

The best predictor of foraging profitability is simply nectar volume. This variable explains over 99% of the variance in the energy available per flower and is highly correlated with foraging profit in both species. Therefore, if these butterflies forage so as to maximize energy intake, they should select the nectar sources with the

greatest nectar volumes, irrespective of concentration, density or corolla length. This would maximize their water intake while they nectar as well, which Watt et al. (1974) have suggested may be important to some butterflies. The usefulness of nectar volume as a cue influencing foraging decisions may be hampered by the large amount of variance in this quantity, both within and among species. A critical factor in a forager's decision making process is the size of its "memory window" (sensu Cowie 1977) used in evaluating the rewards offered by a given resource. If only a few flowers are sampled and used as a basis for foraging decisions, the result is a high variance in the estimates of nectar availability for a given nectar source among sampling estimates. It is not at all uncommon to encounter several empty flowers or several rewarding flowers in a row for several of the nectar sources used by these species. Patchiness in the dispersion of nectar resources may be common in other types of flowers as well (Zimmerman 1981). The result of using only a few flowers for estimating nectar availability might thus result in frequent switching among nectar sources, as is seen in Agraulis vanillae. Using a greater number of flowers to estimate nectar availability would improve the accuracy of the estimate, but would also entail greater costs of sampling, as it would take the insect longer to decide not to forage at an unrewarding species. Such a sampling pattern may be more feasible in butterflies than in other nectarivores, however, as butterflies possess significant lipid reserves that would carry them through periods of energy-deficit foraging while sampling.

Do either of the species considered here select nectar resources on the basis of volume? It seems likely that they do. Agraulis does not visit some available nectar sources, such as Heterotheca subaxillaris, that have exceedingly minute nectar volumes. Furthermore, it only visits Richardia scabra when this flower is growing by itself. This low-reward flower is avoided when in the presence of flowers with higher nectar volumes such as Verbena brasiliensis and Hyptis mutabilis. As previously discussed, Phoebis sennae exhibits even greater selectivity, again seemingly due to differences in nectar volume. It completely avoids several low-volume flower species such as Richardia, Bidens pilosa, and Verbena. It is also more constant than Agraulis when visiting a mixture of flowers differing in nectar rewards. When foraging at a mixed patch of Hyptis and Verbena, Phoebis for the most part avoids the less-rewarding Verbena flowers, even though they are quite similar to Hyptis in shape, color and size. This discrimination, not seen in Agraulis, may be based on differences in inflorescence type between the two nectar species (spike vs. panicle).

Both butterfly species exhibit some evidence of selectivity, which seems to be based on nectar volumes and thus energy contents. Why then do they differ in the degree of their selectivity? One major difference is that foraging by Agraulis occurs mainly in the vicinity of the larval food plant Passiflora incarnata. Phoebis however is apparently much more mobile between patches of its Cassia food plants. Murphy (1983) has shown a relationship between Euphydryas oviposition sites and proximity of nectar sources. In Phoebis and Agraulis, the differences in vagility may be related to the persistence of their

food plants. Passiflora is a long-lived perennial that is available at any one site throughout the butterflies' flight season. The Cassia species fed on by Phoebis are annuals that senesce in some areas before the flight season ends, perhaps favoring greater inter-patch mobility. Thus Agraulis populations appear to be quite sedentary, comparable to other nymphalid butterflies such as Euphydryas editha (Ehrlich et al. 1975; Gilbert and Singer 1973). Phoebis sennae, on the other hand, seems to be more mobile, like some other pierids such as various Colias spp. (Tabashnik 1980; Watt et al. 1977) and may exhibit the "egg-spreading" syndrome described by Root and Kareiva (1984) for Pieris rapae, where the females are highly mobile and lay eggs on widely spaced host plants, possibly to minimize risks of individual plant-related larval mortality. The effects of these divergent mobility patterns to the foraging strategies of Phoebis and Agraulis are potentially manifold. First, the less mobile species is exposed to a lower diversity of resources and therefore has less opportunity to exercise selectivity. Second, as inter-patch flight is less common, energetic expenditures may be lower in the more sedentary species, reducing the selective pressure for energy maximization in foraging. Third, since the more mobile Phoebis are often not in the presence of larval host plants, there may be temporal separation of nectaring and reproductive behaviors. Minimizing the amount of time spent foraging might thus increase reproductive success by freeing more time for mate search, courtship, oviposition site search, etc.

In Agraulis, there is no distinct temporal separation of nectaring and reproductive behaviors. Both types of behavior are alternated throughout the activity period, as larval food plants and

nectar sources are interspersed. Mate search by males may be nearly as effective during nectaring as when they are searching in a more active manner. There may thus be little selection pressure to minimize foraging time. In addition, Agraulis must bask to maintain high body temperatures required for activity. Thermoregulation in flight is not known to occur in any butterfly species (Heinrich 1981), so Agraulis may have to perch frequently to thermoregulate. Nectaring may thus serve multiple functions, including feeding and basking. Feeding is not restricted to the morning hours when it is most profitable (because of lower body temperatures and greater nectar rewards). However, butterflies foraging in the afternoon are more likely to be older individuals that may be more energy stressed due to depleted fat stores.

These species differ in the way they allocate time to foraging versus reproductive behaviors and this may also explain the observed differences in selectivity. Lucas (1983) considered the effect on foraging selectivity of limiting the amount of time available for foraging by an animal. He argues that the "cost" of being non-selective in prey choice is the probability that a forager will miss the opportunity to capture a high-quality food item while the animal is handling or consuming a low-quality item. As the amount of time available for foraging decreases, the probability of encountering a high-quality food item decreases, so the forager should become less selective. Stated in another way, animals with short foraging bouts should be more generalized in their food selection than animals with long foraging bouts. I have presented evidence here suggesting that Agraulis forages in very short bouts, alternating these foraging bouts

with reproductive activities or intraspecific interactions. Phoebis, on the other hand, often forages farther from larval food plants and appears to segregate their foraging and reproductive activities into longer, mutually exclusive periods. Lucas' (1983) model would therefore predict that Phoebis should be more selective than Agraulis, even when foraging in the same flower patches. This is exactly what I observed.

To conclude, then, several diverse factors may interact to affect foraging decisions and selectivity in these two butterfly species. The overall effect of all of these factors produces different patterns of selectivity between these two nectarivores. Morphology of the feeding apparatus influences selectivity by determining which resources are available to a given species. The life history characteristics of a species, such as vagility, food-plant distributions and temporal properties, and allocation of time to various activities, may also influence foraging decisions by affecting the types of resources encountered and the energetic expenditures of the animal. Another factor that may have important consequences to foraging behavior, to be considered in the next section, is the amount of stored energy available to the butterfly and differences in this quantity among species.

Summary

I estimated energy budgets of foraging Agraulis vanillae and Phoebis sennae at their major nectar sources using time-budget data combined with metabolic data from the literature, energetic rewards offered by the various nectar sources, and the rate at which the butterflies exploit these flowers. Using estimated foraging profits,

I sought proximate cues that might be used by energy-maximizing butterflies as a basis for flower selection. Recent theoretical models, as revised in Chapter II, suggested that butterflies should selectively feed on flowers producing nectars with sugar concentrations between 35 and 40%. My data suggest no relationship between nectar concentration and foraging profit. Similarly, floral density is not correlated with foraging profit either. Corolla length and nectar volume are positively correlated with energetic reward and foraging profitability and should be used by the butterflies as a basis for flower selection. Differences in nectar volume alone account for more than 95% of the variance in foraging profitability, and might be used as the sole basis on which flowers are accepted or rejected for inclusion in the diet.

Agraulis and Phoebis showed significant differences in flower selectivity. Phoebis is consistently more selective than Agraulis with regard to energy content of flowers. This results in greater rates of energy intake while Phoebis is foraging than those experienced by Agraulis. This is partly due to morphological differences; Phoebis has a longer proboscis and can feed at highly rewarding flowers with long corollas from which Agraulis is excluded. But Phoebis also avoids several low-reward flower species visited by Agraulis. Agraulis individuals often fail to discriminate between low- and high-reward flowers and frequently switch between them within a foraging bout. These differences in selectivity are probably linked to differences between the butterflies in population structure and time-allocation patterns. Agraulis is a more sedentary species and does not forage far from its larval food plant. Energetic costs of

travel are therefore reduced, and foraging bouts tend to be short since they are frequently interrupted by intraspecific interactions or reproductive behaviors (courtship, chasing behaviors, oviposition search, etc.). Phoebis individuals appear to spend longer periods of time devoted solely to foraging or reproductive behaviors. Recent models have predicted that a species that forages in short bouts should be more generalized in food selection than a species which forages in long bouts, as observed here.

CHAPTER IV
LIPID STORAGE AND DEPLETION IN AGRAULIS VANILLAE AND
PHOEBIS SENNAE : EFFECTS OF ADULT FORAGING

Introduction

The feeding ecology of holometabolous insects may be quite complex, since feeding may occur during both larval and adult stages; the types of food taken during the different stages may be quite dissimilar. Nevertheless, Boggs (1981) has stressed the interdependence of larval and adult feeding and the importance of each to realizing the maximal potential reproductive fitness. She argues that the total expected reproductive output is determined by energy and nutrients acquired through both larval and adult feeding as well as and the proportion of adult energy or nutrient intake allocated to reproduction. Therefore, other factors being equal, a reduction in adult nutrient or energy intake should be accompanied by an increase in the proportion of larval nutrients or energy stores earmarked for reproduction. Boggs' argument was focused at the species level; thus two species that differ in expected adult nutrient intake should show corresponding differences in the allocation of larval nutrients at metamorphosis.

Boggs tested and validated this hypothesis using three species of heliconiine butterflies (Boggs 1981) that differ in the amount of adult feeding. Boggs' predictions and tests were focused on nitrogen budgets and the allocation of nitrogen at metamorphosis to

reproductive reserves. Nitrogen is acquired by feeding adults through pollen feeding, and the extent of pollen feeding varied among the three species, with one species (Dryas julia) not feeding on pollen at all. In accord with the predictions, she found that the proportion of total body nitrogen allocated to reproduction varied inversely with the extent of pollen feeding as an adult. Further, she found that the rate at which these reproductive nitrogen stores declined depended on both the rate of adult nutrient intake as well as the rate of reproductive output of these nutrients.

Boggs remarked that few other data were available concerning the inter-relationship between larval and adult feeding, but that the model should be applicable to other nutrients and dietary components as well. Heliconius butterflies are apparently unique among the Rhopalocera in their demand for nitrogen in the adult diet, as no other butterflies are known to feed on pollen (Gilbert 1972). However, many butterflies feed on floral nectar as adults, and energy intake acquired through this feeding is known to increase fecundity and survival in many lepidopteran species (Stern and Smith 1960; Murphy et al. 1983). In addition, energy reserves are provided for adults through larval storage of lipids, which serve as a major fuel source for adult activities (Stokes and Morgan 1981). We might therefore extend Boggs' (1981) hypothesis and predict that the amount of larval resources allocated at metamorphosis to lipid reserves will vary inversely with the expected adult energy intake, and further, that the rate of change in these lipid reserves will depend on the amount of adult feeding as well as the amount of energy expended on other activities.

Although lepidopterans were thought to use only lipid as an adult energy source (Zebe 1954; Brown and Chippendale 1974), this may only be true in those species that do not feed as adults (Stokes and Morgan 1981). Most lepidopterans apparently can use carbohydrates as a fuel source for initial stages of flight activity, but then switch to lipid oxidation for prolonged flight activity (van Handel and Nayar 1972; Stokes and Morgan 1981). However, lipids are the primary means of storing energy (Brown and Chippendale 1974; Cenedella 1971; Domroese and Gilbert 1964). The amount of stored lipid is known to vary markedly during different phases of adult life. Chaplin and Wells (1982) found that overwintering monarch butterflies (Danaus plexippus) deplete their fat stores over the course of the winter. Walford (1980) and Brower (in press) present data suggesting that migrating monarchs begin building large lipid reserves by extensive nectaring as they reach the southern U.S. The extent of these lipid reserves may determine both the probability of surviving the winter as well as the distance to which they can re-migrate in the spring (Tuskes and Brower 1978).

Adequate lipid reserves of adult butterflies thus appear to be necessary for achieving maximum survival and therefore fitness and are mediated by both larval storage and adult feeding. In Chapter III, I presented data showing that Phoebis sennae forages more profitably in terms of rate of energy intake than does Agraulis vanillae. Assuming that these two species spend similar proportions of adult activity time feeding, Phoebis sennae should have a greater expected adult energy intake than does Agraulis. In fact, unquantified observations suggest that Phoebis may spend a greater proportion of activity time

feeding, as I have observed them feeding during mid- to late-afternoon, when most Agraulis are inactive. In this chapter, I consider data testing the prediction that expected adult energy intake is inversely related to the amount of lipid stored during metamorphosis from resources acquired through larval feeding. In addition, I examine changes in lipid stores and body composition over the adult life span to determine whether differences in adult energy intake correspond to differing patterns of storage or depletion of lipid reserves. Does Phoebis sennae, which has a greater energy intake as an adult, store more lipid through adult foraging or deplete its emergence lipid stores at a slower rate than does Agraulis?

Methods and Materials

I collected late instar larvae, pupae and adults of Agraulis vanillae and Phoebis sennae at various sites on Payne's Prairie State Preserve, Micanopy, Fla. I brought larvae back to the laboratory and reared them to adults. Adults collected in the field were individually placed in glassine envelopes and frozen within four hours of capture. Care was taken during capture to handle the adults by the forewings only, so as not to augment scale loss from the hindwings. Field-collected adults were assigned relative ages by counting the number of scales missing along 1 cm transects in each of five cells of the ventral hindwing (Rs, M₁, M₂, M₃ and Cu). Each transect was made parallel to the anterior vein bordering the cell. Scale loss has been shown to be a reasonable estimator of adult age in other butterfly species (Ehrlich and Gilbert 1973; Watt et al. 1977).

I reared larvae of both species to pupae in the laboratory, where temperature was approximately 24°C and photoperiod was uncontrolled.

Freshly emerged adults were frozen within 12 hours of emergence, after they expelled their meconial wastes.

I measured forewing lengths of the butterflies prior to lipid analysis. Each individual was analyzed for lipid content, after drying to constant weight in a drying oven, using the petroleum ether extraction technique of Walford (1980) and Brower (in press). This technique extracts only neutral lipids and is more suitable for assaying energy reserves than other lipid extractions, as membrane-bound phospholipids are not available as an energy source. I calculated percent lipid for each individual by dividing lipid weight by initial dry weight and multiplying by 100.

I compared body composition characteristics (dry weight, lipid weight, lean weight, percent lipid) of freshly-emerged and field-collected butterflies using analyses of variance programs in the BMDP statistical software package (Dixon et al. 1981). In addition, dry weight, lipid weight, lean weight, and percent lipid of field collected individuals were compared after grouping them into age classes based on the relative amount of scale loss. All analyses of variance were two-way ANOVAs permitting determination of age-related as well as sexual differences in body composition.

Results

Agraulis vanillae shows significant sexual differences in all body composition characteristics, with females being larger and containing more lipids than males (Table 4-1). Females emerge from the pupae weighing approximately 0.117g (dry weight), whereas males emerge at only 0.08g. Of this dry weight, females contain 0.019g of lipids while males contain only 0.011g, or 15.9 and 12.8% of dry

Table 4-1 - Body composition of field-collected and freshly-emerged adults of Agraulis vanillae. [means $\pm$ 1 standard deviation (n)]. F values and probabilities refer to two-way analyses of variance with sex and relative age as grouping variables.

	AGE				F(sex) p	F(age) p
	FRESHLY-EMERGED		FIELD-COLLECTED			
	MALES (10)	FEMALES (11)	MALES (35)	FEMALES (35)		
Forewing length (mm)	-----	-----	39.4±1.5	41.3±1.7	14.5 <0.0001	-----
Wet weight (g)	0.204±0.035	0.303±.051	0.0171±0.033	0.0211±.060	34.8 <0.0001	28.3 <0.0001
Dry weight (g)	0.083±.012	0.117±.011	0.072±.012	0.088±.041	13.9 <0.005	9.0 <0.0005
Fat weight (g)	0.011±.004	0.019±.004	0.005±.003	0.007±.006	21.1 <0.0001	62.8 <0.0001
Lean weight (g)	0.072±.008	0.098±.007	0.066±.010	0.081±.038	10.9 <0.06	2.7 <0.005
% lipid	12.8±3.4	15.9±2.4	7.0±2.4	8.0±3.4	6.4 <0.05	70.1 <0.0001

weight, respectively. Dry weight, lean weight, lipid weight and percent lipid of field-collected individuals are all significantly lower than in freshly-emerged butterflies. This suggests that lipids as well as non-lipid body components are being metabolized during adult life.

As predicted, Phoebis sennae adults emerge from the pupae with less stored lipid than do adults of Agraulis (Table 4-2). Phoebis shows no significant differences between the sexes for body composition characteristics. Forewing length in Phoebis is greater in males. The F and p values presented in both tables 4-1 and 4-2 refer to the two-way ANOVAs using sex and age class as the grouping variables. Although in some comparisons, Levene's test for equal variances indicated significant differences in variance among samples, the significance of all differences was confirmed by Brown-Forsythe and Welch analyses of variance, which do not assume equal variances among groups (Dixon et al. 1981). Phoebis sennae adults emerge from the pupae with only about 4% of their dry weight allocated to lipids, compared with 13-16% in Agraulis vanillae. However, the proportion of dry weight contributed by lipids increases in the field-collected samples, indicating that this species accumulates lipid reserves as an adult through nectar feeding.

One possible complicating factor in comparisons of field-collected and lab-reared butterflies is the conditions under which the larvae were reared. Angelo and Slansky (1982) have shown that for several moth species, larvae reared under adverse conditions may produce smaller adults with lower lipid stores. If the laboratory conditions under which the larvae were reared in this study were less

Table 4-2 - Body composition of freshly-emerged and field-collected adults of Phoebis sennae. [mean $\pm$ 1 standard deviation (n)]. F-values and probabilities refer to two-way analyses of variance using sex and age as grouping variables.

	AGE				F(sex) p	F(age) p
	FRESHLY-EMERGED		FIELD-COLLECTED			
	MALES (9)	FEMALES (9)	MALES (21)	FEMALES (20)		
Forewing length (mm)	34.8±2.4	32.1±2.9	37.3±1.6	36.5±2.0	8.3 <0.006	33.3 <0.0001
Wet weight (g)	0.147±.030	0.127±.059	0.245±.053	0.244±.048	0.5 <0.5	59.0 <0.0001
Dry weight (g)	0.072±.011	0.063±.023	0.130±.037	0.133±.034	0.1 <0.8	52.5 <0.0001
Lean weight (g)	0.069±.010	0.060±.022	0.090±.013	0.091±.017	0.7 <0.5	35.2 <0.0001
Fat weight (g)	0.003±.002	0.003±.002	0.041±.025	0.042±.024	0.0 <0.96	42.2 <0.0001
% lipid	4.1±1.3	4.4±2.7	28.0±13.1	28.9±13.9	0.03 <0.9	55.9 <0.0001

suitable than those experienced by the wild larvae, greater lipid contents of field-collected butterflies might be due to this factor rather than lipid storage from adult feeding. Forewing lengths, which are a general indicator of body size, were not measured in the lab-reared Agraulis vanillae, so it is impossible to test for differences in overall body size between lab-reared and field-collected samples. However, for this species, such differences would cause underestimation of lipid contents at emergence. Since lab-reared individuals were shown to have greater lipid contents than the field-collected individuals, such biases would lessen the difference between lipid contents at emergence and later in the adult life.

In Phoebis sennae forewings of lab-reared individuals were significantly smaller than those of the field-collected individuals (Table 4-2). However, the critical comparison between these two groups with regard to Boggs' (1981) hypothesis is the proportion of the soma allocated to lipids, so the percent lipid comparison should not be affected unless percent lipid is correlated with body size. There is no significant correlation between percent lipid and forewing length among the freshly emerged butterflies ($n = 18$, $r = 0.1156$, $p > 0.05$), even though these individuals varied in forewing length between 26 and 37 mm. The highest percent lipid seen in any freshly emerged individual was only 7%. It thus appears that Phoebis responds to poor larval conditions by producing a smaller adult; however, the proportion of body tissue invested as lipid stores apparently is not affected, as predicted by Boggs (1981). The significant differences in body size between lab-reared and

field-collected samples make comparisons of dry weight, lean weight, and absolute lipid weight impossible to interpret in terms of the effects of adult energy intake on these characteristics.

In order to examine changes in body composition over the adult life span, individuals were assigned to one of six age classes based on scale loss. Freshly emerged butterflies were assigned to age class A, and the field collected butterflies were assigned to the following five categories: B - 80-99% of scales remaining; C - 60-79% of scales remaining; D - 40-59% of scales remaining; E - 20-39% of scales remaining; F - 0-19% of scales remaining.

Agraulis vanillae males and females generally decrease in dry weight throughout adult life (Figure 4-1). It is not known if the relationship between age and scale loss is a linear one, so whether the x-axis can be directly interpreted as age is unclear. Males are smaller than females in all age classes. Age class C females show an increase in dry weight, but this is probably an artifact of small sample size ($n = 6$). Two of the individuals in this sample were unusually large, and if these two data were removed the graph would show a consistent decline in dry weight throughout life as in the males. As seen in Figure 4-2, the decrease in dry weight is due in part to a decrease in lean weight, which seems to occur mainly in later age classes. Again the apparent increase in lean weight of class C females is attributable to the two abnormally large females in this sample. Figure 4-3 demonstrates that the proportion of body composed of lipids declines rapidly early in life, and then levels off in older individuals at about 5%.

Figure 4-1 - Dry weight (g) of *Agraulis vanillae* vs. age class. Age class determination is based on degree of scale loss (see text for details). Circles indicate means, bars show one standard error on either side of the mean, and sample sizes are in parentheses.

Figure 4-2 - Lean weight (g) of *Agraulis vanillae* vs. age class. Age class determination based on degree of scale loss (see text for details). Circles indicate means, bars show one standard error on either side of the mean, and sample sizes are in parentheses.

Figure 4-3 - Per cent lipid (of dry weight) of *Agraulis vanillae* vs. age class. Age class determination based on degree of scale loss (see text for details). Circles indicate means, bars show one standard error on either side of the mean, and sample sizes are in parentheses.

In contrast, Phoebis sennae adults increase their dry weight dramatically, mainly by accumulating lipids acquired through adult feeding. Figure 4-4 shows the relationship between dry weight and age class of Phoebis sennae adults. As mentioned above, analyses of variance indicated no significant differences in weight characteristics between sexes, so data from males and females were pooled. Because of the smaller size of laboratory-reared individuals, the weight of class A individuals is suspect. However, all other classes were composed of field-collected butterflies that did not differ in body size among age classes. These data show that Phoebis increases dramatically in weight during most of the adult life, and then apparently declines. Figure 4-5 shows that this increase in dry weight may be due to slight increases in lean weight, but as seen in Figure 4-6 it is mainly due to storage of lipids acquired through adult foraging. The proportion of dry weight contributed by lipid increases through most of adult life. Up to 0.07 g of lipid was found in some field-collected individuals, or 47% of dry weight. This represents a 10-fold increase in the proportion of dry weight contributed by lipids over the freshly-eclosed butterflies.

Discussion

Boggs (1981) states that little evidence is available from other studies to support her model of larval-adult feeding interdependence. The data presented here suggest that her hypothesis may have broad applicability to many aspects of insect nutrition. Although the original model pertained strictly to nutrients allocated to reproductive reserves at metamorphosis, in this study it was impossible to determine how much of the lipid reserves set aside at

Figure 4-4 - Dry weight (g) of *Phoebeis sennae* vs. age class. Age class determination based on degree of scale loss (see text for details). Circles indicate means, bars show one standard error on either side of the mean, and sample sizes are in parentheses.

Figure 4-5 - Lean weight (g) of *Phoebe sennae* vs. age class. Age class determination based on degree of scale loss (see text for details). Circles indicate means, bars show one standard error on either side of the mean, and sample sizes are in parentheses.

Figure 4-6 - Per cent lipid (of dry weight) of *Phoebis sennae* vs. age class. Age class determination based on degree of scale loss (see text for details). Circles indicate means, bars show one standard error one either side of the mean, and sample sizes are in parentheses.

metamorphosis are used directly for reproduction, i.e., egg or spermatophore production. These reserves are used to fuel all adult activities, most of which are at least indirectly related to reproduction, such as mate searching, courtship, oviposition site searching, etc.

The adaptive advantage of using lipids as a fuel reserve, especially for flying insects, has been known for some time. Lipids contain more energy/mass than other fuel sources such as carbohydrates (9 cal/mg compared to 4cal/mg), and can be stored in anhydrous form rather than in a hydrated state as are carbohydrates (Kleiber 1961; Bailey 1975). However, lipids are not as rapidly mobilized as carbohydrates are, and therefore most lepidopterans apparently use carbohydrates first and then fall back on lipid reserves once carbohydrates are depleted (Stokes and Morgan 1981). The main energy-yielding components of stored lipids are apparently triglyceride fatty acids such as oleic and palmitic acids (Cenedella 1971; Brown and Chippendale 1974).

In her original model, Boggs (1981) was able to assume that larval nutrition and survivorship were invariant among species by comparing three closely related species with similar life histories and food plants. The data here suggest that her model may apply in general to all butterflies, since the two species here are from different families (Nymphalidae and Pieridae) and have completely unrelated larval food plants (Passiflora spp: Passifloraceae and Cassia spp.: Fabaceae). If the assumption of similar life histories and larval nutrition can be relaxed, this model may be a powerful tool for understanding inter-relations between feeding during larval and

adult stages. For example, it may be possible to predict the importance and extent of adult feeding in a variety of lepidopteran species simply by examining lipid storage at metamorphosis.

Other factors, however, may confound this simple relationship between lipid storage at metamorphosis and adult foraging. The longevity of the adult may significantly affect the requirement for stored lipids. In the two species considered here, Agraulis may live up to 21 days as an adult; the longevity of Phoebis is unknown but is presumed to be greater, as overwintering adults are in reproductive diapause and must live several months if they are to survive and reproduce the next spring. In addition, patterns of reproductive expenditure vary significantly among lepidopterans. Species that lay eggs in several large masses, such as Euphydryas editha (Murphy et al. 1983), may require greater lipid stores since forming a batch of eggs produces more of an immediate energetic drain than laying eggs singly. Both species studied here lay eggs singly, although the rate of egg production, total lifetime fecundity, and differences in these quantities between the two species are unknown. Another factor that may affect the magnitude of lipid storage is the vagility of the species. In the two species studied here, there are significant differences in mobility. Agraulis vanillae is a sedentary species; mark-recapture studies indicate that home ranges are restricted to the vicinity of Passiflora food plants. Phoebis sennae engages in extensive inter-patch movements between its Cassia food plants, which may necessitate greater lipid reserves. In this species, these reserves are acquired mainly through adult foraging. In migratory monarch butterflies (Danaus plexippus), lipids may constitute up to

45% of dry weight (Brown and Chippendale 1974). This species also acquires these lipid reserves mainly through adult foraging and not by larval feeding (Walford 1980; Brower in press). The pattern of fat storage and depletion by Agraulis vanillae more closely resembles that seen in Hyalophora cecropia (Saturniidae) (Domroese and Gilbert 1964) or Magicialada cassini (Homoptera) (Brown and Chippendale 1973). In these species, fat reserves laid down at metamorphosis are not augmented by adult feeding, but progressively decline through the adult life span.

Lipid reserves in butterflies may serve as a buffer against environmental variability in species that encounter highly variable conditions as adults. For Agraulis vanillae, the Passiflora food plants required for reproduction may occur in a variety of plant communities. These vary greatly in the amount and quality of nectar sources co-occurring with the larval food plants. Large lipid reserves in newly emerging adults may allow them to take advantage of these nectar-poor food plant patches, or allow emigration to more suitable areas. In Phoebis sennae, adults are able to exploit more energetically rewarding nectar sources due to their longer proboscis, and thus adults can store sufficient lipid reserves to allow great mobility among larval food plant patches that vary in quality. In addition, this species apparently can tolerate variability in food plant quality by producing smaller adults when larvae are faced with suboptimal food plant material or feeding conditions.

Summary

Agraulis vanillae and Phoebis sennae differ significantly in fat storage patterns, as predicted by theory. Boggs (1981) hypothesized

that two species differing in expected adult intake of a nutrient should show corresponding differences in the allocation of that nutrient at metamorphosis. Phoebis sennae, which has a higher adult energy intake, emerges from the pupa with 3-5% of dry weight allocated to lipid. Agraulis vanillae, which is relatively non-selective in adult foraging and obtains less energy through adult feeding, emerges from the pupa with 16-20% of dry weight allocated to lipid. Whereas the lipid reserves of Agraulis vanillae decrease regularly to about 5% of dry weight, Phoebis sennae accumulates lipids and builds reserves up to 40% of dry weight.

CHAPTER V
THE EFFECTS OF ADULT ENERGY INTAKE ON
SURVIVAL AND FECUNDITY OF AGRAULIS VANILLAE

Introduction

Optimal foraging models assume that maximizing the rate of intake of some dietary component, such as energy, will maximize the fitness of the individual, and therefore natural selection will favor those individuals that forage so as to maximize the rate of intake of that component over a given time period (Schoener 1971; Pyke et al. 1977; Mitchell 1981). However, this assumption is rarely supported empirically (Mitchell 1981). Real (1980a) suggests that in some animals where energy is the quantity maximized, the fitness benefits derived from increasing energy intake may not be linear, but concave downwards. In other words, there may be diminishing fitness returns at increasing levels of energy intake. With regard to nectarivores, which obtain mainly energy from nectar (Heinrich 1975), maximizing energy intake in energy-stressed individuals may confer large fitness benefits, whereas non-stressed individuals may realize smaller increments in fitness from behaviors maximizing energy intake. Thus selection pressures favoring behaviors maximizing energy intake may be strong for energy-stressed individuals, but weak for individuals under no energy stress.

The effects of the energy-yielding components of nectar (mono- and disaccharide sugars) on fitness components such as fecundity and longevity of lepidopterans are quite variable. Some species require no adult feeding at all (Carefoot 1973); in others, individuals on water diets realize fecundities equal to those of sugar-fed individuals (Fenemore 1979; Raina and Bell 1978). However, in most species that feed as adults, sugars in the diet result in increased fecundity or survival (Labeyrie 1957; Raina and Bell 1978; Stern and Smith 1960; El-Sherif et al. 1979; Murphy et al. 1983). Yet maximizing energy intake apparently does not necessarily maximize fecundity. El-Sherif et al. (1979) found that the moth Pthorimaea operculella (Gelechiidae) achieved maximum longevity and fecundity when fed 5% sucrose solutions; increasing the sucrose concentration, which presumably increased energy intake, reduced survival and fecundity below that of the 5% diet. These studies all dealt with laboratory strains of pest moth species; their relevance to wild populations is uncertain. In addition, in many lepidopterans the reproductive output achieved by adults may be significantly affected by the feeding success and food plant quality experienced by the larvae (Slansky 1982; Beckwith 1970).

Observations of foraging Agraulis vanillae have suggested that selection for energy maximization during adult feeding may be weak. I have presented evidence that this species is relatively non-selective when foraging at mixed floral arrays and fails to discriminate among flower species varying widely in

energy return. Furthermore, this species emerges from the pupa with relatively large lipid reserves that are depleted throughout adult life. Freshly-emerged individuals apparently spend less time foraging than do older adults, as older individuals tend to forage later in the day when nectar resources are less rewarding. Thus there may be age-related differences in foraging strategies of individuals related to the current energy balance and the benefits to be realized from further energy intake.

In this section, I describe experiments designed to measure the effects of adult feeding and larval reserves on fitness in Agraulis vanillae. Specifically, I wish to test the assumption that increasing energy intake increases fitness. Further, I would like to determine the form of the energy-fitness function, i.e., linear or concave. Fitness will be quantified in several ways, including survivorship, fecundity, and lipid storage. Fitness is a complex function determined by fecundity and survivorship as well as interactions between these variables. No attempt is made here to integrate the various traits into a single model of fitness. Rather, my intent is merely to show that certain life-history traits that affect fitness are sensitive to energy intake by the adult insect. Fecundity is quantified here as the number of fully-formed (chorionated) eggs found in the ovarioles of females and is assumed to be a relative measure of reproductive output. The effects of energy content of the adult diet on lipid storage and survival in males are also considered.

Methods and Materials

Effect of energy intake on fecundity and lipid storage

I collected late-instar larvae of Agraulis vanillae in the field and reared them to pupation in the laboratory.

Freshly-emerged adults were individually numbered, marked and released in flight cages. These cages measured 2.5 x 2.5 x 3.1 m and were located in the shade of a large live oak so that they received no more than one hour of direct sunlight per day. I randomly assigned each butterfly to one of the following four diet treatments: a) fed once a day to satiation with a 0.25% sucrose solution (the butterflies would not imbibe pure water), hereafter referred to as the water treatment; b) 10% sucrose solution (weight/weight), restricted to a maximum feeding bout of three minutes per day; c) 10% sucrose solution, fed once a day to satiation; d) 50% sucrose solution, fed once a day to satiation. Butterflies in the satiation treatments were assumed to be satiated when they had removed their proboscides from the feeding vessel three times. For a randomly selected sample of individuals in each treatment, I timed the feeding duration of each day's feeding bout with a stopwatch. The cumulative feeding time was used to estimate energy intake during adult life by multiplying cumulative feeding time by energy intake rate (joules/s) for the sucrose concentration on which the individual was fed (see Chapter II for explanation of energy intake rate determinations). Cages were checked daily for mortality, and at ages of 1 to 9 days randomly chosen individuals were sacrificed for fecundity or lipid measurements.

Females were preserved in 70% ethanol and later dissected to determine the number of chorionated eggs formed in the ovarioles. Males were frozen and later subjected to a petroleum ether lipid extraction to determine the magnitude of lipid reserves (see Chapter IV for details of the extraction procedure).

Effect of body weight on survival

Body weight is highly correlated with lipid content in both Phoebis sennae and Agraulis vanillae (Phoebis: $n = 59$; wet weight-lipid weight $r = 0.8462$, dry weight-lipid weight $r = 0.9442$; Agraulis: $n = 91$; wet weight-lipid weight $r = 0.696$, dry weight-lipid weight $r = 0.706$; all $p < 0.01$). To determine if body weight (and therefore lipid weight) was significantly related to survivability, freshly-emerged and field-collected adults of Agraulis vanillae and Phoebis sennae were individually numbered, weighed and placed in the flight cages described above. They were not fed, but were provided with water via an enamel pan of moist sand, in which pinned butterflies of both species were placed to stimulate puddling (Arms et al. 1974). Both species were observed to visit the pan to puddle. The cages were checked daily for butterfly mortality.

Effect of eclosion weight on fecundity

To determine if larval feeding success (as measured by weight of the adult butterfly at eclosion) influenced adult fecundity, I collected late-instar larvae of Agraulis vanillae in the field and reared them to pupation in the laboratory. I weighed freshly-emerged females were weighed within 3 hours of

eclosion. Eclosion weight is assumed to reflect in some sense the feeding success during the larval stage (as well as genetic influences). Females were maintained for three days in the laboratory at room temperature by keeping each female in a glassine envelope within a 10 x 14 x 20 cm plastic box maintained at high humidity. Each female was fed for a maximum of three minutes daily with a 30% sucrose solution after warming to flight temperature with a heat lamp. At the end of the three-day period, each female was weighed and preserved in 70% ethanol. At a later date I dissected each female and counted the number of chorionated eggs formed in the ovarioles.

Results

Feeding bout duration varied widely among individual Agraulis vanillae used in the diet experiments. Individuals offered 10% sucrose solutions would feed for durations as short as 55 seconds per day or as great as 1200 seconds per day. With 50% sucrose solutions similar variation was seen, with bouts ranging between 5 seconds and 900 seconds per day. Consequently, there was a wide range of energy contents of diets received by different individuals, even within treatment groups. Individuals in the water treatment (0.25% sucrose) showed a fairly consistent pattern of feeding behavior. Bout duration for the first 1 to 3 days of adult life was quite short (1 to 5 seconds), but later in life lengthened to as long as 325 seconds. As mean uptake rate at this concentration is about 0.7 μ l/s, this corresponds to a daily water intake ranging

between 1 and 225ul. Energy content of diets within this range was negligible (average of 9.4 joules over entire adult life).

There is a significant effect of adult energy intake on chorionated egg production (Table 5-1). Because sacrificed females differed in age (although not significantly among treatments), and because this might affect the number of eggs formed, data from this experiment were analyzed using a one-way analysis of covariance (Dixon et al. 1981) with age as an independent covariate of the dependent variable egg number. Even after statistically removing any possible effects of age on egg production, there was still a highly significant effect of diet on egg production. However, inspection of the group means in Table 5-1 suggests that the relationship between energy intake and fecundity (as measured by chorionated egg production) is not linear. Females in the 10% satiation treatment received on the average about twice as much energy as females in the 10% restricted group, and egg production was almost exactly doubled. The 50% satiation group received more than twice as much energy as the 10% satiation group, yet fecundity was increased only slightly.

Figure 5-1 shows the relationship between total adult energy intake and egg production for all females for which feeding durations were measured. Two features of this plot deserve comment. Although there is a significant correlation between energy intake and egg count ($r = 0.3952$, $n = 30$), egg

TABLE 5-1 - CHORIONATED EGG PRODUCTION OF FEMALE AGRAULIS VANILLAE RECEIVING DIFFERENT ADULT DIETS.
[mean $\pm$ 1 standard deviation (n)].

	WATER	TREATMENT GROUP		
		10% RESTRICTED	10% SATIATION	50% SATIATION
Age at sampling (days)	4.4 $\pm$ 1.4 (12)	5.2 $\pm$ 2.0 (9)	4.9 $\pm$ 1.0 (9)	5.5 $\pm$ 2.3 (12)
Energy intake (Joules)	9.4 $\pm$ 10.4 (12)	424.7 $\pm$ 202.5 (9)	886.3 $\pm$ 732.9 (4)	2143.9 $\pm$ 1379.8 (7)
Chorionated eggs	19.2 $\pm$ 22.4 (12)	26.9 $\pm$ 22.7 (9)	58.1 $\pm$ 16.1 (9)	71.8 $\pm$ 30.2 (12)

Analysis of covariance -
Chorionated eggs vs. treatment F = 9.43, p < 0.0005

Figure 5-1 - Total energy intake (Joules) during adult life versus chorionated egg production. Line is fit by least squares regression. ($n = 30$, $r = 0.395$, $p < 0.05$, $y = 0.105x + 30.68$.)

production appears to level off at energy intakes above 1200 joules. Second, there is wide variation in egg production of females receiving very little or no energy in the adult diet (< 150 joules). In fact, some females receiving virtually no energy in the adult diet produced as many eggs as females receiving the highest amounts of energy. This suggests that much of the realized fecundity of some females may be due to stored resources carried over from the larval period and that variation in fecundity among these low-energy females may reflect variation in larval feeding success. To test this, I sought correlations between eclosion weight of females and the number of chorionated eggs produced after 3 days on a standardized diet. As seen in Figure 5-2, eclosion weight is strongly related to the number of eggs produced ($r = 0.557$, $n = 26$, $p < 0.01$). Egg production was also significantly correlated with forewing length ($r = 0.506$, $n = 26$, $p < 0.01$), final weight after 3 days ($r = 0.724$, $n = 26$, $p < 0.01$), and weight gain over the three day period ($r = 0.596$, $n = 26$, $p < 0.01$). Some of these butterflies gained weight over the course of the experiment, in contrast to field-collected individuals and individuals in the flight-cage experiments previously described. In this experiment however, females were maintained in a relatively cool laboratory (about 24°C) within glassine envelopes, so that metabolic expenditures were minimal and weight gain was possible.

Energy intake of adult males also significantly affects body composition and lipid storage. Table 5-2 presents the data

Figure 5-2 - The relationship between emergence weight *Agraulis vanillae* females and the number of chorionated eggs produced after 3 days on a nectar diet (see text for details). Line fit by least squares regression. ($n = 26$, $r = 0.557$, $p < 0.01$, $y = 287.2x - 22.0$.)

TABLE 5-2 - BODY COMPOSITION AND LIPID STORAGE OF MALE AGRAULIS VANILLAE RECEIVING DIFFERENT ADULT DIETS. [mean $\pm$ 1 standard deviation (n)]. Statistical analyses are analyses of variance for sampling age and energy intake and analysis of covariance (with age and forewing length as covariates) for all other variables.

	TREATMENT GROUP			F	P
	WATER	10% RESTRICTED	50% SATIATION		
Age at sampling (days)	4.1 $\pm$ 1.3 (17)	5.0 $\pm$ 1.6 (13)	4.8 $\pm$ 1.5 (12)	F = 1.6 p = 0.21	
Energy intake (joules)	7.2 $\pm$ 8.2 (17)	529.5 $\pm$ 166.1 (12)	2116.2 $\pm$ 977.2 (7)	F = 60.5 p < 0.0001	
Wet weight (grams)	0.114 $\pm$ 0.036 (17)	0.130 $\pm$ 0.042 (13)	0.204 $\pm$ 0.034 (12)	F = 30.0 p < 0.0001	13
Dry weight (grams)	0.064 $\pm$ 0.014 (17)	0.070 $\pm$ 0.012 (13)	0.098 $\pm$ 0.019 (12)	F = 32.3 p < 0.0001	13
Lipid weight (grams)	0.006 $\pm$ 0.006 (17)	0.006 $\pm$ 0.004 (13)	0.014 $\pm$ 0.006 (12)	F = 10.9 p < 0.0005	
Lean weight (grams)	0.058 $\pm$ 0.010 (17)	0.065 $\pm$ 0.010 (13)	0.084 $\pm$ 0.017 (12)	F = 30.0 p < 0.0001	
% lipid (of dry weight)	8.3 $\pm$ 6.3 (17)	7.8 $\pm$ 4.6 (13)	14.2 $\pm$ 5.2 (12)	F = 5.3 p < 0.01	

from lipid analyses of male Agraulis vanillae on different adult diets. Feeding durations of males in the 10% satiation treatment were not measured; I was therefore unable to determine adult energy intake and they were consequently omitted from the analyses. Statistical comparisons of wet weight, dry weight, lipid weight, lean weight and percent lipid (of dry weight) were performed using one-way analysis of covariance with age and forewing length as covariates (Dixon et al 1981). Increasing adult energy intake decreased the rate at which body weight was lost. However, the lipid contents of the 10% restricted males did not differ from those of water-fed males. At low energy intake levels, stored lipid is apparently depleted at the same rate; increasing the energy intake to levels within the range received by individuals within the 50% group decreases the rate at which stored lipid is depleted. There is no evidence that any individuals stored lipids above the level seen at eclosion from the pupa (about 15% of dry weight). One factor not controlled in this experiment was activity level; all butterflies were maintained in the same flight cages, so amounts of flight activity may have varied among treatment groups depending on energy content of the diets. This might obscure any real differences in rate of lipid depletion between the 10% restricted and water treatments.

Some mortality occurred among all treatment groups during the course of the diet experiments. To determine if mortality was influenced by treatment, I analyzed the mortality data using a clinical life-table approach, which allows comparisons among

treatments when survivorship of all individuals is not known (those individuals withdrawn for egg counts or lipid extractions). Data from males and females were pooled for this analysis. Table 5-3 presents the observed and expected numbers of deaths in each treatment group. Expected number of deaths were calculated using the log-rank method. A χ^2 test showed mortality to be significantly affected by treatment group ($\chi^2 = 9.4$; $df = 3$; $p < 0.025$). Number of deaths observed was close to expected in the 10% restricted and 10% satiation groups, but was much greater than expected in the water treatment and less than expected in the 50% sucrose treatment. I therefore conclude that energy content of the adult diet significantly affected the probability of mortality.

Body weight and survival

The data presented above show that increasing the adult energy intake of males decreases the rate at which they deplete body weight and stored lipids. A better fed butterfly is thus a fatter butterfly. To determine whether differences in body weight were related to mortality, I compared survival of freshly-eclosed and field-collected individuals of both Phoebis sennae and Agraulis vanillae that were maintained in a flight cage with water but no access to food. Table 5-4 presents the data from that experiment. Freshly-eclosed Agraulis were about 0.05 g heavier than field-collected individuals and survived an average of 2.5 days longer. Although field-collected Phoebis were heavier than freshly-eclosed individuals, survival time of both groups was equal. Variance in survival time of

TABLE 5-3 - NUMBER OF OBSERVED AND EXPECTED DEATHS OF AGRAULIS VANILLAE VS. DIET TREATMENT. Expected deaths calculated using log-rank method.

TREATMENT	DEATHS	
	OBSERVED	EXPECTED
WATER	13	6.8
10% RESTRICTED	5	6.0
10% SATIATION	4	4.1
50% SATIATION	2	7.1

$$\chi^2 = 9.4, \text{ DF} = 3, p < 0.01$$

TABLE 5-4 - SURVIVAL IN DAYS OF AGRAULIS VANILLAE AND PHOEBIS SENNAE WITHOUT NECTAR VS. INITIAL WEIGHT. [mean $\pm$ 1 standard deviation (n)]. Butterflies had access to water.

	WET WEIGHT (G)	SURVIVAL (DAYS)
Freshly-eclosed Agraulis	0.246 ± 0.028 (10)	5.9 ± 1.1 (10)
Field collected Agraulis	0.202 ± 0.042 (65)	3.3 ± 1.7 (61)
Freshly-eclosed Phoebis	0.199 ± 0.026 (8)	5.3 ± 0.8 (7)
Field collected Phoebis	0.225 ± 0.056 (39)	5.3 ± 2.8 (33)
F	4.26	10.98
p	< 0.01	< 0.0001

field-collected individuals was higher than in freshly-eclosed individuals. In both species, there were highly significant correlations between initial wet weight and survival time (Agraulis: $r = 0.4955$, $n = 71$, $p < 0.01$; Phoebis: $r = 0.6643$, $n = 40$, $p < 0.01$). These data are plotted in Figures 5-3 (Phoebis) and 5-4 (Agraulis).

Discussion

Adult feeding and energy content of the adult diet have significant effects on several life-history traits affecting adult fitness in Agraulis vanillae, including egg production, fat storage and mortality rate. In addition, data from Phoebis sennae indicate that survival is strongly correlated with body weight, which is increased through adult feeding (Chapter IV). Thus there should be selection on these butterflies to achieve some level of energy intake through adult feeding.

However, data from Agraulis vanillae suggest that the relationship between energy intake and fitness is not linear as assumed by most optimal foraging models. Increasing energy intake of females above a given amount does not necessarily result in corresponding increases in egg production. Additionally, some females are able to produce a large number of eggs with very little adult energy intake. Both of these findings suggest that selection for energy maximization may be quite variable among different individuals of this species. Egg production in this species may be constrained by factors other than energy intake. Abdominal storage space of females may limit the number of eggs that can be produced at any one time.

Figure 5-3 - The relationship between initial wet weight and survival in days of *Phoebis sennae* in a flight cage without nectar resources. Line is fit by least squares regression. ($n = 40$, $r = 0.664$, $p < 0.01$, $y = 31.4x - 1.55$.)

Figure 5-4 - The relationship between initial wet weight and survival in days of *Agraulis vanillae* in a flight cage without nectar resources. Line is fit by least squares regression. ($n = 71$, $r = 0.496$, $p < 0.01$, $y = 20.9x - 0.72$.)

Nitrogen or other nutrients may begin to limit egg production once energy limitations are overcome. Thus increasing energy intake may increase until other constraining factors make egg production insensitive to further increases in energy intake. Selection for energy-maximization may be relaxed once some threshold energy level has been achieved.

For the nymphalid Euphydryas editha, Murphy et al. (1983) showed a somewhat similar relationship between adult diet and fitness. Sucrose in the diet did not significantly affect egg production during early clutches, but increased the size of later egg masses. However, the authors suggested that the potential for later egg masses to survive to maturity was minimal except during wet years and therefore concluded that adult feeding increased fitness only during favorable years. Thus selection pressures for energy-maximization or efficient adult foraging may be variable in this species as well.

Variable or weak selection for foraging efficiency or energy maximization in Agraulis vanillae is consistent with observed foraging behavior in this species. Individuals are relatively non-selective in flower visitation and will frequently switch flower species during a foraging bout even when the flower species differ significantly in energetic rewards offered. These apparently non-selective individuals may be choosing flowers for qualities other than energy, such as amino acid content. There is also significant variation in length of the foraging period among individuals depending on age. Older individuals, which have depleted much of their lipid

reserves, forage later in the day, when energetic rewards are reduced, than do younger, more lipid-rich individuals. It is possible that that some individuals may forage very little (except perhaps to meet water demands, which are apparently minimal) if they have emerged from the pupa with large lipid reserves procured through larval foraging.

Phoebis sennae, on the other hand, is much more selective during adult foraging and apparently requires extensive adult feeding to obtain sufficient lipid reserves. Thus, selection for energy maximization and efficient adult foraging should be stronger in this species than in Agraulis vanillae. The effects of adult energy intake on fitness components of Phoebis were not studied due to difficulty in obtaining sufficient numbers of larvae during the past two field seasons of this study. However, from observing foraging behavior and lipid storage patterns, I would suggest that the effects of energy intake on survival and fecundity would be more pronounced and more nearly linear than in Agraulis. Furthermore, since all individuals of Phoebis apparently emerge from pupae with similar, small lipid reserves, I would expect less variance in fecundity in this species due to differences in larval feeding success. In fact, extensive and efficient adult foraging may be part of an evolved strategy allowing these butterflies to exploit low-quality larval food plants and still realize high reproductive success as adults.

As mentioned earlier, fitness or reproductive success is a complex function influenced by mortality, fecundity, and other

variables. There may be trade-offs involved in adjusting one of these variables. For example, lowering the age of first reproduction may also result in decreased probability of survival later in life. To fully understand the effects of adult energy intake on fitness, it will be important to study the interactions between the fitness components studied here and to integrate these components into a single measure of fitness.

Summary

I fed freshly-emerged adults of Agraulis vanillae on different diets differing in sugar (and therefore energy) content to determine the effects of adult energy intake on survivorship, egg production, and fat storage. Increasing the energy intake of females increased chorionated egg production, but there appeared to be diminishing returns at higher energy intake levels. Males that received more energy in the adult diet depleted their lipid reserves at a slower rate than did males with low energy intakes. For both sexes, mortality was significantly reduced by increasing energy intake. Both Agraulis vanillae and Phoebis sennae showed significant correlations between body weight and survival time when deprived of nectar. Although the various components of fitness are sensitive to energy intake in the adult diet, egg production in female Agraulis vanillae is influenced by larval feeding as well, as suggested by a positive correlation between female body weight at emergence from the pupae and chorionated egg production.

CHAPTER VI
ADULT FORAGING IN AGRAULIS VANILLAE AND PHOEBIS SENNAE:
SUMMARY, SYNTHESIS AND CONCLUSIONS

Foraging optimization models assume that animals should select food items so as to maximize the rate of intake of one or more dietary components. Most models assume that energy intake is of primary importance and therefore predict that foraging animals should structure their diets and foraging activities to maximize the rate of energy intake while foraging. Because floral nectar contains predominantly sugars and water, nectarivores have been suggested to be ideal test subjects for these energy-maximization models of foraging behavior (Pyke 1981a).

A large volume of work conducted on foraging in various bee species has suggested that these insects generally seem to select flowers and behave while foraging so as to maximize energy intake (for references and an excellent review of bee foraging and energetics, see Heinrich [1979b].) This is not surprising; bees partition their behaviors so that no other activities occur concurrently with foraging. Thus no conflicting adaptive goals compromise foraging efficiency. Furthermore, in many bee species foraging is performed by sterile workers whose main function is to provision the hive

with nectar and pollen. This provisioning must not only supply the nutritional demands of the adults but of the larvae as well.

In contrast, foraging behavior in adult lepidopterans is subject to a number of conflicting selection pressures. In these holometabolous insects, feeding may occur during both the larval and adult stages, and feeding success during both stages can significantly affect fitness. Whereas all lepidopteran species feed as larvae, not all species require food as adults to carry out their reproductive activities, and in some species the mouthparts are degenerate, making adult feeding impossible. Even among those species that do feed as adults, there is great variation in the nature, extent and importance of adult feeding. The types of food taken by adults are immensely variable, including blood, pollen, sap, rotting fruit, dung and nectar. The amount of food taken during the adult stage is highly variable as well, as some groups such as satyrids and some nymphalines are rarely observed feeding, while others such as long-lived tropical Heliconius species are highly dependent on adult food resources for fully realizing potential fecundity (Gilbert 1972; Gilbert and Singer 1975).

Important questions to be addressed regarding adult feeding in lepidopterans include: What are the relative importances of larval and adult feeding to maximizing fitness, and consequently how rigorous are the selection pressures exerted on adult foraging behavior? It is clear that the importance of adult feeding spans a continuum among species ranging from species not feeding at all to those for which adult nutrition is

essential. The two species studied here, Agraulis vanillae and Phoebis sennae, appear to occupy different points on that continuum. Their foraging behavior and energetic profitability differ significantly. These differences can be explained in terms of a variety of morphological, ecological and physiological factors that differ between them and affect adult foraging behavior as well as the selective pressures to which such behavior is subjected.

Both species are to some degree selective of nectar sources. Although this selectivity does increase the rate of energy intake, Phoebis sennae is apparently under greater selective pressure to achieve a maximum energy intake during adult feeding. Nectar uptake rates are higher in Phoebis than in Agraulis, even though Phoebis has a longer, slightly narrower proboscis. This requires production of greater pressure drops by Phoebis but results in a greater net rate of energy intake while nectar of any concentration is being extracted. It also reduces the amount of time spent extracting nectar from flowers. This difference between the species is probably due in part to the differences in nectar volumes encountered by the butterflies. Some flowers visited by Phoebis contain up to several microliters of nectar; minimizing time spent at these flowers may be important in minimizing total foraging time. Agraulis, on the other hand, visits mainly low-volume nectar sources with tenths to thousandths of a microliter of nectar per flower. The majority of the time spent at these flowers is

spent finding the nectar (handling time), so increasing the extraction rate would result in negligible time savings.

The male-female dichotomy in extraction rates of both species is curious and suggests that sexual differences in energetic needs, foraging behaviors and selectivity may occur as well. Males of both species have significantly higher extraction rates than do females, even though females are of equal (Phoebis) or greater (Agraulis) body size. Males may be under greater selection pressure to minimize foraging time or maximize energy intake due to the time and energy constraints associated with finding and successfully courting receptive females. In Agraulis, even when densities are high, courtship is relatively infrequently seen, and copulating pairs are rare. Nearly all females collected in the field have at least one spermatophore in the bursa copulatrix, so finding unmated females is probably a very time and energy consuming activity.

In terms of the foraging choices and behaviors exhibited by these two species, differences in foraging success are even more pronounced. Each species chooses a set of nectar sources that is distinctly different from that of the other. Some overlap in nectar sources does occur, but on the average, Agraulis forages at flowers that are energetically less rewarding than those fed at by Phoebis. Differences in energetic rewards offered by the various flower species used by these two butterflies are caused predominantly by variation in nectar volumes available to foragers. Mean sugar concentrations of the nectars do not differ between the resources chosen by the two butterflies.

Although the energy content of nectar in individual flowers is determined by both volume and sugar concentration, concentration alone is not correlated with energetic profitability of foraging in either species. Thus predictions of foraging selectivity based on nectar concentration and its effect on energy intake rates during nectar extraction (Kingsolver and Daniel 1979; Heyneman 1983) have little relevance to foraging butterflies, since other factors such as nectar volume and density of flowers are much more important in determining overall energy intake rates than is nectar concentration. Nectar volume, however, varies tremendously among nectar sources and is the single most important factor affecting foraging profitability. Differences in the energetic profitability of foraging between the two butterflies can thus be attributed mainly to differences in the average nectar volumes encountered. Phoebis sennae feeds at flowers that on the average yield greater nectar volumes than do the flowers visited by Agraulis vanillae. This is because a) Phoebis is more selective than Agraulis, and avoids low-volume flower species such as Richardia scabra, Verbena brasiliensis and Bidens pilosa, which are major nectar sources for Agraulis, and b) because of its longer proboscis, Phoebis can forage at high-volume flowers such as Ipomoea spp. from which Agraulis is morphologically excluded.

Foraging selectivity differs in other aspects as well. Both species often encounter patches of flowers containing several flowering plant species differing in their profitability. In these situations, Phoebis is more successful

than Agraulis at energy maximization because it discriminates among flower species and excludes less rewarding flower species from the diet. Agraulis, however, will alternate visits between flowers differing significantly in energetic reward, even when the flower species involved are distinctly different in color and morphology, and differ by an order of magnitude in energetic reward (Sida rhombifolia and Verbena brasiliensis). Differences in selectivity may be due to differences between the butterfly species in time allocation patterns. Agraulis' foraging bouts are shorter and are often interrupted by intraspecific interactions. Recent theoretical models of time constraints and their effect on foraging selectivity (Lucas 1983) predict that species that forage in short bouts actually achieve higher energy intake rates by using a generalized foraging strategy. Alternatively, Agraulis may be selecting nectar resources on the basis of factors other than strictly energy content. Water content is probably not one of these factors, as selection for water content would result in selection of flowers with greatest nectar volume and would concomitantly maximize energy intake. Amino acid content of floral nectars, however, may be involved in flower selection. Butterfly-visited flowers are known to be relatively high in amino acid content (Baker and Baker 1975), and amino acids in the adult diet significantly increase fecundity of pollen-feeding Heliconius butterflies (Gilbert 1972), although amino acids in the adult diet of a more typical nymphalid, Euphydryas editha, have relatively minor effects on fitness (Murphy et al. 1983). Tests of foraging selectivity of

honey bees (Apis mellifera) have provided little evidence that these insects select nectar resources on the basis of amino acid content (Inouye and Waller 1984). With regard to the butterflies and nectar resources studied here, measurement of amino acid content was impossible with existing technology, so no conclusions can be made about the importance of amino acids in the diet and their effects on flower selection.

The lack of selectivity of nectar sources by Agraulis vanillae may be influenced by several ecological attributes of this species. These butterflies, like some other nymphalids (Ehrlich et al. 1975), have quite restricted home ranges. This may be due in part to the nature of the foodplant; Passiflora incarnata is a rhizomatous perennial that remains available at any given site for several months. Thus adequate oviposition sites can apparently be found with relatively little movement. This has two important consequences for foraging energetics and floral selectivity. First, total energetic demands are reduced because of the low travel costs. Second, a given individual butterfly is probably exposed to only a few potential nectar sources during its lifetime, so the potential for exercising selectivity may be quite small. In fact, some populations of Passiflora used by Agraulis were found to have virtually no nectar source plants in close proximity. Whether these Agraulis populations show greater mobility in order to find nectar sources or simply do without is unknown.

Another ecological factor that may lead to non-selective or sub-optimal foraging could be the constraints placed on foraging

activities by concurrent but conflicting behaviors. Agraulis does not clearly partition the activity period among different behaviors. Feeding individuals may simultaneously be searching for mates or oviposition sites, requiring some modification of foraging behavior. In addition, these butterflies thermoregulate by dorsal basking (Clench 1966) and probably cannot thermoregulate in flight (Heinrich 1981). Frequent perching may be required to maintain high thoracic temperatures required for activity, and foraging while basking may be a secondary goal.

Although Phoebis sennae movement and behavior patterns were not similarly quantified, it appears from qualitative observations that this species differs significantly from Agraulis in these respects. The larval hostplants, Cassia spp., are annuals that are much less predictable in time and space than is Passiflora. Although Cassia plants are available from May/June through October, individual plants appear to be relatively short-lived. Thus, the hostplant that a freshly-emerged Phoebis fed on as a larva may be inadequate for oviposition, and greater mobility may be required for finding suitable oviposition sites. The flight behavior of Phoebis is more rapid, direct, and covers much greater distances in a given time period than does that of Agraulis. Phoebis is frequently observed nectaring or flying in areas devoid of the larval foodplants, suggesting that there may be distinct segregation of foraging and reproductive activities, which could lead to

greater selection for minimizing foraging time or maximizing energy intake in this species.

Certainly Phoebis is more efficient while foraging at the same resource arrays as Agraulis. The greater selectivity of Phoebis has been discussed earlier; Phoebis consistently restricts visitation to the more energetically rewarding nectar sources that are available. In addition, Phoebis spends less time in flight than does Agraulis when foraging at the same nectar sources. Between flower flights are more direct, reducing foraging costs and increasing energetic profitability. The greater floral selectivity of Phoebis, its avoidance of low-reward flowers, and its more efficient flight behavior all suggest that this species is subject to greater selection for energy maximization than is Agraulis vanillae.

The need for profitable adult foraging is further augmented by resource storage patterns during larval feeding and metamorphosis. It is not reasonable to argue that larval feeding strategies have caused the observed differences in adult foraging strategies; undoubtedly, the feeding strategies during larval and adult stages are integrated during the evolution of each species, and modifications in one stage allow or necessitate changes in the feeding behavior of the other stage. The integration of larval and adult feeding strategies, as suggested by Boggs (1981), is nicely illustrated by Agraulis and Phoebis. Agraulis individuals eclose from the pupae with relatively large lipid reserves (12-15% of dry weight in males, 14-20% in females), and the magnitude of fat storage during

metamorphosis has important effects on both survivorship and fecundity of these butterflies. Adult foraging appears to supplement these larval fat stores, but does not always seem to be necessary for maximizing fitness. Some females of Agraulis that are fed only water as adults exhibit fecundities equal to those of females on energy-rich diets. Although energy intake of adults can reduce the rate at which lipid reserves are depleted, Agraulis does not store lipids from adult feeding above the level that is attained at metamorphosis.

Field-collected individuals show a consistent decline in lipid reserves with age, although this decline may not be linear. If scale loss is a linear indicator of age, then these field-collected individuals show a rapid depletion of lipid reserves during the first few days of life, with the rate of lipid depletion slowing when lipid levels fall below 7-8% of dry weight. There appears to be a shift in foraging strategy accompanying the drop in lipid reserves. Older, lipid-depleted individuals forage for longer periods than do younger, lipid-rich butterflies. I suggest that there are correlated changes in reproductive behavior as well; younger butterflies may spend a greater proportion of their activity period in mate search, courtship, and oviposition behaviors than do older butterflies. Once reproductive reserves have been partially depleted, foraging time may increase to reduce the rate of lipid depletion. This would suggest that younger butterflies may be under greater time constraints, and therefore greater selection for energy maximization or time minimization while

foraging. Age-related differences in foraging selectivity and energetics would therefore be predicted.

Phoebis sennae exhibits a totally divergent strategy of adult-larval feeding integration. These butterflies emerge from the pupae with small lipid reserves ($< 5\%$ of dry weight) and require profitable adult foraging to boost these lipid reserves, which increases survivability and probably is required for maximum fecundity as well (Stern and Smith 1960).

Field-collected butterflies show a consistent increase in lipid reserves with age, up to levels as high as 50% of dry weight (compared to maximum of 20% in Agraulis). It is probably impossible for a butterfly to survive with lipid reserves below 3 or 4% of dry weight (no individuals of either species were found with lipid reserves lower than this), and Phoebis responds to poor larval feeding conditions not by reducing lipid storage at metamorphosis, but by not attaining full body size while keeping the proportion of body weight allocated to lipid within the 3-5% range. Given this low level of lipid reserves at eclosion, inefficient or non-profitable adult foraging would be expected to have serious fitness consequences such as reduced longevity or low fecundity. Since this species is more mobile, individuals that do not rapidly acquire lipid reserves sufficient for lengthy flights may be unable to find other conspecifics for mating or suitable oviposition sites, and may therefore not reproduce at all. I therefore suggest that selection for profitable adult foraging by Phoebis is greater than in Agraulis.

Adult Foraging in Lepidopterans -- A General Hypothesis

Adult foraging in lepidopterans, as illustrated by Agraulis vanillae and Phoebis sennae, obviously shows a wide range of variation among species. Although there is probably a continuum of adult feeding strategies, I suggest that most of these strategies can be grouped into two general classes: obligate vs. facultative adult feeders. These adult foraging strategies are closely linked to larval feeding behavior and energetics. For those species that are primarily nectarivorous as adults (and therefore acquire mainly energy through adult foraging), lipid contents at eclosion may be an excellent general indicator of adult foraging strategy, as suggested by Boggs (1981). The relationship between lipid storage at metamorphosis and adult foraging energetics invites further corroboration.

Obligate Adult Foragers

These species, exemplified by Phoebis sennae, for a variety of reasons emerge from the pupae with low energy reserves. This may be due to poor foodplant quality, selection for rapid development that may be fostered by variable environmental conditions (rapid foodplant senescence, heavy predation or parasitism on larvae, etc.), or other undetermined factors. Large lipid reserves may be required for mobility, mate location and/or egg production. These species are under heavy and constant selection pressure for efficient and profitable adult foraging in order to acquire these required lipid reserves. Adult fitness in these species is thus most closely related to adult foraging success. They are expected to exhibit

characteristics of optimal foragers, i.e., high selectivity of nectar resources based on energy content, minimization of foraging costs through efficient flight patterns while foraging, and minimization of foraging time at high-volume flowers via rapid nectar extraction rates. In general, any physiological or behavioral mechanisms that would reduce energy expenditures on non-reproductive activities and maximize lipid storage would be strongly selected for. There may also exist a relationship between proboscis length and foraging strategy, as suggested by Opler and Krizek (1984). I would expect these obligate foragers to have on the average longer proboscides that would increase the range of floral resources available to them.

Because of their requirements for highly profitable adult foraging, these species might be restricted in their ability to exploit different habitats containing the larval foodplants to those that contain a variety of floral resources or those that consistently contain one or more high reward species. Alternatively, obligate foragers may be selected for high mobility to maximize exposure to a variety of nectar sources. It is interesting that over the three field seasons of this study, the population densities of Phoebis sennae fluctuated much more dramatically than did those of Agraulis vanillae. This is a general characteristic of the genus Phoebis (Howe 1975) and may be attributable to fluctuations in nectar plant availability induced by differences in precipitation, which was highly variable among seasons.

Facultative Adult Foragers

These species, illustrated by Agraulis vanillae, probably show more variation in feeding strategies than do obligate foragers, as they may range from species that rarely or never feed (such as some satyrid butterflies and saturniid moths) to those for which adult feeding may be of variable importance. These species in general will emerge from the pupae with large lipid reserves, and the magnitude of these lipid reserves may be closely linked to realized adult fitness. Thus in this category adult fitness is more dependent on larval feeding success than in the obligate forager category. Adult feeding, where it occurs, is seen mainly as a buffer mechanism to compensate for variable environmental conditions encountered by the larvae. In cases where larval feeding conditions are poor, adult foraging activity can be increased to compensate for insufficient reproductive reserves acquired by the larvae. However, individuals that are successful during larval feeding may require little or no adult feeding to realize full fecundity or fitness. Consequently, selection for optimal adult foraging (in the energy-maximization sense) may be weak or absent, and probably variable among individuals. I therefore expect these species to exhibit non-selective adult foraging, inefficient foraging behavior (such as large proportion of foraging time spent in flight), or relatively low nectar extraction rates. In addition, species within this class of foragers may be characterized by shorter proboscis lengths as access to a wide

variety of flowers is unnecessary. These species would be expected to have the ability to exploit a wider range of habitats in which the appropriate foodplant occurs, as abundant nectar resources would not be required for reproduction to take place.

APPENDIX
A SIMPLE METHOD FOR MEASURING NECTAR
EXTRACTION RATES IN BUTTERFLIES

The rate at which nectarivorous animals extract nectar from flowers is one of the major parameters determining the instantaneous rate of energy intake, a quantity that is presumed to be maximized by natural selection (Pyke et al. 1977). The rate of energy intake equals the rate of nectar extraction (ul/s) multiplied by the energy content of the nectar (joules/ul). The rate of nectar extraction has been included in theoretical models of feeding energetics in butterflies (Kingsolver and Daniel 1979) and nectarivorous animals in general (Heyneman 1983). Although this rate has been measured in hummingbirds and incorporated into models of feeding energetics (Hainsworth and Wolf 1972), it has apparently never been measured in butterflies (Kingsolver and Daniel 1979). Here I present a simple technique for measuring extraction rate in butterflies that may be applicable to other nectar feeders as well.

Nectar of a known concentration is loaded into a calibrated microcapillary tube (Drummond Microcaps) that is mounted on a small balsa platform with a millimeter scale alongside the

capillary tube. The platform also includes a perch for the feeding butterfly to grasp. The platform is displaced at a slight angle from horizontal to cause the nectar column to move downward as it is removed. Because many butterflies maintain a body temperature several degrees above ambient (Rawlins 1980), and because extraction rate in poikilotherms is most likely temperature dependent, I placed both the butterflies and the apparatus inside a styrofoam chamber maintained at about 28° C with a heat lamp.

This technique for measuring extraction rates takes advantage of the apparently innate feeding response in butterflies that is released by the contact of the proboscis with a sugar solution. The butterfly is manually placed onto the perch and its proboscis is coaxed into contact with the leading edge of the nectar column in the microcapillary tube. As nectar extraction proceeds, the meniscus at the trailing edge of the nectar column can be timed with a stopwatch as it moves along the scale. I have had best success with 100 μ l microcapillary tubes (as opposed to smaller sizes), because the most difficult part of the procedure is in establishing the initial contact between the proboscis and the nectar. Larger microcapillary tubes have larger internal diameters, thus facilitating this part of the procedure. However, reducing the size of the capillary tube would increase the resolution of the system.

I have used this method with several species of Papilio (Papilionidae), Basilarchia archippus and Agraulis vanillae

(Nymphalidae), and Phoebis sennae (Pieridae) with equal success. All of these species exhibit a similar response to the initial contact of the proboscis with the sugar solution; the proboscis begins a series of probing motions that sometimes pull the tip out of the nectar column. If the tip reestablishes contact with the nectar within a few seconds, feeding begins. Once the butterfly begins feeding, it is no longer necessary to restrain the insect, since it grasps the perch and feeds at it would at a flower. In some species, there is a characteristic folding and unfolding of the wings while feeding.

Although my use of this method has been to investigate the relationship between nectar concentration, viscosity, and extraction rates (Chapter II), this technique may also be useful for studies of adult diet in which the effect of various dietary constituents on longevity or fecundity are studied. In studies of this type, researchers often feed the insects to satiation (e.g., Murphy et al. 1983). Using the method described here, one can control precisely the volume of nectar imbibed by an individual insect by regulating the volume placed within the capillary tube or by simply removing it from the feeding apparatus once a predetermined volume has been consumed.

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BIOGRAPHICAL SKETCH

Peter Gregory May was born on October 2, 1955, to Rolland L. and Sally S. May, in Jacksonville, N.C. Most of his childhood was spent in northern Virginia, where he graduated in 1973 from Stonewall Jackson High School in Manassas, Virginia. He received his college education at St. Andrew's Presbyterian College in Laurinburg, N.C. and George Mason University in Fairfax, Va., where he received his B.S. and M.S. degrees in 1977 and 1979, respectively. It was during this period that he began to develop his skills as a hoopster. In 1979, he moved to Gainesville to enter the Department of Zoology and play short forward for the North Florida Renegades. Behind his strong shooting from the field, the Renegades climbed to a ranking of sixth in the nation in 1983-4. Pete shoots about 70% from the charity stripe and is deadly from inside 20 feet. Despite these skills he is a totally unselfish player and excels at the assist. His biological interests center around avian community and behavioral ecology, plant reproductive ecology, and insect foraging ecology. Pete's hobbies include wildlife photography and sky diving.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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