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INTRODUCTION

Nectar from flowers provides nourishment for animals ranging in size from mites (55) to man. However, few of the organisms that can use these food resources are pollinators. One of the factors affecting whether or not an animal can be a dependable flower visitor is the relationship between its energy demands and the quantity of food it can harvest from the flowers (53, 107, 131, 133, 136, 255). This provides perhaps the most common basis upon which mutual adaptations for pollination have evolved. With some well-known exceptions [including the scents collected by male bees, possibly for territorial marking (64, 284) and as sex attractants (164, 232)], most attractants to flowers are food. The food quantity provided in relation to the energy demand of the flower visitor influences the amount of flower to flower and plant to plant movement. If the food rewards are too great, a flower visitor could restrict its movements, and become a "nectar thief" rather than a pollinator. If the food rewards are too small, the flower visitor learns to avoid that plant species and forages from another. It is probable that the optimal strategy of both foragers and plants would evolve (54) along the lines of an existentialist "game" (246). The "rules" of this game evolve from the foragers' strategy, where time and energy are used to optimal advantage (71, 241). The foragers' behavior is analogous to that of a predator (212, 247), but the evolutionary response of the "prey" is to maximize rather than minimize discovery and exploitation. Numerous theoretical (e.g. 10, 18, 101, 131, 195, 252, 257) and practical aspects (35, 47, 88, 207) of the pollinator-plant evolution have been reviewed.

From the evolutionary perspective it follows that those animals that are the most frequent vagile flower visitors to a given species will be the most dependable pollinators. Thus they are the ones that would most likely determine the evolution of flower signals to increase the frequency of visits to the flower and to increase the percentage of the pollination events per visit. Concurrently, features should evolve to exclude "nectar thieves" (151).

It is likely that natural selection would tend to produce those quantities of food reward that result in the most cross-pollination at the least cost in nectar. Plants probably do not direct more energy to food production for pollinators than is necessary for the flowers to be adequately pollinated: flowers must provide sufficient food to be attractive, yet if the rewards are too rich, the potential pollinator may be restricted to a single plant. Selective pressures would tend to produce enough food reward for optimal pollinators and, at the same time, to provide exclusion mechanisms for poor pollinators and robbers. However, the exclusion of ineffective pollinators is but the first step in a complex pattern of interrelationships that acts to achieve energy balance between specific pollinators and specific plant species.

During the last two centuries, the focus of studies on pollination has been on morphological coadaptations of flowers and their pollinators (9, 60, 73, 103, 151, 155, 157, 210, 211, 229, 230, 233, 251). These adaptations are astonishing in variety and complexity. The hidden food rewards, in contrast, might seem relatively unvarying and superficially uninteresting. However, they determine whether or not a plant is visited in preference to a neighbor, and whether or not the visitor moves between plants. The ecological significance of food rewards and energetics has not received much scrutiny until quite recently. I address myself here to the question of how, in the ecological context of numerous competing plant species, the floral rewards could affect the movements of flower visitors and hence the evolution of flowers.

The topic encompasses several disciplines, each with its own rich historical background. The information that is relevant and available is enormous. It is far beyond the aims of this essay, and my abilities, to review the subject comprehensively. Rather, I am forced to be synoptic, hoping to provide an overview to indicate general patterns and the possible scope, complexity, and nature of ongoing work.

MEASUREMENTS OF POLLINATOR ENERGETICS

The energy costs of foraging can be allocated to different categories. Energy intake during foraging must exceed the energy expenditure of harvesting. Moreover, the profit during the time available for foraging must be sufficient for long-term energy balance, which in obligate flower visitors includes the energy demands for reproduction. *Energy balance* thus may mean different things depending on the activities and duration in question. Suitable methods for measuring the different rates of energy expenditure vary accordingly.

Direct measurements of food consumption, particularly when foods are chemically defined as are sugars from nectar, can be reliable indicators of total energy expenditure. However, since ingested sugars may be stored or converted to lipid or glycogen, it is necessary to continue the measurements for time periods sufficient to achieve steady-state conditions. In hummingbirds and bees that are presumably not accumulating fat reserves, rapid utilization of sugars has made it possible to compute 24-hr energy budgets on the basis of food intake. However, such data by themselves give no indication of the time or conditions under which the food calories are expended.

The standard and probably most reliable indicator of energy expenditure is the rate of either oxygen consumption or carbon dioxide emission. For most animals feeding on nectar sugar, it can be assumed that the respiratory quotient is close to 1.0, and every milliliter O_2 consumed or milliliter of CO_2 liberated is equivalent to an expenditure of 5.0 calories. Nectars containing lipid (15, 16), as well as pure lipid (which yields approximately 9.0 calories per milligram) produced by "elaiophors," have been reported (271), and 1 ml O_2 consumed during lipid utilization represents an expenditure of 4.7 calories. By far the greatest bulk of foodstuff in nectar is sugar, which yields about 4 calories per milligram. Carbohydrate is a poor substrate for long-distance travel because its weight/energy ratio is about one-eighth that of lipid, and birds and some insects (including Orthoptera and Lepidoptera) convert carbohydrate to fat (122, 280). Hymenoptera and Diptera have a respiratory quotient (RQ) of 1.0, indicating that their flight muscles use primarily carbohydrate.

Despite its precision, the greatest drawback of using metabolic rate for energy budgets is its limitation to specific and often experimentally controlled activity states such as locomotion, maintenance metabolism, or temperature regulation. The animals are generally confined to a respirometer jar, in which their activity patterns and metabolic rates may not correspond with those in natural conditions. However, when combined with careful field observations, the measurements can be a powerful tool to infer energy budgets. For example, from timed observations of flight durations, perching, and body temperature during torpor, in conjunction with the corresponding rates of oxygen consumption during these activity states, accurate energy budgets corresponding to the observed rates of food consumption (221, 254, 287) have been calculated for hummingbirds.

Although the extrapolations from laboratory-derived metabolic rates have proven highly useful in calculating energy budgets of free-living hummingbirds, they are less suitable for some other animals. An endothermic insect, for example, may vary its metabolic rate by an order of magnitude in a few minutes while perching (117, 122, 149), yet display no outward sign of this process. Thus observations of discrete activity states such as perching or flying cannot be used in such cases for extrapolations to energy budgets.

A third, though costly, technique of circumventing the above difficulties in determining energy budgets is the use of isotope-labeled water. Monitoring the amount of isotope in the blood after a given amount has been injected gives an indication of the amount of energy expended during the time between injection and sampling (169, 209, 265). Social insects, trap-lining bats (132), and territorial hummingbirds (183, 255, 287) may be ideal candidates for the technique because these animals can be recaptured in the field at given intervals. To my knowledge, however, the method has yet to be used to measure energy budgets of free-living pollinators. Although ideal for long-term measurements of energy expenditure, the method cannot be used to determine the metabolic rate at any one time.

Body temperature is possibly the most reliable indicator of "instantaneous" energy expenditure of free-living animals in which discrete activity states are not apparent by visual inspection. At least 80% of an animal's energy expenditure is

degraded to heat, due to inefficiency at the biochemical and mechanical levels of organization (282). An increase in heat production, usually accompanied by an increase in body temperature (19, 122, 281), thus closely parallels an increase in energy expenditure. If the metabolic rate is large enough, as it is for most pollinators, it can be calculated from body temperature when mass and cooling rates are known (19, 123, 128). The method, though restricted to those conditions where radiant heat input and active cooling are at a minimum, has been useful in examining the energy expenditure of flying grasshoppers (281) and bumblebees (120).

ENERGY EXPENDITURE BY POLLINATORS

Pollinators conform to energy relationships similar to those of other animals. However, many of them are small, highly mobile, and must restrict foraging activity to the sometimes relatively short periods during the day when their host flowers present nectar. Flower-visiting insects are probably the most extravagant utilizers of energy on a weight-specific basis (118, 120, 131, 136, 278). However, large expenditures are often required to make small profits.

One of the generalities applicable to vertebrate animals is that resting metabolism is inversely related to body size (19, 50, 154, 166, 202). The metabolic rates of passerines and nonpasserines have been reviewed on several occasions (154). Both groups of birds have metabolic rates close to those of homeothermic mammals (166). The energy expenditure of some insects while thermoregulating depends similarly on their size. On the basis of whole body weight, the metabolic rate of a bumblebee while incubating is 170 cal (g hr)$^{-1}$ at 0°C. A hummingbird weighing 10 times more than the bee has a weight-specific respiratory rate 2.4 times less than that of the bee, and a bat weighing 10 times more than the bird has a respiratory rate at the same temperature that is 2.8 times less than that of the bird (121). The smaller the animal, the greater the energetic barrier to activity at low ambient temperature. As Bartholomew has pointed out, "as long as they [small animals] maintain high body temperatures, they are never more than a few hours from death by starvation, particularly at low ambient temperatures" (19, p. 348).

The basal metabolic rate (BMR) of homeothermic animals is measured at temperatures where no energy is expended for thermoregulation. Departure from thermoneutrality results in marked changes in metabolic rate, particularly in small animals. For example, hummingbirds weighing 8 g may increase their metabolic rate from about 9.0 cal (g hr)$^{-1}$ at 33°C to 65 cal (g hr)$^{-1}$ at 0°C (105). A stationary bumblebee weighing approximately 0.5 g increases the metabolic rate of its thoracic muscles from 85 cal (g hr)$^{-1}$ to 850 cal (g hr)$^{-1}$ over the same range of ambient temperature while incubating brood (121).

Since many flowers bloom only for short durations, the small high-energy pollinators could face severe energy problems. However, they have evolved a solution to the diurnal fluctuations of food availability—periods of torpidity. Some social insects avoid this torpidity by storing food energy in the nest. A queen bumblebee may use the entire contents of her honeypot in a single night (121, 122). When all available food has been utilized, the bee enters torpor (117). When at 0°C, a torpid

bumblebee has a metabolic rate 1000–2000 times less than when it is regulating its body temperature (121, 149). An important difference between the torpor of a hummingbird and that of an insect is that the bird regulates its body temperature at a lower set-point (288), but the insect does not regulate it at all. Energy saving by torpidity in hummingbirds was first discussed by Pearson (220, 221), who calculated that a male Anna hummingbird (*Calypte anna*) expends 10.3 Kcal during 24 hr as opposed to only 7.6 Kcal when torpid, an energy saving equivalent to the nectar contents of 370 *Fuchsia* blossoms. Wolf & Hainsworth have made similar calculations of the time and energy economy of torpor in tropical hummingbirds (287). The hummingbird *Selasphorus flammula* must visit 313 *Salvia* flowers to match calculated energy expenditure for 1 hr (107).

The rates of increase in body temperature during warm-up are strongly size-dependent and impose severe limits on the feasibility of hypothermia as an energy-saving strategy for larger animals. A bumblebee weighing 0.6 g may warm up at 12°C/min (122), but an animal weighing 300 g warms up about 120 times less rapidly (128). In addition, the energy costs of warm-up are clearly unfavorable for larger animals (19, 222). It costs a 0.5 g bumblebee 7.5 cal to warm up from 13.5°C – 38.0°C (123), equivalent to the energy expenditure during 3.0 min of flight. A sphinx moth weighing 2.0 g requires 30 cal to warm up from 15°C (126), equivalent to the energy expended during approximately 3.7 min of flight (116, 129). A small bat or hummingbird expends about 114 cal during a warm-up from 10°C, corresponding to approximately 1.2% of the total energy budget for 24 hr. In contrast, a 200 kg bear would need as much energy to warm up as it uses during an entire 24-hr activity period (222).

Other than thermoregulation, the highest energy costs are those of locomotion. Flight, particularly hovering (262, 282), is metabolically the most expensive mode of locomotion, although for a given distance of travel, it can be energetically less costly than walking (263). For insects and birds, the energetic cost of flight has been shown to vary markedly with load (26, 123) and flight speed (262), but it is relatively independent of ambient temperature (25, 27, 113, 123, 129). The above generalities, however, are insufficient to allow the preparation of accurate energy budgets for specific animal species. The following discussions concern energy expenditures in common classes of pollinators.

Bats

The pollinators of over 500 Neotropical plants are Microchiroptera (272). These animals may at times rely on fruit, using flowers as a secondary source of food (17). Some of the smaller species of nectivors, e.g. Australasian Megachiroptera, are known to enter torpor at night (20). Few data are available on the energetic costs of bat flight, but those available (260) indicate that it is similar to bird flight, which agrees with theoretical considerations (264).

Birds

The most common bird pollinators include the honeycreepers (Drepanididae) of Hawaii, the sunbirds (Nectarinidae) of Africa and Asia, some parrots (lorikeets)

from Australia, some honeyeaters (Melliphagidae) of Oceanea and Australia, and hummingbirds (Trochilidae) from America. Except for the latter group, the birds perch while visiting flowers, and their energy relations during foraging, flight, and temperature regulation are not known to differ in any significant way from those of other birds whose energetics have been recently reviewed (50, 154). Except lorikeets, which may derive large portions of their energy supplies from pollen (53), most of the birds [including hummingbirds (254, 273)] also feed on insects.

When breeding, both male and female hummingbirds require relatively large amounts of food energy. The males require time and energy to defend territories (254, 287). The females do not enter torpor at night while incubating (49), and they must have sufficient time for insect collecting to feed their young.

Hummingbirds range in weight from approximately 2.5 to 12 g. The weight-specific metabolic rates that have been measured during flight are close to 43 ml O$_2$ (g hr)$^{-1}$, or 215 cal (g hr)$^{-1}$, regardless of body size (108, 165), but metabolic rate during flight is related to the weight-relative wing area (72).

Bees and Other Insects

Except for some social Hymenoptera, most insects enter torpor at relatively frequent intervals, usually arousing only when preparing to fly (122). When inactive, their metabolic rate continues to decline with decreasing temperature. The metabolic rate in a torpid bumblebee at 10°C is near 0.5 ml O$_2$ (g hr)$^{-1}$, and about four times this rate at 20°C (149). These rates are similar to those observed in other insects (150). The great range of metabolic rates of "resting" insects is undoubtedly due, in part, to occasional or persistent endothermy.

The metabolic costs of rest and walking have not been differentiated in insects; however, it is probable that the metabolic costs of walking, at least at slow speeds, are very near those during rest, relative to the costs of flight. The metabolic cost of flight varies markedly between different types of flight, such as gliding and hovering. Sotavalta suggested that the rate of fuel consumption varies with the 1.4 power of body weight (250), but a comparison of the energy expenditure of a few insects (using various types of flight) weighing from several milligrams to several grams showed no dependence of energy expenditure on body weight (126). Rates of power output during flight in objects ranging in size from aphids to pigeons (156) and up to DC-8 jet transport planes have been compared (263, 264). Honeybees (*Apis mellifera*) utilize 10–11 mg sugar/hr of flight (30, 31, 240, 250), corresponding to a metabolic rate of 77 ml O$_2$ (g hr)$^{-1}$, or 385 cal (g hr)$^{-1}$, near that of flying bumblebees (*Bombus* sp.) (123). Sphinx moths (Sphingidae) have a metabolic rate during flight that is near 60 ml O$_2$ (g hr)$^{-1}$, slightly lower than that of flying bumblebees, (116, 129). However, as they range in weight from $\geq$ 100 mg to over 6 g (128), their total fuel consumption per hour of flight corresponds to about 8–480 mg of sugar.

The metabolic rate of butterflies (Papilionidae) has not been measured in free flight or flight at 100% lift, but those with large wings, permitting low wing-loading should, by extrapolation from moths (116), locusts (281), and birds (72) have low metabolic rates during flight. Many species of butterflies bask (119, 269), which

reduces or eliminates the need for energy expenditure by endothermic warm-up (274). Not having to rapidly accumulate large energy profits to feed larvae, they often wait for sunshine before initiating activity. Moreover, unlike bees, they take the time to bask in the sun rather than foraging without pause.

Except for fruitflies and blowflies, few data on the metabolic rates of Diptera during flight are available (51, 59, 293). Fruitflies tend to have a weight-specific metabolic rate about one-third that of bees. Hovering syrphid flies, on the basis of endothermy, probably have a metabolic rate at least as high as that of bees. Although endothermic by shivering, syrphids practice considerable energy economy by basking (130). In the Arctic, small flies have been observed to bask in heliotropic flowers (139).

The numerous energy-saving mechanisms observed in many nectivorous animals suggest that energy supplies have historically been, and are, sometimes limiting to survival.

FOOD REWARDS IN FLOWERS

With the rare exception of lipid in the nectars of some flowers (16), by far the largest dry weight of nectar is represented in sugar. The sugars are primarily the monosaccharides glucose and fructose and the disaccharide sucrose. Sucrose predominates in most flowers with tubular corollas and its hydrolysates, glucose and fructose, in open flowers (8, 109, 227, 256, 291). Nectar also contains amino acids and other components (15, 16). While these may be of great significance in nutrition, they are probably not a significant source of food energy, for they usually comprise less than 0.03% of the total dry weight of the nectar (H. G. Baker, personal communication).

Various methods of nectar analysis are available. The volume of nectar per flower may be determined by centrifuging individual flowers or by withdrawing the nectar, using capillary tubes of various sizes (16, 29, 32). The concentration of sugars in samples of several microliters of nectar can usually be measured with a pocket refractometer (107, 109, 118, 255, 292). The biochemical composition of the nectar is usually detected using chromatographic techniques (291) and a variety of other detection methods, depending on whether sugars (227) or amino acids (15, 16) are the components of interest.

It is assumed that 1 mg of sugar, regardless of type, yields about 4.0 cal., probably a reasonable estimate for most ecological questions. However, in honeybees, for example, there are physiological differences in the ability to taste (93), live on (270), and utilize in flight (187) various sugars, some of which are found in nectars. Hummingbirds void essentially no sucrose from the cloaca, implying that nearly all ingested is fully utilized (110). Generally, the sugars found in nectars are the ones for which honeybees have the greatest preference (290, 291) and the ones most readily utilized (187, 270). To honeybees, mixtures of glucose, sucrose, and fructose are more attractive than the individual sugars (290), but hummingbirds prefer pure sucrose (256).

The total caloric rewards available in flowers vary greatly. For example, nectar available in flowers of different plants in Central America (106, 107, 132, 255) varies

from less than 0.03 mg to approximately 1800 mg in *Ochroma lagapus,* a range of 60,000 times (P. Opler, personal communication). Most Holarctic flowers of the north temperate (29, 33, 74, 93, 125, 152, 228, 244) and Arctic regions (137) contain <1 mg sugar per floret and are visited by bees. The amount of sugar in "bird flowers" (12, 109, 255) is considerably larger than that in "bee flowers," although it overlaps with them. "Bat flowers" contain some of the largest amounts of sugar. Up to 15 ml of nectar is produced per flower per night by some bat-pollinated flowers in West Africa (17) and Costa Rica (132). As is discussed later, the amount of nectar per floret is undoubtedly only one of several variables affecting the profits that a flower visitor can obtain from a given plant.

The concentration of the nectar of open flowers is highly variable, ranging from less than 10% to near 80% (33). In part, this range is known to be caused by environmental conditions that foster desiccation or dilution (216, 242). However, the concentration of nectar in flowers with tubular corollas is much more independent of environmental conditions. In bird, bat, and "butterfly flowers" (275), the nectar is usually dilute (15–25%), whereas that of bee flowers is often more than 50% sugar. Environmental factors affecting nectar secretion have been discussed (142, 245).

Whether or not a given caloric reward is presented as dilute or as concentrated solution is important in the energetics of foraging. Sugar presented in dilute solution sets an absolute limit on the amount that can be taken at any one time. Since endotherms require more food energy at low temperatures than at high, it is of interest that nectar from high elevation hummingbird flowers tends to be more dilute than that from low elevations (106). Baker recently suggested a possible functional significance for this difference (14). The rate of nectar uptake by hummingbirds is markedly dependent on its viscosity (106), which is temperature-dependent. The lower temperatures in the highlands increase the viscosity of the nectar, but the lower concentrations produced counteract this effect so that the rate of uptake can remain high.

There is some evidence to suggest that alpine plants produce more nectar than those of lower elevations (245, 261), and that those plants residing north of the Arctic circle produce more than those growing at lower latitudes (137). Nevertheless, honeybees do not accumulate much honey north of the Arctic circle (138), presumably because low temperature either greatly restricts their activity or requires them to consume honey for temperature regulation as fast as it is collected. Bumblebees, on the other hand, because of their prodigious endothermy, are able to forage for 24 hr a day in the Arctic, even at ambient temperatures below the freezing point of water (43, 237), and they have been observed foraging in rain and snow (286). Some minimum amount of nectar must obviously be present to attract pollinators, but the range of nectar amounts within which pollination is optimal may be narrow and variable from one locality to the next.

Several attempts have been made to relate seed with nectar production in genetic strains of plants varying in nectar production, but the results have not been clear-cut (223, 224). However, recently F. L. Carpenter and R. E. MacMillen (personal communication) have measured seed-set in Hawaiian Ohia trees (*Metrosideros col-*

lina) as a function of nectar availability, and found that seed-set declines significantly above and below some optimal degree of nectar availability.

Pollen is an important food reward in many flowers. With some exceptions (53), however, its importance is not in its energy content, but in its protein, which is used for egg maturation and larval growth. Pollen is probably a relatively more important food item for solitary bees than for social bees. A considerable portion of the energy resources collected by social bees is used in heating the nest (89, 117, 121), which accelerates brood development. This energy is derived from sugar. The solitary bees, which dispense with such energy expenditure, accumulate only enough food reserves in the nest to feed the larvae, and should thus have a much smaller need for food energy than do social bees.

For social bees, the demands for food energy are often so great relative to protein that pollen often appears to be collected only incidentally to nectar collecting. It is often discarded, and it thus has been concluded that nectar is the primary attractant for honeybees to flowers (226, 228). Free (81) observed that honeybees collect pollen only when there is no nectar, but Gary et al disagreed (97). It is probable that no generalities can be gleaned from isolated examples, since the preferred foods depend on needs in the hive (84), which vary greatly from one instance to the next.

The total amounts of pollen produced by some flowers have been measured (53, 173, 225, 266). Honeybees take approximately 1000 pollen grains from a flower of *Trifolium pratense,* visiting on the average 284 flowers per load in 24 min (44). *Colias* butterflies visiting *Phlox glabberima* unintentionally take a similar number of pollen grains from each flower (173).

The labor required to collect a load of pollen is often less than that required to collect a load of nectar. A pollen-gathering bee, for example, may only visit 7–120 apple blossoms per trip; one collecting nectar visits 250–1446 (234). But bees collecting pollen pollinate a greater percentage of the flowers they visit (83). Honeybees foraging from vetch (*Viccia* sp.) visit the same number of flowers per unit time whether they are collecting only nectar or both nectar and pollen (277). Weaver (279) has shown that 1 lb of white clover honey represents approximately 17,330 foraging trips. Since bees visit about 500 flowers during an average foraging trip of 25 min, each pound of the honey represents the food rewards from approximately 8.7 million flowers, and 7221 hr of bee labor. As long as energy supplies are limiting, as they often are to social bees, the supply of pollen is usually secondarily limited.

FORAGING PROFITS

The foraging profits of individuals are ultimately related to reproductive or hive success; several studies have linked the two. For example, time-labor factors of individual honeybee foragers on selected crops (219, 279) and as a function of flight distances (30, 31, 68, 69, 236, 237) have been translated to total honey production per hive. More recently, time-labor factors of flower visiting by birds in relation to nesting have been investigated (53, 254).

Factors affecting foraging profits of individuals are examined more specifically below. Foraging economics of honeybees (276, 277, 279), bumblebees (118, 120,

125), and hummingbirds (107, 221, 254) on different plant species have been calculated. It is not necessary that a forager be rewarded at every flower it visits. Honeybees visit and pollinate the flowers of a nectarless variety of muskmelon, but only as long as those flowers are intermingled with others bearing nectar (37). The precise mechanisms whereby bees assess the suitability of flowers are not known. However, bees can learn to associate a scent (158) or a color in a single reward during the 2 sec before feeding (204). The information resides initially only in the short-term memory, from which it fades within a few minutes (205). It can be assumed that the rate at which the reward is presented or becomes available must not drop below a minimum dictated by short-term memory in order for conditioning to occur. (Long-term memory may last for a month.) The food rewards that a given plant species yields must ultimately be assessed in terms of the quantity that can be collected per unit time. This quantity is a function of the distance between florets and the speed with which food can be extracted from them. For example, bumblebees usually visit the flowers of *Chelone glabra* at only 2.8 per min, in part because up to 30 sec may be required to enter a single blossom (127). The relatively great effort required to search for and enter the widely distributed blossoms may be energetically worthwhile since each blossom (foragers excluded) contains on the average 3.3 mg of sugar. In contrast, *Trifolium pratense* may contain only 0.05 mg of sugar per floret, but the florets, arranged into inflorescences, are probed at a sustained rate near 40 per min by the long-tongued *Bombus fervidus.* While foraging from capitula of *Hieracium* sp. (Compositae) growing in patches, the sustained rate of probing florets by short-tongued bees (*Bombus terricola*) averages 110 per min. The amounts of nectar per floret of *Hieracium* are minute (usually not visible to the unaided eye). The high rates of probing, probably necessary for an energetic profit, might not be possible if the florets were not in dense inflorescences and the plants in relatively dense colonies.

The absolute distance between flowers and the ease of entry into them may not always be the only relevant variables to foragers. The effective distance is related to the time of flight from one flower to the next, and larger objects are more attractive from a distance and are visited by a more direct line of flight than small ones (161). It is of critical energetic importance that flower signals be conspicuous, so that search times are minimized and the line of flight from one flower to the next is direct and unimpeded. Ideally flowers should be located outside the foliage and marked by color patterns that contrast sharply with the background. As Lovell has indicated, conspicuousness has a profound effect on the rate of food discovery (189–191). Thus, if the rewarding flower is not conspicuous, the forager may fail to detect it and continue foraging from less rewarding flowers.

Crowding of flowers into inflorescences, or the presence of large petals, makes targets more conspicuous to potential flower visitors from a distance, thus aiding discovery (286) and shortening the flight path between successive flowers visited. However, a large target at close range obscures the "bullseye"—the nectar or pollen source. Additional time and energy is saved by close-in signals. The honey guides (58, 199, 251) and scent guides (7, 182) act to direct the movements to the nectar

without delay. Since the forager can visit more flowers when its time at each is decreased, the flowers could produce less nectar, and the pollinator could visit more flowers while maintaining a similar profit margin.

The rate at which florets can be manipulated, which could make the difference between profit and loss (125), depends also on various morphological features of the flowers and foragers. Hummingbirds, for example, are able to extract nectar from flowers of a wide range in length of corolla tube. However, the rate at which the nectar can be extracted decreases markedly with increasing corolla length for a given forager (109). Similarly, the rate at which different species of bumblebees manipulate the florets of *Trifolium pratense* is directly related to tongue length (see 140 for review). Rates of visitation of short-tongued bumblebees to campanulate flowers of *Uvularia sessifolia* may be sufficiently low so that they are energetically "excluded," although physically only impeded (125).

Hummingbirds need only to maintain a daily energy balance at which input equals output. During the breeding season, however, the net profit must be sufficient, after individual energy requirements are met, to leave time for territorial defense by males and for insect catching to feed the young by females. Total energy expenditure is approximately the same in the breeding and nonbreeding seasons, but the time allocated for different activities shifts (253, 254).

For Lepidopterous pollinators, some foods required for reproduction are drawn from energy stores derived from leaves on which the larvae have fed. Some moths rely on these reserves for their entire food supply. Other moths and butterflies (275) may lay a few eggs without feeding, but their life spans and reproductive potentials are greatly reduced unless they feed (99).

Heliconius butterflies have lifespans possibly longer than 6 months (98), during which food reserves accumulated from the larval stage are exhausted and the insects rely nearly exclusively on the food derived from flowers, both as a protein source for egg production and as their energy source. These butterflies provide an interesting contrast in their relations with their hosts compared to high-energy hymenopterous pollinators. Because of their slow gliding flight and their small energy investment to offspring, spread out over a long time, their rates of energy intake and expenditure are very low. The butterflies readily meet these requirements by visiting less than a dozen flowers a day, whereas a bumblebee may have to visit some flowers in its habitat at a rate of 10–20 per min to make an acceptable energy profit (125).

A social bee worker must collect food energy in great excess of what it expends (95), and is usually also under the rigid constraints of time, particularly where the environment is marked by seasonality. Such a time limit may be particularly severe in bumblebees, which must bring in sufficient profit to allow rapid buildup of the colony, followed by the production of reproductives, in a single season (231). The foraging speed in different bees may be a reflection of selective pressures on foraging profits. *Bombus* visits flowers at nearly twice the rate of honeybees (41, 66, 86), and the rate of foraging of a variety of solitary bees (289) is at least half that of honeybees and often less than one-fourth that of a *Bombus* (127). Although the parasitic bumblebee *Psithyrus* is similar in size to eusocial bumblebees, its rate of flower

visitation is several times lower than that of *Bombus* on the same species of flowers (B. Heinrich, unpublished). *Psithyrus* does not need to collect a large profit since it does not feed its own larvae.

Because of their large size, some sphinx moths, birds, and bats have very high net rates of energy expenditure relative to the food energy of most flowers. One of these pollinators weighing 3 g, for example, expends approximately 11 cal per minute of flight, which is energetically equivalent to the sugar contained in 15 μl of a 20% sugar solution. Due to the high rate of energy expenditure during locomotion, the heavier animals must necessarily have high rates of food intake; this can be accomplished by visiting only flowers with high food rewards or visiting flowers at a very rapid rate.

Hovering greatly accelerates the rate at which flowers can be visited. The ruby-throated hummingbird (*Archilochus colubris*), for example, may visit *Impatiens biflora* blossoms at a rate of 37 per min, whereas bumblebees foraging from the same flowers at the same place and time visit them at 10 per min (127). However, although hovering permits the making of a rapid profit when food rewards per flower are ample, it is also the most rapid means of accumulating an energetic debt when they are not.

When flowers are tightly clumped, as on compact inflorescences, a forager that perches presumably can visit as many florets per unit time as a hoverer, but without incurring the high energetic costs. Thus the hoverer necessarily reduces the spectrum of flowers from which it can forage, but it has an energetic advantage over others. While foraging from large inflorescences, bees have the option of reducing both the percentage of flight time and their body temperature, and energy expenditure could drop nearly an order of magnitude while nectar gathering on a restricted group of flowers continues (118). Torpor during foraging (118) appears to be a reserve mechanism observed only if high-energy flowers are no longer available in the habitat. These mechanisms may permit the animals to maintain an energy balance, but probably preclude them from making a rapid profit. Analogous low energy foraging behavior is observed on a continuous basis in ants foraging from *Polygonum cascadense* (Polygoniaceae) (133).

Foraging profits by social insects depend markedly on the distance of the food source from the hive. The energy expenditure in flight to and from the hive, though great, is often negligible in comparison to the food energy that could be collected during the same time (30, 32, 277). For example, a bumblebee visiting 40 clover blossoms per minute (66) potentially collects enough sugar (2 mg) in this minute for 6 min of flight, that is, for one round trip to a food source nearly 1 km from the hive at a speed of 18 km/hr (61). However, a foraging distance of 1 km costs the bee 6.7 min of foraging time equivalent to the nectar content of 267 clover blossoms. Thus at 1 km from the hive, the clover blossoms are worth much less energetically than they are at 0 distance from the hive. Eckert (68) has calculated that when a food source is 2–3 km from the hive, a honeybee can make 20 round trips per hour, but at a distance of 14 km it can make only 1 trip per hour. Beütler (30) reached similar conclusions and Hamilton & Watt analyzed more general aspects of resources and foraging distance (112).

In view of these time-energy relations, it is perhaps not surprising that bees have a strong preference for foraging close to the hive (90, 97, 167, 177). Ribbands, in a review on foraging distance (235), concluded that 0.4 km is a reasonably "economical" distance for foraging. However, whether or not a given distance is economical depends on the amount of sugar with which the bee can return, which in turn depends on honeystomach contents and nectar concentration. At a distance of 1.2 km, hive gain may be reduced by 32% in a good year for nectar and up to 83% in a poor year (235, 236).

The amount of food brought back appears to be maximized in that the bees start with a relatively "empty" honeystomach, although they take more sugar with them before departing to collect food from a dish at a great distance than at one nearby (30). During a good honeyflow, honeybees weighing approximately 70 mg when empty return on the average with about 27 mg nectar in their honeystomachs (capacity is 40 mg). During a poor honeyflow they return with about 12 mg (95).

Foraging Strategies

The flowers of different species of plants in any one habitat may provide nectar, pollen, or both, and are generally of diverse morphology. A large range of behavior is required to harvest the food rewards (124, 127).

The food rewards of flowers are not visible from the exterior. They are of widely varying quantities and are distributed in numerous ways, ranging from dense aggregates of tiny droplets to widely distributed high-energy packets. How the foragers go about harvesting these resources profoundly affects their energy balance and the minimum amounts of food acceptable to them.

Although the ways in which profits or potential profits are assessed by the flower visitors are not known, it is obvious that they decisively affect behavior. A honeybee's recruiting (94, 214) and foraging intensity (278), flight speed (94), volume of nectar uptake (93, 213), and flowers visited (45, 267, 268) are markedly affected by both the amount and the concentration of the available food resources. The distances flown (68, 69, 235) and the weather conditions acceptable for foraging (90, 167, 168, 177) also depend on the relative value of the food resource. Few bumblebees forage for food resources yielding low caloric rewards at low ambient temperatures, where they must expend energy for thermoregulation (118) and would not make caloric profits. On the other hand, they forage for similar food rewards at higher ambient temperatures, where a small margin of profit can be made (125). Foraging on marginal food resources, however, is usually not initiated if more rewarding food from other flowers is available (127). The greater the food rewards of the flowers, the more energy the bees are willing to expend to produce a higher body temperature, resulting in a higher flight speed, greater rate of flower visitation, and the ability to carry greater loads of nectar (123). In stingless bees (Meliponinae) in Central America (148) and in hummingbirds (253–255), the amount of energy used in aggression and defense of food resources also depends markedly on their caloric worth. Competition for food resources by *Bombus* is primarily by way of foraging efficiency. Aggression between them, although not unknown (42),

is rare in most species; it has not been observed as a consistent feature of their behavior on any of over 100 species of plants in Maine (127). The food rewards of flowers in the north temperate regions are usually minute and probably not worth defending. Also, defense of foraging areas requires efficient recruitment (148), which has not been observed in bumblebees. However, given a comb of honey available to both *Bombus* and honeybees, the honeybees will attack the larger bumblebees (141).

Flower Constancy

An individual forager has, at any one time, a limited repertoire of behavior. Bees specialize, and aspects of their flower constancy have been reviewed (87, 102). Flower manipulation and the rate at which food is harvested, involves learning (134, 162, 279). Furthermore, bees (Apoidea), Lepidoptera (104, 275), and possibly other flower visitors, acquire a "search image" (as do predators) (212, 247) during foraging, as they learn to be attentive to specific stimuli associated with their food items. Presumably both recognition of specific flowers and their manipulation are sharpened during flower fidelity and increase the amount of food that can be collected from the flowers per unit time.

The immediate reasons for restriction of foraging, at least for some periods of time, to specific species of flowers are varied. On the one extreme are some solitary bees that fly only for a short time of year when their hosts are in bloom. These bees usually do not visit a great range of different flowers and often have preferences for pollens from specific plants (36, 57, 143, 184, 185). Possibly, such preferences in the adult could arise, in part, from larval food conditioning, as in blowflies (62), but this has not been investigated. Honeybees forage for a great variety of plants occurring throughout the season (258), but they have weak spontaneous preferences (65, 179) biased toward native flora (159). In the honeybees, the weak inborn preferences have been exploited through selective breeding to produce lines preferring alfalfa, *Medicago sativa* (197, 215). Different lines of honeybees also have different "preferences" for red clover (*Trifolium pratense*), probably based on relative tongue and corolla lengths (3). The selectivity of the bees, as in other animal foragers (71), is reduced or obliterated when the availability of food is low (76). In some habitats, there may be only a few plant species suitable for a flower visitor, and the flower visitors are then relatively faithful because of exclusion from alternate food sources.

A third type of flower constancy is on the basis of the individual, within a less constant species. It arises from recruitment and conditioning. Individual honeybees are specialists (82). In any one hive of social bees, different individuals may forage from different species of flowers, even though the availability of specific foods is communicated. Attempts to condition honeybees to selected crops have had limited success (80). Unlike those of solitary bees, the social bees' long-term food requirements relative to the flowering period of most species of plants do not allow close species-specific foraging fidelity; the bees of a colony must "track" the different plant species blooming one after another throughout the season (96, 197). Despite the probable energetic advantage of innate responses giving "errorless" foraging behavior at specific plants, the behavior of the foragers must be relatively plastic particularly in noncommunicators such as bumblebees that rely on a succession of

rewarding flowers. Innate preferences would cause them to dismiss many potential sources of food. Although species-specific preferences are observed in bumblebees, these are usually attributed to differences in ease of nectar extraction, which is related to tongue length (39, 42, 134, 135). The relatively pure pollen loads of honeybees, in contrast to the mixed pollen loads of bumblebees (4, 23, 78, 79, 87, 102, 193) that consist of 1–7 plant species (40, 114), may indicate that individual honeybees are more flower constant than bumblebees. The pollen carried by honeybees is about 3% mixed, but in bumblebees it may be 32% mixed (28). However, if the contents of the pollen loads are a function of the propinquity of flowers at the foraging site, as Betts suggested (27, 28), then the availability of flowers of different species at the foraging site and differences in size of the foraging areas between honeybees and bumblebees could affect the purity of pollen loads.

"Majors" and "Minors"

In a given area containing numerous species of concurrently blooming plants, some individual bumblebees restrict themselves primarily to one species, their "major" (124). Other bees at the same site may have different majors. However, unlike honeybees, most individual bumblebees also have second and third specialties, their "minors." The latter are visited at relatively low frequency unless they suddenly provide more food (B. Heinrich, unpublished).

Whether or not a bee adopts a given plant as its major depends, in large part, on the food rewards it encounters. If the bees forage where they make the most profit, why do some individuals major from some flowers of low nectar production in the same area where there are flowers of high nectar production? The most obvious answer is that any one area contains many bees that deplete the nectar-rich flowers first, so that all of the flowers are eventually nearly equal sources of food to unspecialized bees that begin to forage and sample the flowers for the first time. It is to their advantage to specialize, even to flowers of lower nectar production. When the high-yield flower species are already occupied by a high population of bees, it matters little on which flower the newly-fielded foragers specialize. Consistent with this hypothesis is the fact that nectar-poor flowers are sometimes entirely avoided in those areas where high-yield nectar flowers occur, while they may be mobbed with bumblebees in other areas where the high-yield flowers are absent or where the bee population is very high (B. Heinrich, unpublished).

Minoring and sampling involve some cost in comparison to strict specialization at any one time. However, the cost may be necessary in the absence of communication such as that of honeybees, for each individual bumblebee must rely on its own foraging experience to find the best food resources from flowers. Majoring on the appropriate flower species, arrived at after sufficient sampling, is the best strategy as long as the flowers remain in the field. However, the flowering season of some plants is short, and rich resources could be missed if the bees did not sample new flowers as they appeared.

Spatial Constancy

Like flower specificity, site specificity reduces a forager's random movements, permitting it to maximize the energy return per given energy investment. Thus individ-

ual honeybees may restrict successive visits to the same highly rewarding flowers of a saguaro cactus (201) and they may return from one day to the next to within 5 yd of where they were marked in a patch of *Epilobium* (46). While flower constancy reduces uncertainty in food uptake arising from physical differences in the flowers, site fidelity reduces uncertainty in food uptake arising from spatial heterogeneity.

The site constancy of honeybees has long been known (48, 206) and has been of practical interest in the production of genetically pure crop plants. Optimum planting practices to avoid "contamination" have been studied using genetic marker plants (2, 6, 38, 56, 75, 285) and dyes (147, 259). For the most part, contamination drops off precipitously 10 m beyond the marker plants, as in wind pollination (21, 22). Contamination of insect-pollinated crops is more dependent on the number of flowers within a plot than on isolating distance; seed plots of clover with few blossoms results in high contamination up to 450 m (285). Gene dispersal by way of insect-dispersed pollen has also been studied in nonagricultural situations using genetic markers (153); vital dyes and radioactive pollen have been used to study pollen dispersal by hummingbirds (183, 239). Although it is clear from these and many other studies that many pollinators are highly site specific, numerous data indicate that site specificity is reduced as the food resources become smaller or more dispersed (38, 46, 178, 201, 207, 276). Despite the high site specificity of flower visitors, pollen is occasionally transported 1.6 km (38), perhaps by wandering pollinators. Predominantly self-incompatible *Oenothera organensis* sets abundant seed even on plants isolated in separate canyons (70). The sphinx moths, its pollinators, may be less site specific than social Hymenoptera associated with nests.

Another aspect of site specificity is the tendency of many pollinators to repeat specific foraging paths. Foraging paths probably can be considered as elongated foraging areas, in that a path consists of a number of spatially separated foraging sites, no one site containing sufficient food to provide all of the animal's needs. Indeed, the spatially separated plants visited by Euglossine bees in the Central American tropics provide only a few blossoms at any one time, forcing the bees to move from one plant to the next (145). Visiting the different flowers or flower patches in sequence rather than at random reduces the probability of revisiting empties and allows maximum time for refilling in the flowers visited. However, the effect is reduced if many individuals utilize the same flowers, unless they forage in groups, as has been observed in some bats (132). Other bats trap-line singly (13).

Group-foraging bats reappear at specific flowers at regular intervals. Heithaus et al (132) pointed out that the foraging strategy appears to be similar to that proposed by Cody (54) for flocks of finches foraging for a different renewable resource (seeds) in the Mojave desert. Many days may elapse before given desert plants mature more seed, and the same area is picked over by birds again. However, most flowers produce nectar for many hours, and the bats appear at the flowers at regular intervals during the same night. Bumblebees also learn the location of individual plants, visiting them in sequence (200). However, they often repeat the same foraging path several times during a single foraging trip (127).

Foraging along specific paths may be more ubiquitous in the tropics than elsewhere. The behavior appears not only in bats and bees, but also in some humming-

birds (255), butterflies (99), and possibly sphinx moths (132). Many of the flower resources utilized by trap-lining pollinators in the tropics occur in relatively isolated calorically rewarding packets; the food from "mass-flowering" species is not harvested by trap-lining pollinators. In the tropics, the probability of food rewards at a given site remains high for a long time, since plants may remain in bloom for several months (99, 145, 230, 255). All of these factors, which probably encourage trap-lining behavior, are less likely in temperate regions with their typically dense and ephemeral carpets of bloom.

Site constancy as a component of the forager's harvesting strategy involves knowledge of more than the location of a foraging site and the location of flowers within this site. The learning of spatial inter-relationships on the blossom itself should affect movements and hence yield. At least to the human observer, the numerous florets on an inflorescence look similar. Presumably a forager cannot determine which of them contains nectar until it probes, and the manner in which an inflorescence is manipulated should affect the percentage of "empty" florets encountered. The fewer the probes, the less likely that the florets will be revisited but the greater the energetic cost of flight during foraging, as more inflorescences need to be visited. Also, the more random the probing, the more empties will be encountered. It can be predicted that when the rewards per floret are rich, profits would increase if the florets were probed in a pattern, and if a high percentage of the available florets were probed.

Numerous observations suggest that such optimization "strategy" is used by bees foraging from inflorescences. For example, bumblebees usually first visit the lower flowers of vertical inflorescences, gradually working up from the older to the newer blossoms. The arrangement of the flowers acts to minimize revisitation of freshly emptied florets. Furthermore, since in many cases the anthers of the florets mature before the pistils (protandry), pollen is carried from the uppermost flowers of an inflorescence of one plant and deposited on the stigma of the lower flowers of another (157).

When foraging from the horizontal inflorescences of composites (in which florets mature at the periphery before they do in the center), bees probe the florets at the perimeter of the blossom in an approximate circle. The individual florets usually contain only minute amounts of nectar, and in *Hieracium* sp. only 13% of the 43 open florets per blossom are probed by bumblebees (127). On *Trifolium pratense,* the bees visit 18% of the 30 open blossoms per inflorescence. However, they visit 81% of the 6.2 florets on the inflorescences of *Prunella vulgaris,* which have relatively large amounts of nectar. In the latter flowers, the energetic cost of revisitation of a flower is small in comparison to the possible reward of probing an unvisited flower. However, most bees visit most of the florets on an inflorescence without revisiting empties, which suggests that they can keep track of the florets they have already visited. Recently Ortiz-Crespo (personal communication) determined that captive hummingbirds have the ability to avoid some of the flowers they have visited previously. The ability to avoid revisiting a proportion of empties is also possible without exact knowledge of the location of each flower in a clump, if the animal visits flowers in a small area, moves to another area, and subsequently avoids the first area. Such behavior is facilitated if the forager holds a territory, follows a foraging path, or has other site specificity.

FLOWERING STRATEGIES

The evolution of the various aspects of a plant's flowering biology is molded in large part by the foraging behavior of the flower visitors. The flowering biology will, in turn, influence the foraging behavior of flower visitors. However, the flowers can be considered the "active" partners in the evolutionary relationship in that they have retained those features that promote cross-pollination.

One of the prerequisites for the evolution of a successful pollinator-plant relationship is at least temporary fidelity of the flower visitor. Such fidelity is based, in large part, on the availability of a minimum food reward. In an area containing numerous species of competing plants, the precise amounts of food that a pollinator encounters per blossom may be of critical importance to ensure continuing fidelity. However, if some of a plant's flowers are emptied, the energetic balance could shift so that the plant cannot be visited repeatedly on a sustained basis.

Uniformity in Food Rewards

A tightening of the energetic "fit" between a plant species and the energy needs of its pollinators depends on maintaining the mean food rewards per flower constant. Such a fit may be achieved by a variety of mechanisms involving flower morphology, signaling devices, blooming times, or combinations of these.

In view of the attractiveness of nectar and pollen of a given species to nearly all flower visitors, those flowers pollinated by high-energy pollinators offering high food rewards must evolve mechanisms to exclude other primarily low-energy foragers. The long tubular corollas of "hummingbird" and "hawkmoth" flowers have probably evolved as mechanisms to exclude flies, bees, and other nonpollinating foragers ("nectar thieves"). Chemicals acting as poisons to some foragers (16, 67, 218, 266), and "nectar guards" (151) may have similar functions. The exclusion is seldom absolute; nectar thieves learn to breach these morphological barriers (82) and, when little else is available, foragers will gather poisoned nectar (67). However, as long as some nectar thieves are excluded at some time, the mechanisms may have adaptive significance. In some cases, however, nectar robbing may not be as deleterious as supposed. For example, seed production in red clover may be increased rather than decreased in the presence of nectar robbing bees (115), suggesting that the flowers provided more than ample nectar and that lower nectar availability to the actual pollinators increased their vagility among flowers. In undisturbed environments with native plants and pollinators, however, plants probably do not evolve to have spare nectar to feed nectar thieves, unless they cannot avoid being robbed.

Rather than excluding nectar thieves by physical features, the nectar that a flower produces can be retained for its pollinators by presenting it only at those times when they are active. For example, hawkmoth and bat flowers typically produce their nectar in the evening or at night, or they open their corolla only at these times (17, 73, 132, 217, 233). In some Loranthaceae, the physical presence of the bird (Nectarinidae) is required, as manipulation of the flower by the bird's beak causes it to snap open (63).

As soon as a flower of a plant has been visited and pollinated, its removal would reduce the energetic cost of foraging by increasing the average food reward from other flowers. Several features of flowers with this effect have been observed. Perhaps the simplest is that of ephemeral blossoms such as those *Oenothera,* which wilt a few hours after opening (186). A variation with the same effect occurs when the blossoms remain on the plant much longer when not pollinated, as in *Clarkia* (180, 198) and possibly *Trifolium incarnatum* (34), or when they remain on the plant only until visited and presumably pollinated. In *Helleborus niger,* the sepals are large and white, but after the flower is pollinated they become functional leaves (188). Some orchid flowers live for only 5 minutes, while others last 9 months (230, p. 159).

Wilting physically excludes pollinators from depleted blossoms. But exclusion, resulting in energy economy both to the pollinator and ultimately to the plant, can be achieved also by ethological means. Most pollinators rapidly learn to avoid unrewarding flowers. This behavior is reflected in the signaling by many flowers. Blossoms may change color and markings (100, 146, 243), scent production (182), and geometric outline (146) after being pollinated. Such signaling has recently been shown to restrict bee visitors to the unpollinated (presumably filled) blossoms of two tropical legumes (146). Similarly, bumblebees in Maine restrict their visits to newly opened blossoms of *Rosa nitida,* almost completely avoiding day-old blossoms (127). The energetic advantage of signaling and the resultant behavior is readily apparent from a hypothetical example: If the flowers of a bush are rewarding only on the day they open, but their appearance does not change and they are retained for 4 days rather than 1, 4 times as much nectar per flower would have to be provided to give the same energy reward per unit time to a forager. In other words, if the empties were not advertised as such, the pollinator would be obliged to visit at least three empties for every full one.

A more direct, though perhaps costly, mechanism for maintaining a constant quantity of food reward per flower is refilling stimulated by nectar removal. This has been reported in isolated instances (217). It can be expected that such a mechanism would occur in flowers having poor defenses against nectar thieves or in those flowers that require many pollen grains to set fruit, which might benefit from multiple visits by a pollinator. Watermelon blossoms, for example, require approximately eight honeybee visits before normal fruit development occurs (1).

Uniformity in amount of food reward per flower could also be approached if the food reward per flower were arranged into numerous packets, rather than being concentrated into one. For example, if an inflorescence of 1000 florets is visited by a pollinator that takes nectar from only 10 of them, the amount of food per average floret is diminished by only 1% during each flower visit.

In an inflorescence, "fine tuning" in the amount of food energy available may be achieved by the sequence of blooming in the individual florets relative to one another. The more synchronous the bloom, the more food is available per inflorescence. While it may be necessary for florets of some inflorescences pollinated by energetically demanding pollinators to bloom synchronously, others with similar amounts of food per floret, but pollinated by low-energy pollinators, could bloom over a much longer period of time.

Trees—A Conflict

Large plants such as trees face special problems with regard to cross-pollination by animals. If the amount of food reward per flower and the flower distribution are adequate to attract a given pollinator, they may also restrict it to the same plant. The site specificity of honeybees has long been considered a problem in the pollination of fruit trees when nectar supply is ample or bee populations are low (90, 207). The bees generally restrict their visits to one or two trees per foraging trip (81). At least theoretically, however, honeybees and presumably other social bees could affect some cross-pollination of isolated, widely separated trees even though they restrict their visits to a single tree; because bees carry pollen on their body hairs, the pollen could be exchanged among nest-mates in the hive (91, 92). Bees, if isolated, usually do not carry viable pollen after 12 hr (160), but some pollens are viable for at least 24 hr (77).

In fruit orchards, most of the pollination appears to be accomplished when bee populations are high, the food resources are depleted, and the bees begin to wander (90, 207). These circumstances suggest a possible mechanism for pollination of some massive-blooming trees by normally site-specific bees.

Many forests in temperate regions are composed of relatively few species of trees. The blooming of any one common species could provide a temporary superabundance of food if its flowers offer sufficient food to attract flower visitors. However, the temporary abundance probably could not be locally depleted to create a wandering population of pollinators, since it is unlikely that large pollinator populations would have built up when there are not sufficient flowers to feed them at other times of the year.

It is therefore probable that only a few species can be insect-pollinated in such a situation, and the most common ones would be preadapted for wind-pollination. Many groups of plants that are wind-pollinated in the temperate regions are insect-pollinated in the tropics, and wind-pollination has been considered to be derived from insect-pollination (10, 283). Gregarious flowering has probably been selected in wind-pollinated trees, where staggering of blooms of different species is unnecessary. Most wind-pollinated trees in temperate regions bloom in early spring (283), while animal-pollinated plants bloom throughout the whole growing season, usually one species after another.

It has recently been shown that many trees in the Central American tropical dry forests are outcrossed (24, 77). Massively blooming trees there are pollinated by relatively low-energy site-specific bees (77). One possible advantage of the massive bloom could be that it serves to attract large numbers of potential pollinators. The ample food rewards should initially retain the bees at the same tree and condition them to feed from the flowers of that species. However, having been adequately rewarded at the plant for a period of time, the bees may be motivated to fly long distances to seek another tree of the same species when the local food supply is depleted. Such a "conditioning-depletion" hypothesis presupposes the availability of a relatively large number of flower visitors (only some of which need be the actual pollinators) rapidly depleting the food resources in a synchronously blooming plant.

In this case the "nectar thieves" that remain site specific may aid in speeding the depletion of the resource and promoting vagility of the pollinating bees that move to other trees.

Another strategy for widely separated trees is to provide fewer, but exceptionally rewarding, flowers, and to rely on the highly mobile, energetically demanding pollinators discussed previously. As indicated by Colwell (55), such a strategy presupposes that the flowers can be adequately protected from nectar thieves, and it relies on the presence of long-distance flyers.

One could also speculate that low-energy site-specific foragers could act as pollinators of trees that are also visited by long-distance flyers. The long-distance pollinator could carry pollen from one plant to the next, while the local low-energy pollinators could act as "spreaders" of this pollen to the numerous blossoms of the plant. Suggestive evidence for such a mechanism has recently been found in *Metrosideros collina* (Myrtaceae) visited by honeycreepers (Drepanididae) and insects (52). The flowers of *Metrosideros* provide the relatively large amounts of nectar typical of bird flowers, yet insects are not excluded from them. Seed-set is relatively low in flowers from which insects, which take most of the nectar, are excluded. This might suggest that the insects reduce nectar quantities enough to force most birds to forage from more than one tree (L. Carpenter, personal communication).

Ecological Constraints

Given equal food rewards, foragers adopt the more common flowers as a target, and the rarer suffer a minority disadvantage (171). This behavior presumably has an energetic advantage, for, by visiting the most numerous flowers, the frequency of flower visitation is maximized. It is thus to the plant's advantage to bloom synchronously if it produces low food rewards per flower. By blooming synchronously, a rare plant that does not employ trap-lining pollinators counteracts its minority disadvantage, and one yielding low food rewards per flower may increase the potential profits to acceptable levels for a given flower visitor.

Synchronous bloom, while it may provide an acceptable profit margin to flower visitors, does not necessarily attract them. If the bloom occurs in a time niche already occupied by another plant providing a greater profit, the plant may remain unvisited. But the minority disadvantage can be overcome by Müllerian mimicry (194, 257) or by providing more food reward than competing plants.

Competition of flowers for pollinators has often been observed in environments containing crop plants or introduced species (76, 85, 111). Mosquin (208) observed that in the spring and at the end of summer, the insects in Alberta compete for flowers, but during the summer there is much nectar, and the plants compete for pollinators, leading to selective pressure for earlier and later flowering. Differences in blooming time of 7–10 days may be sufficient to adversely affect pollination (203), and, at least in *Clarkia biloba,* the blooming time can be advanced by one week in one generation by selection of seeds from plants that were earliest to bloom (181).

The hypothesis that the timing of the blooming period of plants has evolved under the selective pressure of the pollinators (172, 238, 257) in the same way that fruiting times may be related to seed dispersal by birds (248, 249) can be investigated by

examining the flowering times of different plant species in different ecological contexts. In the Arctic, with its short growing season, those plants pollinated by bumblebees tend to have overlapping blooming periods during the relatively short growing season (237). In Missouri, on the other hand, there appears to be a peak of blooming in the spring, followed by a second peak in the fall (5). In Maine bogs (undisturbed environment), the flowering of plants is also synchronous, and species bloom one after another from early spring until late fall (124, 127). At any one time, in a given bog, there are usually no more than 3–4 species in bloom, although the species composition of plants varies widely from one area to the next since most of the plants occur in colonies. Some of the shrubby bog plants of the Ericaceae, such as *Rhododendron angustifolia,* form flower buds in the summer and fall, and bloom before their leaves appear in the spring. Others, like *Kalmia angustifolia,* bloom after they have set new leaves, and still others, such as *Chamaedaphne calyculata,* are evergreen. The plant's energy reserves for flowering are thus stored in many species and expended at the appropriate time, presumably when the flowers can be adequately pollinated.

Numerous widely dispersed plants beneath the forest canopy in the tropics rely on trap-lining bees (145), hummingbirds (183, 255), bats (15), butterflies (99), and possibly hawkmoths (132). This foraging strategy necessitates the presentation of relatively high food rewards per flower or inflorescence. The high food rewards per flower, in turn, encourage the evolution of mechanisms to exclude other foragers, thus resulting in closer specialization and one-to-one relationships with specific pollinators (55). A lengthening of the blooming period is encouraged in such relationships, since successful pollination depends more on dependability of a given food reward at all times rather than on avoiding competition from other plant species by blooming in a specific time niche. The plants bloom for long periods, presenting a few blossoms at a time (10, 145, 255). *Anguria* plants pollinated by trap-lining *Heliconius* butterflies, for example, may stay in continuous bloom for several years. Individual inflorescences may present 0.3–0.5 flowers per day for several months (99). In contrast, many dry forest trees present their flowers synchronously (144). Physical features of the environment, as well as seed predators and seed dispensers, possibly also provide selective pressures on blooming times.

Weeds face unique problems with regard to pollination since they usually have not evolved in close association with a particular set of pollinators or competitors. In addition, colonization from a few pioneer individuals has encouraged selfing (11), thus releasing them from dependence on neighboring plants and pollinators. However, those weeds that are outcrossed may evolve mechanisms allowing them to "fit in" in any of a variety of ecological contexts where there is disturbed habitat. Such plants must have competitively superior flowering strategies. In Maine, most of the weedy plants (such as *Rubus hispidus, Epilobium angustifolium, Prunella vulgaris, Impatiens biflora, Asclepis syriaca*) are characterized by having large amounts of nectar and, in most cases, by blooming for a long period of time (127). The flowers are always highly attractive to bees, and in most cases they are considerably more attractive than nonweedy plants. This suggests that the large amounts of nectar and the long blooming period give such plants the competitive edge in attracting pollinators from a wide variety of conceivable neighboring plants.

Flower Variety

Most plant communities contain numerous species of plants pollinated by the same species of pollinators or by different species with similar energy budgets. On the basis of potential food rewards, the pollinators can profitably forage from a wide range of flowers of different plant species. However, the most readily available food rewards usually become depleted (125), and it is to the flower visitor's advantage to specialize to gain an additional small margin of profit.

Forager specialization is economical to the plants since it prevents straying by the foragers that would result in wastage of pollen and nectar (nectar thieving). When straying results in the production of sterile hybrids, the penalty to the plant is considerably greater. It has been suggested that the optimum assortment of flowers in a habitat is one in which straying by the pollinators between different species of plants is minimized (170, 188, 191).

The less diverse the flowers of different plant species in a habitat, the less is the energetic advantage of specialization by foragers, and the greater the potential advantage of flower visitors that wander from one plant species to the next. However, it has been observed that flowers of similar appearance often bloom in different habitats and at different times, and that plants may display floral differences or character displacement in zones of overlap (124, 127, 174–176, 196).

Although flower color is a major signaling mode that acts to allow pollinators to differentiate one species from another, it is not sufficient to prevent straying if other flower parameters are equal. Bumblebees visit different colored morphs of the same species indiscriminately (163, 192), as long as the food rewards of both remain equal. However, they stray little between flowers differing widely in morphology and food rewards, in addition to color and scent (127). There is probably a limit to the number of similar types of flowers than can simultaneously bloom in a given habitat and retain flower-faithful foragers. If so, each type of flower could be considered to occupy a "morphological niche." Each exploits a different pollinator or different specialized behavior of a given pollinator. From the perspective of community ecology, flower constancy, an important aspect of foraging energetics of the pollinators and of the strategy of cross-pollination in plants, may thus provide a mechanism affecting the divergent and convergent evolution of flowers.

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