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Approaches to nectarivore-plant interactions in the New World

Acercamientos a las interacciones nectarívoro-planta en el Nuevo Mundo

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ABSTRACT

During the past two decades, the emphasis of research on animal-flower interactions has changed dramatically. Valuable data continue to be collected using the traditional approach of descriptive natural history: detailing pollination mechanisms, tallying animal flower-visitors, and refining or applying the concept of "pollination syndromes" (sets of floral traits associated with particular animal taxa). Most recent studies, however, utilize animal-flower interactions to make quantitative tests of general hypotheses in evolutionary ecology. Some topics of special interest in recent years are: (1) "coevolution" between plants and pollinators (in particular, the selective consequences to plants of variation in floral traits, or of variation in animal visitors); (2) the relationship between nectarivore morphology and the energetics of locomotion, and the relationship between the animal's energetic requirements (or other nutritional needs) and the food resources provided by flowers; (3) the role of animals in sexual selection among plants and the evolution of plant breeding systems; (4) the influence of animal pollinators on gene flow in plant populations; (5) the determinants of territorial behavior in nectarivorous animals; (6) nectarivore search patterns and the economics of foraging; (7) the relationship between social structure and niche width in populations of flower-visiting animals; (8) interspecific competition and the organization of nectarivore guilds; (9) interspecific competition, interspecific facilitation, and community pattern among animal-pollinated plants; and (10) changes in the ecology of animal-flower interactions among different communities. Many studies utilize techniques that were first developed to study the pollination of crop plants or horticultural cultivars, but few of the recent, conceptual approaches to natural animal-flower interactions have re-invaded applied research.

Two major directions for future research, in fact, are the application of "post-revolutionary" concepts of animal-flower interactions to (a) agricultural research, especially in regions with many animal-pollinated crop plants, and to (b) conservation research, especially research on ecological effects of habitat fragmentation. Other gaps in our knowledge on animal-flower interactions include: (1) the particularly intriguing interactions between hawkmoths (Lepidoptera: Sphingidae) and moth-pollinated flowers; (2) the relationship between the foraging energetics of many flower-visitors and nectar availability in flowers; (3) the ontogeny of foraging in vertebrate (and invertebrate) nectarivores; (4) the short-term and long-term dynamics of nectarivore guilds; (5) the relationship between mechanisms of interaction and community pattern among plants that use the same animals as pollinators.

Key words: Coevolution, competition, energetics, foraging, pollination.

RESUMEN

Durante las dos últimas décadas, el énfasis de la investigación sobre interacciones animal-flor ha cambiado dramáticamente. Aún se sigue colectando valiosa información usando el método tradicional de historia natural descriptiva, es decir, describiendo mecanismos de polinización, contabilizando visitantes de flores y refinando o aplicando el concepto de "síndromes de polinización" (grupos de características florales asociadas con taxa animales en particular). Estudios más recientes, sin embargo, utilizan las interacciones animal-flor para probar cuantitativamente hipótesis generales en ecología evolutiva. Algunos tópicos que han despertado especial interés en años recientes son: (1) "coevolución" entre plantas y polinizadores (en particular, las consecuencias selectivas para las plantas debidas a cambios en características florales, o debidas a variación en el tipo de visitantes); (2) la relación entre la morfología de los nectarívoros y la energética de su modo de locomoción, y la relación entre los requerimientos energéticos del animal (u otras necesidades nutritivas) y los recursos alimenticios provistos por las flores; (3) el papel de los animales en la selección sexual entre plantas y en la evolución de sistemas de reproducción en las plantas; (4) la influencia de polinizadores animales en el flujo de genes en poblaciones de plantas; (5) los factores determinantes del comportamiento territorial en animales nectarívoros; (6) la "búsqueda óptima de alimento", o sea, patrones y economía de la búsqueda de alimento en los nectarívoros; (7) la relación entre estructura social y amplitud del nicho en poblaciones de animales visitantes de flores; (8) competencia interespecífica y la organización de gremios de nectarívoros; (9) competencia interespecífica, facilitación interespecífica y patrones de la comunidad de flores polinizadas por animales; y (10) cambios en la ecología de interacciones animal-flor entre distintas comunidades. Aunque muchos de estos estudios utilizan técnicas que fueron desarrolladas originalmente en estudios de polinización de plantas de cultivo, pocas aproximaciones conceptuales recientes a las interacqiones animal-flor han reinvadido la investigación aplicada.

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Dos de las principales direcciones de futura investigación son, de hecho, la aplicación de conceptos "postrevolucionarios" de interacciones animal-flor a (a) investigación en agricultura, especialmente en regiones con un gran número de cultivos polinizados por animales y a (b) investigación en conservación, especialmente investigación sobre los efectos ecológicos de la fragmentación del hábitat. Otras brechas en el conocimiento de las interacciones animal-flor incluyen: (1) las interacciones entre polillas (Lepidoptera: Sphingidae) y las flores que ellas polinizan; (2) la relación entre la energética de la búsqueda de alimento de muchos visitantes de flores y la disponibilidad de néctar en las flores; (3) la ontogenia de la búsqueda de alimento en nectarívoros vertebrados e invertebrados; (4) la dinámica de los gremios de nectarívoros a corto y largo plazo y (5) la relación entre los mecanismos de interacción y patrón comunitario entre plantas que usan los mismos animales como polinizadores.

Palabras claves: Búsqueda de alimento, coevolución, competencia, energética, polinización.

INTRODUCTION

Interactions between flower-visiting animals and the plants they inadvertently pollinate have intrigued biologists for centuries. Throughout the second half of the 19th century and the first six decades of the 20th, most research on these interactions stressed a botanically oriented approach that fitted descriptive studies into a general evolutionary framework (Baker 1983). By the mid-20th century, a tremendous body of information –and a daunting terminology– had been amassed on "anthecology" of North Temperate and (some) tropical plants (Proctor & Yeo 1973, Faegri & van der Pijl 1979). The mass of descriptive studies and idiosyncratic data threatened to discourage conceptually oriented, hypothesis-testing approaches.

Two decades ago, though, the study of animal-flower interactions was revolutionized by three reviews. Grant & Grant (1965) carefully examined pollination in the plant family Polemoniaceae from the viewpoints of both plants and animal flower-visitors. Baker & Hurd (1968) used a comprehensive, modern ecological framework to discuss numerous features of the micro- and macro-evolution of plant-pollinator interactions. Heinrich & Raven (1972) alerted a wide readership to the role of energetics in animal-flower relationships. These reviews (and others) coincided with the growth of "evolutionary ecology" as a general approach to ecological field studies. Because the underlying concern of evolutionary ecology is the fitness consequences of different "tactics" (*e.g.*, see Schoener 1971, Emlen 1972, Pyke *et al.* 1977, Pianka 1983, Pyke 1984), animal-flower interactions were an obvious choice for investigation: the consequence to plants of ecological events at pollination is variation in seed set or in the genetic "quality" of seeds (Waser 1983b), whereas the consequence to flower-visiting animals, many of them highly energy-limited, is variation in net energy intake (Heinrich & Raven 1972, Heinrich 1983b). At the same time, the theory of interspecific competition came to dominate community ecology (cf. MacArthur 1972, Cody & Diamond 1975, Diamond 1978), and here too animal-flower interactions offered many opportunities for investigation (cf. Feinsinger & Colwell 1978, Waser 1983a).

The 1970s saw an explosion of studies that tested ecological or microevolutionary hypotheses with animal-flower systems. Under the impact of numerous additional researchers in the 1980s, pollination ecology is approaching the status of a "hard" science, with an established theoretical framework (which, of course, is still evolving) and an established research protocol. Rigorous hypothesis-testing studies take place alongside studies on the natural history of new systems. Inferences drawn from studies on animal-flower interactions are increasingly realistic. There is now widespread recognition that pollination is just one step, and often a relatively unimportant step in proximate terms, along the route from flower production by one generation to recruitment into the next (*e.g.*, Stiles 1978, Heithaus *et al.* 1982, Wheelwright & Orians 1982, Rathcke & Lacey 1985). Consequently, pollination ecology is being rapidly integrated into balanced perspectives on plant life history phenomena, plant demography, and other arenas of animal-plant interaction such as seed predation, seed dispersal, and herbivory. Likewise, the realization that animals need not be expected to forage "optimally" at flowers (Heinrich 1983a, cf. Pyke 1984), and that interspecific competition is not a uniformly important feature of animal (or plant) assemblages (Strong *et al.* 1984, Feinsinger *et al.* 1985, Diamond & Case 1986), has encouraged objectivity in recent research on the ecology of flower-visiting animals.

This review will sort recent theory, research approaches, and empirical results into a series of arbitrary categories. Given the breadth of the subject, I can highlight only a few points and only a restricted geographic region (the New World, particularly Central and North America). For more comprehensive reviews, readers should consult Faegri & Van der Pijl (1979), Feinsinger (1983a), Jones & Little (1983), Real (1983b), Willson (1983), Willson & Burley (1983), and Rathcke & Lacey (1985). Furthermore, I will bypass the mass of literature on the intricacies of the pollination event itself, including pollen-stigma interactions, the genetics and evolution of compatibility systems, pollen biochemistry, and pollen tube growth (*e.g.*, Heslop-Harrison 1975, de Nettancourt 1977, Frankel & Galun 1977, Heslop-Harrison & Shivanna 1977, Mulcahy & Ottaviano 1983). With those disclaimers, we can now discuss the evolutionary ecology of animal-flower interactions.

"COEVOLUTION" OF FLOWER-VISITORS AND PLANTS

In broad terms, angiospermous plants and flower-visiting animals undoubtedly influence one another's evolution and have done so at least since the Cretaceous (Baker & Hurd 1968, Regal 1977, Mulcahy 1979). Apparently, though, precise "coevolution" or "reciprocating evolution" (Baker & Hurd 1968) between particular plants and particular pollinators is exceedingly rare. Recent reviews (Feinsinger 1983a, Schemske 1983, Howe 1984a, Kiester *et al.* 1984) point out that plant-pollinator "coevolution" is very diffuse. Most plant demes apparently experience simultaneously the selective pressures from several pollinator populations, whose densities (hence, relative selective impacts) may fluctuate over time, as well as conflicting selective pressures from seed predators, seed dispersers, and neighboring plants. Demes of most flower-visiting animals, free to roam widely in search of the most profitable floral resources, are even less susceptible to selective influences of particular plant species. In fact, I am unaware of any study clearly documenting microevolution in nectarivores in response to the selective influence of particular flowering plants.

Recently, however, several studies have documented (1) geographic variation in floral traits within plant species, apparently as a microevolutionary consequence of spatial changes in the pollinator milieu; (2) the selective consequences, measured by differential pollination success or reproductive output, of intrapopulation variation in floral traits; and (3) the selective consequences of visitation by different animal species.

(1) Many correlational studies exist. Grant & Grant (1965) documented many cases in the Polemoniaceae of intra- and interspecific variation in floral traits that corresponded to shifts in the pool of available pollinators. Miller (1981) showed that elevational shifts in traits of the columbine *Aquilegia caerulea* (Ranunculaceae) corresponded to a shift in the frequency of the hawk-moth *Hyles lineata* (Sphingidae) relative to the frequency of longer-tongued hawk-moths (primarily in low-elevation deserts) or bumblebees (primarily at high elevations).

(2) Waser & Price (1981, 1983b, 1985) showed that bumblebee pollinators were significantly less effective at pollinating rare white-flowered plants than blue-flowered plants in a population of the larkspur *Delphinium nelsonii* (Ranunculaceae). As a result, white-flowered plants set only 30-45% as many seeds as blue-flowered plants, and the authors inferred that the white-flowered morph was maintained in the population only through spontaneous mutation. Paige & Whitham (1985) showed that a population of *Ipomopsis aggregata* (Polemoniaceae) shifted from red to whitish flowers through its flowering season, as hummingbirds became more scarce and hawkmoths predominated in the local pollinator pool; through clever experiments the authors showed that with hummingbird pollination red flowers indeed produced more offspring than white flowers, while the reverse was true late in the season. Schoen & Clegg (1985) documented the effect of flower color on outcrossing rate and reproductive success as a male parent in bumblebee-pollinated *Ipomoea purpurea* (Convolvulaceae); they found that bees visited the pigmented morph significantly more frequently than the white morph, but that both morphs outcrossed at similar rates and the white

morph was actually favored as a pollen donor.

(3) Results of Schoen & Clegg (1985) show clearly that counts of animal visitors to flowers may have little relevance to the importance or effectiveness of different pollinators (also see Kalin-Arroyo *et al.* 1985). This fact was recognized in the 19th century but has been stubbornly ignored ever since, particularly in applied pollination studies, where most studies determine the "important pollinators" of crop plants through tallies of visit frequencies alone. Primack & Silander (1975) provide an objective index for estimating pollinator effectiveness, but it is better yet to measure effectiveness directly by monitoring the reproductive consequences of single pollinator visits (Motten *et al.* 1981, Tepedino 1981, Price & Waser 1982, Handel 1983, Spears 1983). Schemske & Horvitz (1984) used the last method to demonstrate that *Calathea ovandensis* (Marantaceae) flowers visited by euglossine bees had much greater reproductive outputs than flowers visited by butterflies (Table 1). Many more such studies are needed to document the selective forces leading to the evolution of particular floral traits.

TABLE 1

Effectiveness of different visitors as pollinators of *Calathea ovandensis* flowers (Schemske & Horvitz 1984). Hymenoptera included *Euglossa heterosticta, Eulaema cingulata, Exaerete smaragdina, Bombus medius,* and *Rathymus* sp. Lepidoptera included several species of Hesperiidae plus *Eurybia elvina* and *Heliconius ismenius.*

Efectividad de distintos visitantes como polinizadores de flores de *Calathea ovandensis* (Schemske & Horvitz 1984). Los Hymenoptera incluyen *Euglossa heterosticta, Eulaema cingulata, Exaerete smaragdina, Bombus medius,* y *Rathymus* sp. Los Lepidoptera incluyen varias especies de Hesperiidae, *Eurybia elvina,* y *Heliconius ismenius.*

Visitors	Number of visits observed	Total fruits set from observed visits	Fruit-set per visit
Hymenoptera	1,817	140	7.7%
Lepidoptera	757	1	0.1%

BEYOND "POLLINATION SYNDROMES"

General Considerations

Because each taxon of flower-visiting animal has a unique combination of sensory perceptions, energetic needs, behavioral traits, flight capabilities, social systems, capacities for learning, and nutrient constraints, individuals of each will use somewhat different criteria in choosing flowers at which to forage. If each taxon exerts selective effects on the plant demes it exploits, such as the effects documented by Schemske & Horvitz (1984), then widely different plant species sharing a common taxon as "most effective pollinator" (Stebbins 1970) will tend to converge, over evolutionary time, on a broadly similar set of phenotypic features, or a "syndrome" (Faegri & van der Pijl 1979).

The floral features that vary among pollination syndromes, thoroughly reviewed earlier by Faegri & Van der Pijl (1979), have been re-reviewed recently enough that only brief mention needs to be made here. Kevan (1983) and Scogin (1983) discuss the visual cues that attract many animals to flowers and sometimes serve to guide them into contact with the reproductive parts. Both authors stress that different taxa of visually oriented animals perceive the electromagnetic spectrum in a variety of ways, such as bees' well-known ability to perceive ultraviolet reflectance and absorbance patterns. Williams (1983) discusses olfactory cues that attract some animals, in particular the odors that attract neotropical euglossine bees to certain species of orchids; research on odors characterizing other pollination syndromes, and on behavioral responses by other animals, has progressed little since Faegri & Van der Pijl's (1979) review.

Considerable research (some of it reviewed in following sections) has been performed on variation among pollination syndromes in the quantity and constituents of nectar, the usual "primary attractant" (sensu Faegri & Van der Pijl 1979) that lures animals to flowers. Simpson & Neff (1983) describe not only the variation in nectar, but also the occurrence of two much more unusual floral secretions that attract particular bee groups: lipids and resins (see also Armbruster 1984). Simpson & Neff (1983) also review briefly the many cases where pollen, not nectar, is the food resource collected by animals; Buchmann (1983) reviews the phenomenon of "buzz pollination", in which bees induce the release of pollen by clinging to dehiscent anthers and shivering their indirect flight muscles. Finally, the well-known cases where animals use flowers for protection or brood places (see Feinsinger 1983a) have experienced a flurry of recent research. With every new study, interactions between figs (*Ficus*, Moraceae) and the tiny agaonid wasps that pollinate them are revealing greater and greater complexity in such features as phenologies, extent of parasitism, and wasp sex ratios (Janzen 1979, Wiebes 1979, Bronstein 1986). Recent investigations show that the supposedly tight ecological relationship between North American *Yucca* (Agavaceae) and *Tegeticula* moths is actually quite unpredictable from site to site and season to season (Aker & Udovic 1981; J. Addicott, personal communication, 1985). These examples point out the value of long-term, detailed studies on purportedly coevolved systems.

A Few Examples of Syndromes

(1) Many orchids of the lowland Neotropics are pollinated exclusively by male euglossine bees that land on the flower but extract neither nectar nor pollen. Although some bees visit many orchid species and some orchids attract many bee species (Ackerman 1983), in general the fragrances emitted by a particular orchid attract only a subset of the pool of euglossine species in the area. Bees apparently extract either the fragrance compounds or other compounds; it is possible that these are used as precursors to pheromones used in mating (Williams 1983, Williams & Whitten 1983). Current research involves careful characterizations of the chemical constituents of fragrance spectra; intrapopulation variability in fragrance spectra; the biochemical pathway between fragrances (or other compounds) produced by the orchids and the mating pheromones of the bees; and the role of those pheromones in bee behavior (N. H. Williams, personal communication, 1985; cf. Williams 1983, Williams & Whitten 1983).

(2) Hawk-moths (Lepidoptera: Sphingidae) are large, usually nocturnal or crepuscular, fast-flying nectarivores that imbibe nectar through long proboscides. Most flowers they visit have long tubes, are pale in color, and secrete moderate to copious volumes of quite dilute nectar. Hawk-moths and moth-pollinated plants are quite frequent in warm temperate, subtropical, and tropical biota (Gregory 1963-64, Cruden 1970, Cruden *et al.* 1976, Miller 1981, Grant & Grant 1983, Martínez del Río & Burquez 1986). Moth species vary widely in body mass, body and wing shape, and proboscis length (Casey 1976, Bullock & Pescador 1983, Heinrich 1983b, W.A. Haber, personal communication, 1982). Likewise, moth-pollinated plants vary widely in spatial dispersion of flowers, tube length, and nectar production. Consequences and correlates of such phenotypic variation in terms of microevolution of moths and plants, ecology, foraging behavior, community dynamics, and energetics (see section below) have scarcely been investigated other than in the studies cited above and in ongoing work by W.A. Haber (in Costa Rica) and S.H. Bullock (in Mexico).

(3) In Central and South America, large bees pollinate a great diversity of plant species with large, brightly colored flowers (reviewed by Frankie *et al.* 1983). An equally diverse set of plants, usually having numerous small flowers, is pollinated by small solitary, semisocial, and social bees (Janzen 1967, Heithaus 1979a, 1979b, 1979c, Wille 1983). Much research remains to be done on these two "syndromes", for example in terms of floral characters, patterns of nectar production, bee foraging behavior, the influence of bee behavior and sociality on pollen movement, flowering phenologies, and community dynamics of bees.

(4) Butterflies are frequent visitors to tropical and temperate flowers, for example many flowers in the Chilean Andes (Kalin-Arroyo *et al.* 1983, in press). Although some plants appear to be adapted specifically for butterfly pollination (Cruden & Hermann-Parker 1979, Murawski & Gilbert 1986), the diversity of flower forms that butterflies actually visit is quite extensive, ranging from brush-like blossoms on many Compositae and Mimosoideae to tiny flowers of some

Labiatae to the "typical" tubular yellow-on-orange blossoms. Butterflies are critical to pollination among the Andean flora (Kalin-Arroyo *et al.* 1983, in press), but elsewhere the ability of butterflies to carry large pollen loads and transfer them effectively is debated (Murphy 1984). Butterfly pollination remains somewhat of an enigma.

(5) Pollination by hummingbirds (Trochilidae) has been extensively studied in North and Central America. Most hummingbirds that migrate to North America have short, straight bills (Brown & Bowers 1985) and forage at plants having tubular, red corollas of moderate length (Grant & Grant 1968, Brown & Kodric-Brown 1979). In Central and South America and the West Indies, though, hummingbirds have a variety of bill shapes (Feinsinger & Colwell 1978, Stiles 1978, 1981, Snow & Snow 1980, Feinsinger 1983a, Kodric-Brown *et al.* 1984). Most fall into two basic categories, short straight bills (like those of the migrants to North America) and long, often curved bills (suchs as those of the hermit hummingbirds, Phaethorninae). Flowers adapted for pollination by short-billed species tend to resemble their North American counterparts in shape and in rate of nectar secretion, but sport a great diversity of colors. Short-billed hummingbirds also visit a variety of flowers in other "syndromes", such as bee-, moth-, bat-, and passerine-pollinated species. Some short-billed hummingbirds also rob the flowers normally pollinated by their longer-billed relatives (McDade & Kinsman 1980). Long flowers, which include most species of *Heliconia* and representatives of numerous other plant families, come in a great variety of shapes and colors. Most secrete copious volumes of sugar-rich nectar. Several detailed, long-term studies have taken place on particular hummingbird-plant interactions in the West Indies (*e.g.*, Snow and Snow 1972, Feinsinger & Swarm 1982, Feinsinger *et al.* 1982, 1985, Kodric-Brown *et al.* 1984) and Central America (*e.g.*, Stiles 1975, 1978, 1981, 1985, Feinsinger *et al.* 1986), but detailed long-term studies from South America have not been published.

(6) Research on bat pollination, reviewed earlier by Baker (1961, 1973), has increased in recent years (*e.g.*, Heithaus *et al.* 1974, 1975, Marshall 1983, Hopkins 1984, Dobat 1985), but the body of data, like that on hawkmoth pollination, is still less extensive than that on diurnal, more easily quantified interactions.

(7) Other than a possible case of rodent pollination in Costa Rica (Lumer 1980), pollination by non-flying mammals has rarely been investigated in North and Central America. Evidence from undisturbed South American habitats (Janson *et al.* 1981) suggests that pollination by arboreal mammals may have been more widespread before human hunters arrived on the scene, and it is possible that some neotropical trees and lianas currently assigned to bird-, bat-, or even bee-pollination syndromes actually evolved in response to pollination by primates or other arboreal mammals.

How Useful is the "Syndrome" Approach?

Of course, many other pollination syndromes can be identified among New World plants (Baker & Hurd 1968, Faegri & Van der Pijl 1979). In my opinion, however, continued emphasis on "pollination syndromes" is unproductive. Such emphasis leads one to expect animals to use the same set of cues in choosing flowers as pollination ecologists use in assigning plants to syndromes, whereas in reality a foraging animal chooses among potential food items on the basis of perceived benefits and costs. Perceived benefits and costs are determined by many proximate criteria that do not fit easily into "syndromes", such as the dispersion and density of flowers, previous activity by other foragers of the same or different species, and the extent of food limitation. Thus, any one animal may actually forage at a much greater variety of flowers than a "field guide to syndromes" would indicate. Emphasis on syndromes diverts attention from the very real ecological (and evolutionary) role of nectar robbery by animals in the same taxon as, or different taxa from, the "legitimate" pollinator (Baker *et al.* 1971, Lyon & Chadek 1971, McDade & Kinsman 1980, Roubik *et al.* 1985). Likewise, to classify plants into one or another syndrome the ecologist must ignore the many flowers pollinated by two or more distinct taxa, and the different selective effects these may have (*e.g.*, Baker *et al.* 1971, Waser 1982, Schemske & Horvitz 1984). Finally, emphasis on syndromes diverts attention from the unifying concepts that prevail in animal-flower interactions regardless of the taxa involved. The first such concept to discuss is the relationship between metabolic demands of the pollinator and food available in the flowers visited.

METABOLIC NEEDS OF POLLINATORS *VERSUS* FOOD AVAILABLE IN FLOWERS

Not Everything is Mutualistic

From a nutritional standpoint, the mutualism between plants and flower-visiting animals dissolves into a series of skirmishes. In general terms, the most fecund plant phenotype is that which maximizes the ratio [effective pollen transfer/energy expended in attracting pollinators]. The numerator of the ratio is highest if the flower produces sufficient food to attract an effective pollinator, but not so much food that the pollinator becomes sluggish and sedentary (Heinrich & Raven 1972, Carpenter 1976, Feinsinger 1983a). In some flowers, at least, the production of "floral rewards" is costly enough to exert selection for a decreased denominator as well (Southwick 1984). In other words, a famished, harried pollinator is often the most effective from the plant perspective because to achieve a neutral or slightly positive energy (or nutrient) budget, the food-limited animal must visit many flowers.

Naturally, the "optimally foraging" animal will operate quite differently (Carpenter *et al.* 1983, Pyke 1984). It is often assumed that the most fit animal phenotype is that which maximizes net energy intake, the ratio [energy ingested/energy expended], over a fixed time or, under some conditions, that phenotype which minimizes the time spent obtaining a fixed amount of energy. Thus, the energetics of animal-flower interactions involve a delicate interplay between conflicting selective pressures; the balance shifts according to the density of animals relative to flowers and according to many other ecological variables (Heinrich & Raven 1972, Heinrich 1979a, 1983b).

A foraging animal requires many types of nutrition: a balanced intake of different amino acids and/or of protein; vitamins; trace elements or compounds; fatty compounds; and, of course, carbohydrates. Floral nectaries can secrete any or all of these; at present, the limits to what can be secreted are largely unknown. Because carbohydrates seem to be the major "currency" in animal-flower interactions, they have received the most attention from researchers.

Measuring the energy content of nectar

The pattern of carbohydrate production among individual flowers has several aspects, each potentially subject to natural selection, and all of which have ecological and evolutionary implications to animal flower-visitors. These aspects include (1) the volume of nectar a flower secretes; (2) the energy content of each microliter of nectar or of the total volume; (3) the temporal pattern of secretion; (4) the extent of variation among the flowers on a plant, or among plants in a deme, in each feature 1-3; and (5) patterning of this variation within the plant according to inflorescence size, shape, and location.

To measure nectar volumes, my colleagues and I use Drummond brand micropipettes. To extract nectar from curved flowers or other flowers with hard-to-reach nectar chambers, we use flexible Intramedic brand polyethylene tubing; the nectar thereby extracted is then transferred into a Drummond micropipette for accurate measurement. Flowers of many species can be repeatedly sampled; if this is done, cumulative measurements from repeatedly sampled flowers should be compared with total nectar accumulated by flowers unmolested throughout the sampling period, for repeated sampling can either stimulate or depress secretion rates (Feinsinger 1978, Cruden & Hermann-Parker 1983). In other plants, only destructive sampling is possible, so one must begin with a very large number of flowers and then measure the accumulated nectar in a random subsample of these at regular intervals (*e.g.*, Stiles 1975, Feinsinger *et al.* 1982).

A clear distinction must be made between measuring nectar secretion, and measuring nectar availability or standing crop. Secretion patterns provide the baseline data on food presentation by the plant, analogous to "primary productivity" in ecosystem studies. The animal arriving at a flower patch encounters, however, the standing crop, which is a function not only of underlying secretion patterns but also of the foraging by all previous visitors, as well as a function of post-secretion evaporation or dilution (cf. Gill & Wolf 1975, 1979, Feinsinger 1978). Therefore, nectar available to the incoming animal may differ greatly from the pattern in which nectar is secreted (Feinsinger *et al.* 1985), a fact frequently ignored by researchers.

The energy content of nectar can be determined by using a hand refractometer reading in dregrees Brix (percent sucrose equivalence, or weight of solute/total weight solution). I recommend the Reichert (American Optical) Model 10431, a sturdy instrument much less expensive than better-known models but equally accurate; we use clear Plexiglass chips to flatten the nectar droplet against the prism. The reading in degrees Brix is converted to grams sugar/liter of solution, or micrograms/microliter, using Table 88 in the CRC Handbook of Chemistry and Physics (1978-1979). The refractometer reading is located in Column 1 of that table, and the grams sugar/liter (= micrograms/microliter) is read from Column 4 (Bolten *et al.* 1979). One microgram of sucrose provides 0.01648 joules, or one microliter of a sucrose solution that is 1 microgram/microliter provides 0.01648 j. For example, consider a flower that secretes 15 microliters of a 20% sugar solution. A solution of 20% sugar contains 216.2 grams/liter of sugar, or 216.2 micrograms/microliter (CRC Handbook of Chemistry and Physics 1978-1979). Thus, each microliter contains 3.563 j, and the entire volume of 15 microliters contains 53.45 j. The energy content of a given percent sucrose solution is approximately equal to the energy content of the same percentage monosaccharide solution; thus, energy value of nectar is quite independent of the identity of the sugar constituents, although other solutes in the nectar may bias the refractometer reading slightly (Inouye *et al.* 1980).

Pollinator energetics and nectar patterns

How much carbohydrate "fuel" is needed by a foraging animal, and what features influence this requirement? Body size is one obvious factor; all else equal, a large flower-visitor requires a greater energy intake per unit time than a small one. Endothermy, practiced not only by vertebrate nectarivores but also by many flower-visiting insects, requires an additional energy input (Heinrich 1975b, 1975c, 1983b). The mode of locomotion employed during foraging –hovering flight, flapping flight, or landing and walking–affects total energy expended and therefore required. Except for a verbal argument by Heinrich (1975c, 1983b) and a disputed model of Pyke (1981; see Miller 1985), the costs and benefits of these three foraging modes have not been rigorously examined. Continuous hovering flight allows rapid visits and thus high intake rates, but to land instead and walk among flowers obviously conserves energy. Thus, for a bee that lands and walks, or a hummingbird that perches while feeding, foraging at an inflorescence of many small flowers consumes much more time but only slightly more energy than foraging at a single large flower with the same total nectar volume. For a hummingbird or hawkmoth that continues to hover while feeding, though, the time difference translates into a considerable energy difference.

Just how many flowers must a hawkmoth, for example, visit in order to strike a positive energy balance? Moth-pollinated flowers vary greatly in nectar volumes and concentrations (W.A. Haber & G.W. Frankie, unpublished manuscript). Let us use two examples: the herbaceous Costa Rican weed *Hippobroma longiflora* (Lobeliaceae), secreting 40.1 ± 16.0 microliters•flower^{-1}•night^{-1} of nectar with sucrose equivalence 13.6% ± 2.1%; and the vine *Ipomoea alba* (Convolvulaceae), secreting 8.3±2.1 microliters•flower^{-1}•night^{-1} of nectar with 39.0% ± 2.2% sucrose equivalence. Using the method described above (Bolten *et al.* 1979), we calculate that each microliter of *Hippobroma* nectar provides 2.361 j, *versus* 7.53 j·microliter^{-1} for *Ipomoea* nectar. Thus, a full flower provides 94.7 j or 62.5 j, respectively. Casey (1976; also see Bartholomew & Casey 1978, Heinrich 1983b) studied the energetics of hovering in various sphingids ranging from 0.12 to 6.25 g, and found that a 1 gram hovering sphingid uses 1154 – 1593 j·h^{-1}, just to balance the energy expended in hovering. Thus, a 1 g sphingid must visit 12 – 17 full *Hippo-*

broma flowers or 18 – 26 full *Ipomoea* flowers per hour. Undoubtedly, forward flight is less energetically costly than hovering in place (cf. Gill 1985), but also the moth must obtain a positive, not neutral, energy balance while foraging in order to maintain at least a neutral energy balance over the entire 24-hour cycle.

Such estimates of the hawkmoth-flower energetic relationship stimulate many speculations and questions. They imply that sphingids will only bother to visit flowers that secrete quite copious nectar. Even though the speed at which hawkmoths can travel long distances cuts down on their transit costs, they are expected to visit isolated plants only if the reward is correspondingly great; thus, plants occurring in widely scattered populations will experience stronger selection for copious nectar production than plants typically occuring in dense clumps. Hawkmoths are expected to choose flowers having not only high secretion rates but also high standing crops, *i.e.*, flowers unvisited by other sphingids and protected from other nectarivores; thus, hawkmoth flowers might be expected to protect their nectar better (physically, and biochemically through repellent compounds in floral tissues) than flowers in many other syndromes. Like hummingbirds (Diamond *et al.* 1986, Karasov *et al.* 1986), hawkmoths might be expected to process nectar quickly and to extract sugars efficiently, but this has not been investigated; even crop capacities of hawkmoths are unknown, although W.A. Haber (personal communication, 1986) has observed captive hawkmoths imbibing, over a 5 minute period, quantities of nectar equal to their body weight. Presumably, energetic requirements differ between the sexes; this has not been investigated. To cut down costs of thermoregulation and maximize the intake of undiluted nectar, hawkmoths are expected to forage only when weather conditions are ideal; hence, moth-pollinated plants may experience very erratic pollination success (Martínez del Río & Burquez 1986).

Not all hawkmoths have a 1 gram mass. In fact, body size in sphingids spans nearly 2 orders of magnitude. Bartholomew & Casey (1978) present the empirical equation.

$$Y = 1243\,X^{0.81}$$

where Y is $j \cdot h^{-1}$ required for hovering and X is mass in g. Thus, a 0.1 g hawkmoth requires only 192.5 $j \cdot h^{-1}$, whereas a 6 g animal (and some hawkmoths are even larger) requires 5306 $j \cdot h^{-1}$. How do internal diameters of proboscides, and intake rates, vary with mass? This is unknown. Clearly, though, large moths cannot effectively utilize flowers with small nectar volumes. For example, Heinrich (1983b) calculates that a 6 g hawkmoth would need to visit 580 *Kalmia latifolia* flowers each minute just to keep even. Is there a compensatory advantage for large body size? Heinrich (1983b) proposes that large moths can fly farther, in search of nectar sources or host plants for oviposition, than small moths. Furthermore, large moths may have access to richer nectar sources than small moths. Bullock & Pescador (1983) found a significant positive correlation, across species, between wing length and proboscis length; the correlation even holds within species, where individuals may vary more than threefold in mass and twofold in proboscis length (Casey 1976; see also Miller 1981). In general, long-tubed moth flowers provide more nectar than short-tubed species (Opler 1983; Haber & Frankie, unpublished manuscript). At present, though, there is little evidence from the New World that large, long-tongued hawkmoths specialize on long-tubed, richly rewarding flowers, although this relationship apparently does exist on Madagascar (Nilsson *et al.* 1985).

One other morphological feature affects hawkmoth energetics: wing loading, the ratio of body mass to total wing area. Casey (1976) examined moths of similar mass but different wing loading and found that the energy expended in hovering increased sharply with increasing wing loading or increasing wing disc loading (ratio of body mass to the area of the disc defined by the tips of the wings during flight). Thus, moths with long wings expend less energy in hovering than moths of equivalent mass but short wings (Table 2). What are the costs of long wings? Do they enforce slow flight (cf. Gill 1985) and thus increase transit times between far-flung flowers? How do mass, wing loading, and wing disc loading correlate with choice of flower species and flower dispersion? What is the range of hawkmoth "foraging tactics"? The data will be

TABLE 2

Effect of wing length and shape on the power output required to hover, among hawkmoths (Sphingidae) of similar body mass (Casey 1976)

Efecto de la forma y longitud del ala en la potencia requierda para vuelo estacionario en polillas (Sphingidae) de masa corporal similar (Casey 1976).

Species	Mass (g)	Wing span (cm)	Wing loading ($g\ cm^{-2}$)	Wing disc loading ($g\ cm^{-2}$)	Required power ($cal\ h^{-1} g^{-1}$)
Protambulyx strigilis	1.20	12.8	0.057	0.009	5.7
Manduca sexta	1.21	11.0	0.082	0.016	7.7
Agrius convolvuli	1.20	8.7	0.195	0.020	8.7

difficult to collect, but the results are sure to be intriguing.

Likewise, what is the relationship between sugar concentration and flower choice by hawkmoth? Sugar concentration varies greatly among the nectars of hawkmoth flowers (Haber & Frankie, unpublished manuscript). Undoubtedly, internal tongue widths and nectar extraction rates vary greatly among hawkmoths. Perhaps, then, there are parallels between hawkmoth feeding energetics and the much better studied feeding energetics of butterflies. Kingsolver & Daniel (1969) proposed a biophysical model for the mechanics of nectar extraction by butterflies, and after making a number of assumptions proposed that maximum net energy intake would occur at a sugar concentration of 20-25% sucrose equivalence regardless of the butterfly considered. Recently, more sophisticated studies in biophysics and bioenergetics (May 1985b, c, Pivnick & McNeil 1985) have shown that many of the earlier assumptions were unrealistic, and that optimum sugar concentrations varied among butterfly species and even between sexes. Through controlled laboratory experiments in which butterflies' proboscides were inserted into capillary tubes with predetermined flow rates and "nectar" constituents, May (1985a, b) has even determined the fitness consequences of flower choice in butterflies.

Likewise, wing disc loading has been investigated much more thoroughly in another taxon than in hawkmoths. In hummingbirds, wing disc loading clearly relates to the energy expended while hovering (Epting & Casey 1973). Hummingbirds with high wing disc loading (heavy for their wing length) expend more energy than hummingbirds with equivalent masses but longer wings. The most efficient flight speeds of the former, however, may be much higher than those of the latter, so that even if they expend more energy per unit flight time birds with high wing disc loading may cover a long distance with less total energy expenditure (Gill 1985).

At one time it appeared that wing disc loading (and required energy output for hovering) was clearly related to a simple dichotomy in hummingbird foraging behavior: hummingbirds with high wing disc loading defend territories at dense clumps of flowers that yield abundant energy, whereas behaviorally subordinate species or sexes that are excluded from these rich nectar pockets, foraging instead on dispersed, nectar-poor flowers, have low wing disc loading and low foraging costs (Feinsinger & Chaplin 1975, Feinsinger *et al.* 1979b). Continued investigation has revealed a more complex picture. The relationship we originally proposed seems to be restricted to hummingbirds having moderately short, straight bills and foraging primarily at ornithophilous flowers. Small, behaviorally subordinate (in encounters with larger territory-holders), bee-like hummingbirds frequently forage at small insect-pollinated flowers and also tend to have high wing disc loading (P. Feinsinger, unpublished data). Here, high loading may permit exceedingly precise probes into numerous closely packed flowers in rapid succession. Many hermit hummingbirds (Phaethorninae) and other long billed hummingbirds also have high wing disc loadings but are rarely bellicose; for them, the relationship between wing disc loading and most efficient flight speed (Gill 1985) may be most important, for these birds often fly many hundreds of meters between isolated flowers each holding a copious supply of concentrated nectar (Stiles & Wolf 1979, Feinsinger 1983a).

Copious, concentrated nectar averaging around 35% sucrose equivalence at sea level) in fact characterizes most flowers adapted for pollination by long-billed hummingbirds. Until recently this fact (Stiles 1975, Bolten & Feinsinger 1978, Feinsinger *et al.* 1982, unpublished data) was unreconciled with other assertions that most hummingbird flowers secreted quite dilute nectar, averaging around 20-25% sucrose equivalence at sea level (Baker 1975, Pyke & Waser 1981) or with biophysical models showing that the net energy hummingbirds gained from nectar actually declined with increasing sugar concentrations (*e.g.*, Heynemann 1983). In 1982, however, Ewald & Williams showed that at least one hummingbird species fed by extremely rapid licking (ca. 0.06 seconds per lick), squeezing the nectar from the tongue each time the tongue was exserted through the tightly closed mandibles. For the hummingbird examined, each lick meant an intake of about 1 microliter of nectar. Kingsolver & Daniel (1983) showed that, if the nectar volume in a flower was sufficiently small to be extracted with one or a few licks, net energy intake would indeed be maximized (at sea level) at 20-25% sucrose equivalence; but if the nectar volume was sufficiently large to require multiple licks, net energy intake at sea level would be maximized at 35-40% sucrose equivalence! Secretion rates and standing crops in long-tubed hummingbird-pollinated flowers, which also have high sugar concentrations, greatly exceed those in short-tubed hummingbird-pollinated flowers (Feinsinger & Colwell 1978; Feinsinger *et al.* 1982, 1985, unpublished data, Beach *et al.*, unpublished manuscript). Thus, the model fits very well the data on nectar in hummingbird-visited flowers. Apparently the Kingsolver-Daniel (1983) explanation does not extend to hawkmoths, however, for long-tubed flowers pollinated by hawkmoths have more dilute nectar, not more concentrated nectar, than short-tubed ones (Haber & Frankie, unpublished manuscript).

Pollinator physiology and nectar constituents

The chemical composition of sugar in nectar varies widely, and to some extent is associated with pollinator taxon (Baker & Baker, 1983a, 1983b, 1983c). For example, most flowers adapted for hummingbird, hawkmoth, or butterfly pollination are rich in sucrose, whereas those adapted for pollination by bats, passerine birds, or bees are hexose-rich. The distinction between nectars of hummingbird- and passerine-pollinated flowers is especially intriguing: it occurs even among closely related species, such as those in the genus *Erythrina* (Baker & Baker 1983b, 1983c). Current research addresses the physiological basis and behavioral consequences of sugar preferences in nectar-feeding birds (C. Martínez del Río, personal communication, 1986).

Baker & Baker (1975, 1983b) have also performed the definitive studies on the distribution of other organic compounds among floral nectars. In particular, amino acid concentrations and constituents vary widely among nectars, and, like sugars, appear to correlate with expected preferences, of pollinators, considering metabolic needs, requirements of nutrients for reproduction, and the availability of alternate protein sources in the normal diet. For detailed information, readers should consult the Bakers' thorough reviews.

Pollen and animal metabolism

Many animals visit flowers to extract pollen, not nectar (Simpson & Neff 1983). The role of pollen in diets of the bee family Apidae is well known (Vivino & Palmer 1944, Haydack & Tanquarry 1963, Heinrich 1979a). Gilbert (1972) describes the means by which *Heliconius* butterflies extract nutrients from pollen, and describes the consequences of this procedure to the fecundity and longevity of the insects. Through complex laboratory experiments, Howell (1974) detailed the importance of pollen in the diet of female (and male) bats (see also Simpson & Neff 1983). Foraging on pollen is more difficult to observe and quantify than foraging for nectar, which may explain the paucity of research on pollen consumption by animals other than honeybees.

Do plants "manipulate" pollinator foraging?

Let us examine more closely the conflict between patterns of nectar production that maximize effective pollination for plants, and patterns that maximize net energy intake by pollinators. At times, flower-visiting animals, individually or collectively, can "manipulate" plants by choosing the most rewarding food sources and virtually ignoring others, but at other times, when nectar is limiting to pollinator populations, plants can "manipulate" pollinators because at least some pollinator individuals will be forced to forage at plants that secrete just enough nectar to provide a positive energy balance.

An interesting pattern occurs in flowers adapted for hummingbird pollination. Long-billed hummingbirds are only sporadically food-limited (Stiles 1975, 1978, 1981, Feinsinger 1983a, unpublished data). Individuals are very selective among species of long-tubed flowers adapted for pollination by them. Most species of long-tubed flowers secrete high mean nectar volumes with low variance. Short-tubed flowers pollinated by short-billed hummingbirds, however, in habitats where these birds are often food-limited as a group, secrete low mean nectar volumes with exceedingly high variance (Feinsinger 1978, Feinsinger 1983a, 1983b). Previously I interpreted these "bonanza-blank" patterns of nectar secretion as features that created intermittent reinforcement schedules for hungry foragers, prolonging hummingbird attention to flower species having such patterns and maximizing pollen movement while minimizing energy expended on nectar (Feinsinger 1978, 1983a, 1983b, Ott *et al.* 1985; see also Soberón & Martínez del Río 1985). It is likely, however, that plants visited by numerous food-limited foragers simply experience a relaxation in selective pressure to minimize variation, such as the pressure that long-flowered plants presumably experience. To the short-billed hummingbird the standing crop resulting from a bonanza-blank pattern in underlying nectar secretion would be indistinguishable from the pattern of standing crop were all flowers secreting at equal rates, considering haphazard visits from previous foragers. Thus, individuals in a food-limited animal population would be unlikely to discriminate against plants with "sloppy" secretion patterns. Bonanza-blank patterns have also been discovered in plants visited by those bees that are often food-limited at the population level (*e.g.*, Brink 1982, Frankie & Haber 1983, Herrera & Soriguer 1983).

The "bonanza-blank" model extends to interspecific mimicry. Many examples occur of nectarless plants that resemble nectar-producing species flowering nearby (see reviews by Heinrich 1975c, Wiens 1978, Feinsinger 1983a, Dafni 1984). As long as mimic plants are rare relative to rewarding ones, pollinators may fail to distinguish the different species, and the mimic plants could achieve pollination with no energy expended on feeding animals. At this time, there is little evidence that these situations are truly model-mimic phenomena (Bierzychudek 1981a). It is clear, though, that pollinators exert strong selective pressures on patterns of nectar secretion (and, presumably, on production of pollen as food) by plants, and that these selective pressures vary with the relative numbers of pollinators and plants even as this ratio changes through a single flowering season.

THE ROLE OF ANIMALS IN SEXUAL SELECTION AND BREEDING SYSTEM EVOLUTION IN PLANTS

The pollinator:flower ratio, the predictability of pollinator visitation, and the foraging behavior of individual flower-visiting animals may also play a role in the evolution of plant breeding systems. Recent papers propose schemes for animals' influence on the evolution of particular breeding systems (*e.g.*, Beach & Bawa 1980, Givnish 1980, 1982, Beach 1981, Kress 1983, Baker 1984) or, more generally, the evolution of the great diversity of breeding systems that exist among angiosperms (Bawa & Beach 1981, Wyatt 1983).

Recently, the possible influence of pollinators on sexual selection in plants has drawn considerable attention (Janzen 1977, Willson 1979, 1983, Stephenson & Bertin 1983, Willson and Burley 1983, Bell 1985). Underlying the theories and research on sexual selection is the "Bateman Principle" (Bateman 1948, Charnov 1979), which proposes an asymmetry in the costs of producing male and female gametes. The principle holds that female gametes are more costly to produce than male gametes; thus, fewer female gametes are produced. Consequently, maternal fitness is unlikely to be limited by the number of male gametes available; rather, given an overabundance of male gametes, maternal fitness is likely to vary with the genetic quality of the male gametes successful in fertilization, and selection should act on females to discriminate among these gametes or, on the basis of phenotype, among the males providing them. Conversely, paternal fitness is likely to be severely limited by the scarcity of female gametes; hence, intense competition for access to female gametes is likely to occur among male gametes or among males.

At first glance the Bateman Principle appears to be a panacea capable of explaining numerous phenomena in angiosperms. First, in many native and cultivated plant populations the number of fruits matured appears to be limited by resources available to the maternal plant, not the number of pollen grains received (Willson 1979, Stephenson 1981, 1984, Motten 1986, Stephenson & Winsor 1986). Second, many hermaphroditic plants produce far more flowers than the number of fruits that are matured even when all flowers are doused with compatible pollen (Stephenson 1981); this result is interpreted either in terms of selective fruit abortion on the part of females, selection to maximize male reproductive function by dispersing pollen to as many other plants as possible (Janzen 1977, Bell 1985), or both (Bawa & Webb 1984, Sutherland & Delph 1984, Sutherland 1986a, b). Third, careful hand pollinations have shown that some plants selectively mature fruit based on the genotype of the pollen source (*e.g.*, Bertin 1982, 1985, Lee & Bazzaz 1982, Bookman 1983, 1984), whereas pollen grains germinate and produce pollen tubes wherever possible. Fourth, there is tremendous variation in the rates with which pollen tubes from different paternal donors, or even the same donor, grow down a style (*e.g.*, Mulcahy 1983, Mulcahy *et al.* 1983, Marshall & Ellstrand 1985, 1986); not only has this variation been shown to have a basis in the gametophyte (pollen tube) genome, but also strong correlations have been shown between the speed with which tubes of a particular donor grow down a particular plant's style and the vigor of the resulting offspring (Mulcahy 1979, 1983, Mulcahy *et al.* 1983). Fifth, intense competition among growing pollen tubes for access to a flower's ovules (Mulcahy 1979, Marshall & Ellstrand 1985, 1986) is exacerbated by various maternal mechanisms, such as long styles (Mulcahy 1983, Mulcahy *et al.* 1983), or stigma receptivity delayed until many grains from diverse donors have been deposited (Kress 1983, Galen *et al.* 1986). Sixth, mixtures of pollen from several donors have been shown experimentally to increase seed set and seed "quality" in recipient plants compared to the results of single-donor pollinations (Schemske & Fenster 1983, Schemske & Pautler 1984, Marshall & Ellstrand 1985, 1986).

In short, most current thought on sexual selection supports the Bateman Principle, and suggests that maternal reproduction can be highly selective: either male gametophytes (pollen tubes) compete intensely for access to ovules, ensuring that only the fastest growing tubes –which may produce the most vigorous offspring– end up contributing to zygotes; or, unable to mature all embryos in any event, plants selectively mature only the potentially most vigorous offspring after zygote formation has occurred. Thus, animal pollinators are relegated to a minor role in maternal reproductive function among plants, other than effects of the diversity of pollen loads they deliver (Mulcahy 1979, Ellstrand 1984, Marshall & Ellstrand 1985, 1986), although of course they still are given a leading role in reproduction through paternity (*e.g.*, Janzen 1977, Bell 1985).

Field evidence for the Bateman Principle, though, is not nearly so conclusive. Bierzychudek (1981b) pointed out that many studies document plants that receive inadequate pollination for full seed- or fruit-set, and other studies (*e.g.*, Snow 1982, McDade 1983, McDade & Davidar 1984, Zimmerman 1984, Hainsworth *et al.* 1985) also demonstrate that maternal reproduction of plants is frequently limited by pollen loads brought by animals. For example, most hummingbird-pollinated flowers in cloud forest at Monteverde, Costa Rica receive fewer compatible pollen grains [as indicated by the number of pollen tubes reaching the base of the style, assessed with Martin's (1959) technique] than the number of ovules available for fertilization (Feinsinger *et al.* 1986; W. H. Busby & S. Kinsman, unpublished data).

Enticing though it is, then, the Bateman Principle should be applied with caution: real plant populations experience spatial, temporal, and interspecific variation in the relative importance of pollen and female resources as limits to maternal reproductive output. In my opinion, recognizing the interplay of pollen *versus* resource limitation that natural plant populations experience opens up many more opportunities for theory and research than does passively accepting the popular paradigm of the Bateman Principle.

THE INFLUENCE OF ANIMAL POLLINATORS ON GENE FLOW AMONG PLANTS

The extent of gene flow among plants determines deme size and obviously affects microevolution of plant populations (Levin & Kerster 1974). The terms "neighborhood area" and "neighborhood size" have more precise definitions than "deme size", and are in general use. Neighborhood size is an index to the number of individuals among which gene flow occurs over the course of a generation, whereas neighborhood area is simply the area occupied by those individuals (Levin & Kerster 1974). Each concept, neighborhood size and neighborhood area, has different implications to local adaptation and microevolution of plants.

Breeding systems of plants, and dispersal patterns of seeds, obviously influence gene flow. The foraging behavior of flower visitors, and the number of successive recipients to which they carry pollen from a single donor ("pollen carryover"), obviously have a major impact as well (Handel 1983, Lertzman & Gass 1983). Handel (1983) details techniques for tracing pollen movement from source to recipient flowers, and thoroughly reviews the literature on pollinators and gene flow; thus, I will deal with a few aspects only.

Accurate means exist for monitoring the dispersal of individual pollen grains from particular source flowers to recipient stigmas. These are often so costly and time-consuming that sample sizes of recipient flowers are severely limited. At the other extreme, many studies, such as most of those reviewed by Levin & Kerster (1974), use large samples of pollinator flight distances to estimate roughly the distance that pollen moves. Because pollen is often carried for several successive flights, because the extent of such pollen carryover varies greatly among pollinators, and because the number of grains carried also varies greatly among pollinators, pollinator flight distances may often be very poor indices to actual pollen flow (Schaal 1980. Handel 1983, Lertzman & Gass 1983). Recently, many researchers have compromised on a technique that yields large sample sizes yet is less biased than tallies of pollinator flight distances: tracing the movement of a pollen analog, fluorescent dye.

Powdered dyes whitish in visible light but highly colored under fluorescent light are available from various North American manufacturers. Small amounts of dye can be applied to newly dehisced anthers with, for example, a flat toothpick; after foraging has taken place, possible recipient stigmas can be collected and examined under a fluorescent light for the presence of dye. Ideally, stigmas are examined under a compound microscope equipped with an epifluorescence system [the same microscope used to count pollen tubes (Martin 1959)], which allows the detection of single grains of dye; but a dissecting microscope, or even just a hand-held ultraviolet light source, is sufficient for relative estimates to be made. The fluorescent-dye technique has flaws. Handel (1983) points out that dye dispersal is only an index to actual pollen flow and cannot be used to estimate true pollen dispersal distances without exhaustive testing (see also Waser & Price 1982). Even pollen flow itself is at best only an index, and perhaps not a very good one, to actual gene flow, because the success of pollen at fertilization may vary with distance from the donor plant (Waser & Price 1983a). Still, for comparative studies fluorescent dyes, used properly, provide reasonable relative indices to pollen movement by animals, indices certainly preferable to those derived from pollinator flight distances (Thomson *et al.* 1986).

What are some aspects of pollinator foraging (and flowers) that affect pollen dispersal and gene flow? (1) Pollinators do not move in random directions after leaving a particular flower. Levin *et al.* (1971) and Hodges & Miller (1981) discovered marked directionality in the flight paths of pollinators and, consequently, in gene flow (see also Handel 1983, Handel & Mishkin 1984). (2) Variation in the extent of pollen carryover has been investigated thoroughly by a few researchers only (*e.g.*, Thomson & Plowright 1980, Price & Waser 1982, Waser & Price 1982, 1984, Lertzman & Gass 1983). Apparently, deposition of pollen from a particular donor flower does not always follow a smooth decay curve; instead, some may be retained through visits to several succeeding flowers, to be deposited by chance much later in the animal's foraging bout. (3) By influencing the movement patterns of pollinators, average nectar volumes and the pattern of nectar variation among flowers will affect pollen dispersal distances and neighborhood size (Waddington 1981, Zimmerman 1982, Ott *et al.* 1985). (4) The spacing between plants can influence both neighborhood size and area. Area changes because pollinators must move farther among more widely spaced plants to obtain the same amount of food (Levin & Kerster 1974, Beattie 1976). Both neighborhood size and neighborhood area change if the identity of the pollinators themselves changes with altered flower dispersion (Linhart 1973, Feinsinger 1978, Linhart & Feinsinger 1980). (5) Different pollinator species visiting the same flowers will move pollen different distances, so that the relative frequencies of different visitors will have marked effects on neighborhood size (Schmitt 1980, Waser 1982). For example, flight distances of butterflies tend to have higher means and much higher variances than flight distances of bees (Schmitt 1980); hummingbirds may move pollen much longer (Webb & Bawa 1983) or much shorter (Murawski & Gilbert 1986) distances than butterflies; and different species of hummingbirds may move pollen in different ways (Linhart 1973, Linhart & Feinsinger 1980).

"FORAGING STRATEGIES" OF FLOWER-VISITING ANIMALS

We turn to the ecological determinants of foraging choices made by flower-visiting animals, choices whose consequence is pollen movement among flowers. Animal-flower systems are nearly ideal for testing general theories in foraging behavior. Foraging choices made by nectarivores have consequences not only to their own food intake, but also to the plants involved; as discussed above, this feedback loop leads over time to the patterning of rewards by plants. In many cases the rewards themselves are easily quantified by the ecologist; costs and benefits of different foraging choices are estimated with relative confidence; many nectarivores are exceedingly easy to observe and even to manipulate while foraging; patterns of rewards are easy to mimic experimentally; and the risk of predation, which confounds foraging studies on other trophic groups, is not a significant factor at least for some nectarivores. Thus, in recent years "foraging tactics" of nectarivores have attracted more research interest than has any other aspect of animal-flower interactions, and some of these studies have contributed substantially to the growth of foraging theory in general (Pyke *et al.* 1977, Pyke 1984).

Territoriality: Why, When, and How

Many nectarivores defend territories at dense clumps of flowers. Unlike those of many other animals, nectar-centered territories are often very responsive to rapid temporal shifts in resource density, intruder pressure, and the energetic needs of the resident. This flexibility facilitates research on the ecological determinants, behavioral correlates, and consequences of territoriality.

Territoriality has both benefits (potential increases in gross energy intake) and costs (excluding intruders through displays or chases). Like other animals, nectarivores are expected to be territorial (a) when energy is limiting; (b) when territoriality, here defined as defense of an area within which the resident controls or restricts the use of resources, results in a greater net energy gain than non-territorial foraging; and (c) when other aspects of daily life, or of fitness, do not suffer as a consequence of territorial behavior.

Carpenter & MacMillen (1976), Kodric-Brown & Brown (1978), Gass & Montgomerie (1981), Ewald & Orians (1983), and Hixon *et al.* (1983), among others, discuss various models for changes in the cost:benefit ratio with variation in floral density or intruder pressure. At low flower densities, territorial behavior is disadvantageous because resources are indefensible. At high flower densities, territorial behavior becomes disadvantageous because either (a) nectar becomes so abundant that the increment in gross energy intake provided through flower defense vanishes; (b) intruder pressure rises to the point where costs exceed benefits; or both. These researchers tested the models on Hawaiian honeycreepers (Carpenter & MacMillen 1976) or hummingbirds (Kodric-Brown 1978, Ewald & Orians 1983, Hixon *et al.* 1983), and in general found a good fit: birds abandon territorial behavior when flowers become either sparse or exceedingly dense. Gill & Wolf (1975, 1979) performed parallel studies on African sunbirds (Nectariniidae); their detailed results show a clear energetic basis for rapid changes in territorial behavior.

Nectar-feeding birds also show remarkable flexibility in the mechanisms employed in the defense and exploitation of territories. Ewald & Orians (1983) showed that Anna hummingbirds (*Calypte anna*) made predictable shifts in the frequency of passive displays relative to active chases as intruder pressure and quality of territories changed (see also Frost & Frost 1980). Lyon *et al.* (1977) showed that territorial hummingbirds discriminated among the species of hummingbird intruder, expending the most effort on those species most likely to lower the nectar supply drastically. Paton & Carpenter (1984) showed that rufous hummingbirds (*Selasphorus rufus*) foraged heavily at the periphery of their territories early in the day, preserving the territories' core for later in the day. Gass *et al.* (1976; also Gass 1978, 1979, Gass & Lertzman 1980) have documented a remarkably close fit of size and number of rufous hummingbird territories to the nectar resources available. In the montane North American meadows through which these hummingbirds migrate, flower density varies on a daily time scale, yet hummingbirds respond extremely quickly to this variation (Carpenter *et al.* 1983). On most days the meadows are fully occupied by territories each of which provides its resident with just enough nectar to equal or exceed slightly the daily energetic requirements.

Do other foraging modes maximize net energy intake?

Some non-territorial hummingbirds, and other nectar-feeders, visit scattered flowers in a quite regular, repeated sequence. "Traplining" behavior was first described in female euglossine bees (Janzen 1971) and has since been reported for male euglossines (Ackerman *et al.* 1982) and two very different functional groups of hummingbirds: the long-billed species that exploit nectar-rich but scattered flowers (Linhart 1973, Feinsinger & Colwell 1978, Gill 1978, Stiles 1978, 1981), and those short-billed individuals that are habitually excluded from territories (Feinsinger & Chaplin 1975, Feinsinger 1976). Often, long-billed "high-reward trapliners" allow plentiful nectar to accumulate in flowers between revisits (Feinsinger, unpublished data; see Feinsinger *et al.* 1985), but "low-reward trapliners" appear to keep nectar levels exceedingly low by attuning revisit frequencies to rates of nectar secretion (Feinsinger 1976, Gill 1978), thus passively excluding other foragers from their traplines. To my knowledge, F. B. Gill's ongoing research on Costa Rican hermit hummingbirds is the only rigorous investigation of the economic costs and benefits of traplining behavior.

In contrast to the solitary foraging modes discussed above, some nectar-feeders apparently forage in groups. Passerine birds in Trinidad (Feinsinger *et al.* 1979a) and bees in Costa Rica (Frankie 1976) appear at flowering trees in distinct "waves"; at least the passerines may form reasonably cohesive single- or mixed-species flocks. Some bats, too, appear at rich resource concentrations in "waves" (Heithaus *et al.* 1974, 1975, Sazima & Sazima 1977, Howell 1979, Howell & Roth 1981). Whether or not these reflect cohesive bat flocks using a common roost is not conclusively determined. In a detailed energetic analysis, Howell (1979) showed that the energetic benefits of group foraging outweighed those the bats would obtain were they solitary foragers. The consensus is that group foraging may be advantageous for animals encountering discrete, massive crops of nectar-rich flowers, such as large *Puya* and *Agave* plants or large *Erythrina* trees, where the flower crop is far too large for territoriality (cf. Carpenter & MacMillen 1976) but where some energy may be saved, in comparison to haphazard solitary foraging, by avoiding areas where others in the flock are seen to forage.

Search patterns and the economics of foraging

An animal undertaking a foraging bout makes a series of choices that affect its diet and its energy intake (Pyke *et al.* 1977, Pyke 1984). In order, these choices are: (1) upon choosing the habitat, which "patch types" to visit; (2) which foraging path to employ within the patch while searching for potential food items; (3) which of the items encountered to utilize; and (4) when to abandon the patch and move on to another.

At each step, the choice that yields the highest net energy gain depends on characteristics of the forager and of the resource. Often, theory and research are couched in terms of "optimal foraging", but as Heinrich (1983a) points out optimality arguments may be misleading and tautological; there are too many possible ways of defining "optima". A more objective way to approach foraging decisions may be to ask, do the choices that foraging animals make provide them with a higher net energy gain than if they were foraging in a stereotyped or a haphazard pattern? In colloquial terms, do animals forage in ways that get them "good deals" in terms of energetic costs and benefits (see also Waddington 1983)?

(1) Patch choice. In general terms, foraging nectarivores are expected to choose the patch providing the highest expectation of energy yield per unit time (Pyke *et al.* 1977, Pyke 1980, 1984, Carpenter *et al.* 1983). How does a forager obtain information on expected yield? Some early models of foraging assumed that foragers were omniscient, but more sophisticated models incorporate time (and energy) spent in sampling from various patches. Nectarivores live in a world of especially rapid changes in the nectar value of patches (cf. Pleasants & Zimmerman 1979). Up-to-date knowledge of the local region's possible patches is therefore essential, and many foragers may sample widely after their daily energy requirements are met. For example, many territorial hummingbirds spend increasing amounts of time off the territory late in the day, and non-territorial species as well appear to spend some afternoon hours assessing possible foraging sites for the crucial early morning hours of the following day (Feinsinger 1976, Gass & Sutherland 1985; F. G. Stiles, personal communication, 1986). In fact, data an observer obtains during a nectarivore's sampling period, if taken out of context, could easily be misinterpreted as "non-optimal foraging".

In a sense, social nectarivores pool sampling effort and thus decrease the total sampling effort of the "individual", or colony. For example, in a colony of bumblebees (which do not recruit), as each forager goes through a trial and error process the distribution of bees adjusts slowly to the distribution of good and poor patches on a particular day (Heinrich 1976b, 1979a, 1979b, Pyke 1980). A colony of eusocial bees having "scouts" that recruit foragers to rich patches, such as meliponine bees (Johnson & Hubbell 1974, 1975, Hubbell & Johnson 1978, Wille 1983) or honeybees (Visscher & Seeley 1982), may be as close to an "omniscient forager" as possible: streams of nectar and pollen harvesters are dispatched to good patches almost as soon as these become available.

(2) The foraging path. After choosing a patch, the nectarivore is expected to choose the path that (a) minimizes the distance, or energy expended, between successive food sources and (b) minimizes the chances for revisiting the same flower in a single foraging bout. Kamil (1978) showed that Hawaiian honeycreepers appeared to minimize revisitation, spreading their foraging evenly over the inflorescences in their territories. Attempts to duplicate these results with territorial hummingbirds have failed (Miller *et al.* 1985; P. Feinsinger, unpublished data, C. Murcia, unpublished data), but "traplining" behavior, where it occurs, may

meet both the distance- and the revisitation-minimizing criteria.

Most studies on choice of foraging path have involved bumblebees. Pyke (1978a, b) investigated bees foraging at *Delphinium nelsonii* flowers, which are arranged spirally on the spike. First, he showed that the angle at which bees turned as they went from one inflorescence to the next was one that reduced the chances for revisitation (Pyke 1978b). Second, he showed that the path a bee took among the flowers on a given spike was one that increased nectar intake and reduced movement costs. Pyke interpreted these foraging movements in terms of "optimal choice" of foraging path.

Recent investigations (*e.g.,* Heinrich 1979c) have produced less clearcut results and have thrown some doubt on Pyke's "optimal choice" interpretation. For example, some bumblebees may forage in stereotyped patterns regardless of the vertical distribution of nectar in a flower spike (Corbet *et al.* 1981). Still, in a careful study Waddington and Heinrich (1979) showed that *Bombus edwardsii* were capable of modifying their foraging path in response to the distribution of nectar on artificial inflorescences. When rewards were concentrated among the lowest flowers, bees quickly learned to start from the bottom of each "inflorescence" and to depart before reaching the empty topmost flowers. When instead the rewards were concentrated among the topmost flowers, bees quickly learned to begin each inflorescence in the middle and to depart from the top. When rewards were evenly distributed among flowers, bees switched to foraging throughout each "inflorecence", beginning near the bottom and departing only when the top was reached. Thus, foraging paths appear to involve both stereotyped and learned behaviors.

(3) Food choice. The criteria influencing food choice and diet breadth are more clearcut, and more widely investigated, for other animals than for nectarivores (see reviews by Schoener 1971, MacArthur 1972, Pulliam 1974, Charnov 1976, Pyke *et al.* 1977, Pyke 1984). Heinrich (1976b, 1979b) and others (Laverty 1980, Harder 1983, 1985) have shown clearly, however, the determinant of flower choice by individual bumblebee foragers: net energy return as perceived by the forager. Net energy return is a function of actual nectar volumes and of handling time, which for a given bee is a function of flower morphology and previous experience. Likewise, Lewis (1986) demonstrated the importance of learning in flower choice by the butterfly *Pieris rapae.*

Another criterion affecting flower choice by bees is variance in nectar rewards. Caraco (1980, see also Caraco *et al.* 1980) proposed that foraging animals operating on neutral or positive energy budgets would tend to be "risk averse", choosing patches or food types with low variance in the rate of return, whereas foragers operating on a negative energy budget, given some possibility of encountering an unusually rich reward quickly, would switch to "risk prone" foraging in patches or at resources yielding high variance in the rate of intake. Waddington & Holden (1979), Real (1981), Waddington *et al.* (1981), and Real *et al.* (1982) showed experimentally that various hymenopteran foragers (wasps, bumblebees, or honeybees) tended towards "risk aversion", usually choosing artificial flowers with low variance in nectar volumes over differently colored flowers having the same mean but high variance. These results may explain the scarcity of bonanza-blank patterns of nectar secretion in plants whose pollinators are not often food-limited as a group. Conversely, when food is scarce for pollinators, the theory of risk-sensitive foraging predicts a switch to risk-prone behavior (Caraco 1980, Caraco *et al.* 1980), such as that provided by a bonanza-blank nectar secretion pattern. Certainly, more research is crucial to understanding the relationship between risk-sensitive foraging and food limitation.

(4) When to leave the patch. Foragers may make this decision based on their perception of the rate of return from the current patch *versus* the expected rates of return in alternative patches, modified by the costs of transit. Some foragers' perceptions can apparently be quite accurate. For example, Hartling & Plowright (1979) showed that bumblebees stayed foraging longer at one artificial inflorescence as distance to the next inflorescence was increased.

When costs and benefits of alternative patches are not so well known, nectarivores may use standard "stopping rules", leaving after encountering a given number of empty flowers in sequence. Stopping rules may be flexible, though. For example, Best & Bierzychudek (1982) found that bumblebees switched from a "stopping rule" of 4-5 flowers in early morning to 1 flower in late afternoon. A few of the many other studies dealing with the decision of when to leave a patch include Howell & Hartl (1980), Waddington (1981), Marden & Waddington (1981), Schluter (1982), Hodges (1985), and Wolf & Hainsworth (1986).

Finally, at least one study has dealt not with flexible "stopping rules" for entire patches, but rather with flexible stopping rules for the effort spent at individual flowers. Whitham (1977) showed that bees foraging on flowers of *Chilopsis linearis* (Bignoniaceae), early in the day when most flowers held large nectar volumes, achieved a higher net energy intake by leaving the last drops of nectar in the flowers than by spending the time necessary to extract these dregs. Later in the day, however, when nectar levels were low overall, bees stayed longer and extracted the dregs. This result parallels cases of "partial prey consumption" by predators, in which animals cease feeding on one prey and begin searching for others long before extracting all possible energy and nutrients from the first (Sih 1980).

NICHE WIDTH AND SOCIAL STRUCTURE OF NECTARIVORE POPULATIONS

The collective result of decisions made by individual foragers is a characteristic pattern of resource use by the species population to which they belong, one aspect of the population's "niche" (Whittaker *et al.* 1973, Feinsinger *et al.* 1981). A population of specialists all having similar specialties will have a narrow niche; a population of generalists will have a broad niche, but so will a population of specialists each having a somewhat different specialty. Obviously, a broad-niched population composed of generalist flower-visitors will have a quite different impact on flower pollination than a population with an equally broad niche but containing a diversity of specialists.

Bumblebees studied by Heinrich (1976b, 1979a, 1979b) exemplify populations with specialized individuals but broad niches. On the basis of perceived rewards (see Laverty 1980, Harder 1983, 1985, Plowright & Laverty 1984), a naive bumblebee forager learns to forage at a "major" plant species and one or more "minors" (see review in Feinsinger 1983a). Perceived rewards are affected by species-specific flower complexity, rate of nectar secretion, flower dispersion, and, most importantly, the extent to which existing foragers already visit the flowers. Thus, all else being equal, a naive forager will tend to choose flowers of species underutilized by other bees. The net result is that foragers from any one bumblebee population are distributed broadly over most flower species available (Johnson 1986), even though each bee makes quite specialized choices and each plant population experiences quite constant pollinators.

In contrast, some bees remain specialized on particular plant species regardless of conditions, and the population maintains a very narrow niche. Strickler (1979) showed that *Hoplitis anthocopoides* collected pollen from one plant species only, and was more effective at doing so than less stereotyped bee foragers.

Coexisting meliponine bee species in Costa Rica have a variety of niches (Johnson & Hubbell 1974, 1975, Hubbell & Johnson 1978, Wille 1983). Foragers from non-recruiting species visit a wide variety of flower species and dispersions; thus, the population has a broad niche. At any one time, though, a population of a species that recruits foragers has a narrow niche, as all foragers are concentrated at especially rewarding resources, where they overwhelm other bees. Visscher & Seeley (1982) showed that healthy wild colonies of honeybees (*Apis mellifera*) resembled recruiting meliponine species, with numerous scouts sampling from various patches but recruiting in such a way that foragers were pooled in patches of the plant species that were most rewarding at any one time; energy-stressed colonies engaged in much less sampling and remained with particular plant species for long times; but, because different colonies experienced different degrees of energy stress, the net result was that honeybees as a whole were dispersed over all appropriate flower species. Thus, the niche of feral honeybees might be as broad as the niche of a bumblebee population, but very different foraging techniques are responsible.

At any one time the niche of a territorial hummingbird population is apt to be quite narrow, as only a few plant species are likely to provide resources worth defending (Feinsinger 1976, 1983a). Over time, though, the niche becomes quite broad as plant species going out of, or coming into, flower are respectively discarded from, or added to, the list of defensible resources. Subordinate, short-billed hummingbirds have access only to scattered flowers of many species; thus, populations of low-reward trapliners, for example, are broad-niched at any one time. Likewise, long-billed high-reward trapliners often forage at numerous species having long-tubed flowers. We have found individuals carrying as many as 16 pollen species simultaneously (Feinsinger *et al.* 1987). Relative to long-tubed flowers, then, populations of high-reward trapliners have broad niches; but considering all hummingbird-pollinated flowers they could potentially visit, these species have quite narrow niches, as they rarely visit the less rewarding short-tubed flowers (Feinsinger 1983a).

INTERSPECIFIC COMPETITION AND GUILD ORGANIZATION IN NECTARIVORES

In recent years the field of community ecology has been racked by dissension over the importance of competition among natural populations, and its role in structuring communities (*e.g.*, Lewin 1983a, 1983b, Schoener 1983, Strong *et al.* 1984, Diamond & Case 1986). Many critics of competition theory point out that evidence for resource limitation, the precondition for ecologically (and evolutionarily) important competition, is difficult to collect; that the extent of resource limitation is likely to vary widely in space and time; that the relationship between resource limitation, even when it occurs, and "character displacement" among coexisting species is very complex and tenuous. Animal-flower interactions provide excellent systems for examining the role of competition, because production, availability, and use of resources are easily monitored; because interactions are extremely dynamic, as plant populations go into or out of flower over quite short time spans; because many nectarivores are highly visible, and their competitive interactions are highly visible as well; and because, for some groups at least, there is a clearcut and easily tested relationship between morphology and resource use.

"Tongue" length of bumblebees varies among and within species (Heinrich 1976a, Morse 1977, Harder 1983, 1985). Tongue length strongly affects efficiencies of nectar extraction from flowers with different corolla lengths (Inouye 1980, Harder 1985), and thus constrains foraging choices. Often, nectar from flowers with different corolla lengths is fed on by different bee species. Thus, some bumblebee assemblages may be structured by competition (Inouye 1977). Many recent studies have been performed in Scandinavia and Finland (*e.g.*, by I. Hanski, H. Lundberg, A. Pekkarinen, E. Ranta). One of the most convincing studies, however, was performed in North America by Inouye (1978). Inouye investigated meadows where long-tongued *Bombus appositus* coexisted with short-tongued *B. flavifrons.* Normally, *B. appositus* workers majored on long-flowered *Delphinium barbeyi,* and ignored short-flowered *Aconitum columbianum; B. flavifrons* majored on *Aconitum* and ignored *Delphinium.* When one bee species or the other was experimentally removed, however, nectar welled up in the unutilized flower species, and the remaining bee species began utilizing those flowers even though they were less efficient at extracting nectar than the "normal" visitor (Inouye 1978, 1980). Thus, exploitative competition certainly occurs among bumblebees (see also Heinrich 1976a). Even though such competition may play a minor role in the evolution of the tongue length of a particular bee species, it may play a larger role in assembling, from a pool of potential colonists, groups of coexisting bumblebee species (Bowers 1985a, b).

Meliponine bees in Central America compete intensely for access to rich nectar sources. Using artificial nectar sources, Hubbell & Johnson (1977, 1978) and Johnson (1981) showed that behaviorally subordinate species were often the first to discover new food and exploit it, but when larger, recruiting species discovered rich resources they overwhelmed and displaced the smaller, non-recruiting bees. Interactions among meliponine species at natural nectar sources undoubtedly are more complex, but apparently interspecific competition among meliponines, or between meliponines and other bees, characterizes densely flowering trees (Roubik 1978, 1980, 1983, Frankie & Haber 1983, Wille 1983) and may affect bee community structure (cf. Hubbell & Johnson 1977). The year-around dynamics of meliponine-flower associations have not yet been investigated thoroughly.

Guild structure and seasonal dynamics in nectar-feeding birds, however, have been investigated at several Central American sites and on Trinidad and Tobago. Feinsinger & Colwell (1978) reviewed earlier studies and distinguished five "roles" that nectar-feeding birds appeared to fill: territorialists, high-reward trapliners, low-reward trapliners, and two roles not mentioned previously: generalists (who fit in between territorialists and low-reward trapliners) and "territory-parasites". We pointed out that a hummingbird's morphological and behavioral phenotype guided it towards one or another role, but that some birds might change behavioral roles with changes in resources or in the local array of other nectar-feeding birds.

In general, studies performed in large tropical "old fields", or patches of anthropogenic successional vegetation, have revealed extremely dynamic interactions among hummingbirds (Colwell 1973, Feinsinger 1976, 1980, Wolf *et al.* 1976, Feinsinger & Swarm 1982, Feinsinger *et al.* 1985). The density of flowers may vary by two orders of magnitude over the year. During seasons of nectar scarcity, a small number of bird species, filling widely different roles, coexists. During flowering peaks, however, numerous additional species enter from nearby and distant habitats (see also Feinsinger 1980). By monitoring throughout an annual cycle the nectar available within flowers, Feinsinger *et al.* (1985) documented the extreme resource limitation that led to intense competition and forced "secondary" species to emigrate during times of flower scarcity, *versus* the superabundant nectar that allowed the coexistence of many species at other times.

Canopies of some tropical forests may likewise provide seasonal bursts of resources that support extremely dynamic hummingbird assemblages (Feinsinger & Colwell 1978, W. H. Busby, unpublished data). Nectar availability appears to be much more constant, however, in the understory of these forests, as well as in natural gaps such as those caused by treefalls (Stiles 1975, 1985, Feinsinger *et al.* in press; but see Stiles 1977). As a result, most of the nectar available (at least to short-billed hummingbirds) in flowers of the understory or gaps is utilized on a daily basis throughout the year. Hummingbirds of tropical forest understory appear to be quite sedentary, and there are few transient populations. Such habitats tend to have one or a few species of short-billed hummingbirds exploiting short-tubed hummingbird-pollinated flowers, and one or a few species of hermit hummingbirds or other long-billed species exploiting long flowers.

Thus, structure and dynamics of hummingbird assemblages vary with the nature of the habitat and resources involved. The extraordinarily dynamic assemblages of tropical old-fields exemplify communities where the intensity of competition, and community structure, vary seasonally (Feinsinger 1976, Feinsinger *et al.* 1985). The distinction between those old-fields (and some forest canopies), with their hordes of migrant nectarivores, and the relatively stable resource regimes (and nectarivore assemblages) of forest understories points out that the "organizing principles" of superficially similar species assemblages may in fact differ greatly. Monitoring the entire annual cycles of other tropical nectarivore taxa or guilds will surely reveal even more about the variable role of competition in community structure.

SPECIES INTERACTIONS AND COMMUNITY PATTERN AMONG PLANTS

Plants belonging to different species but using the same animal pollinators may influence one another's pollination through several different mechanisms:

(1) Neighbors may influence the frequency with each other's flowers receive visits from animals, (a) either by drawing animals away from each other (resulting in competition) or (b) by collectively luring animals into a patch (resulting in facilitation) (Schemske 1981, Thomson 1982, 1983, Rathcke 1983, Real 1983a, Waser 1983a, 1983b).

(2) If animals visit plants of different species in succession, "interspecific pollen

transfer" may occur (Rathcke 1983, Waser 1983a). (a) If pollen rubs off on flowers of other species, paternal reproductive success declines as the number of grains dispersed to conspecific flowers, and the number of conspecific plants reached, declines (Waser 1978b, 1983a, Rathcke 1983, Campbell 1985a). (b) Interspecific pollen transfer may lower maternal reproductive success if: (i) heterospecific grains occupy scarce space on the stigma, or induce it to close, thereby limiting access by conspecific grains (Waser 1978a, b, Waser & Fugate 1986); (ii) heterospecific grains have allelopathic effects on conspecific grains (Sukhada & Jayachandra 1980, Thomson *et al.* 1981); (iii) heterospecific grains result in hybridization and gamete wastage (Stiles 1975, Waser 1983b); or (iv) the cumulative number of conspecific grains received by stigmas declines (Campbell 1985b, Campbell & Motten 1985, Feinsinger *et al.* 1986, Motten 1986).

The collective results of mechanisms 1 through 2biv may be quite complex, especially at extremes in flower density (Rathcke 1983, Thomson 1983). Unless sudden flowering bursts overwhelm the pollinator pool, however, effects on visit frequencies (mechanism 1) may be minor compared to effects on pollen transfer (Waser 1983b). Furthermore, at least some studies suggest that stigma packing (2bi) and allelopathy (2bii) by the heterospecific pollen grains that stigmas receive are inconsequential compared to the impact of conspecific grains lost (mechanisms 2a and 2biv) (Campbell 1985a, 1985b, Campbell & Motten 1985, Kohn & Waser 1985, Feinsinger *et al.* 1986).

The possible effects just listed suggest that plants of different species flowering simultaneously are likely to suffer reproductive depression relative to plants flowering at different times from one another. Natural selection or selective immigration could, then, lead to divergent flowering times among the species in a pollination guild. Thus, competition could be responsible for apparently regular dispersion among the flowering seasons of co-occurring plant species (*e.g.*, Heithaus 1974, Heinrich 1975a, Stiles 1975, 1977, 1981, 1985, Feinsinger 1978, 1983a, Pleasants 1980, 1983; see reviews by Rathcke & Lacey 1985, Wheelwright 1985, Armbruster 1986).

If, through competition for pollination, flowering peaks become dispersed throughout the growing season or (in tropical climates) throughout the year, then the animals that visit these flowers are provided with a constant supply of food. Thus, the animals can develop sedentary life styles and can specialize on nectar or pollen. From the plants' perspective, this means that animals that can pollinate them are constantly available. Thus, a causal chain could link the mechanisms of interaction among plants, 1 - 2biv above, to the existence of phenological pattern among coexisting plants, the existence of stable nectarivore assemblages, even to an accelerating interdependence and coevolution between flowers and flower-visitors (Heinrich & Raven 1972, Stiles 1977, 1981, Waser & Real 1979, Feinsinger 1983a).

Alternatively, the competitive mechanisms proposed above could lead to morphological displacement in location of the reproductive parts, among plants simultaneously using the same pollinators (Waser 1983a). Morphological displacement would minimize the amount of interspecific pollen transfer (mechanism 2), such that rare species might actually benefit from using the foragers that come to more common, popular neighbors (mechanism 1b). Thus, a causal chain could lead from mechanism 1b above towards a pattern of convergence in flowering seasons among some coexisting plants, rather than towards the divergence expected among morphologically similar flowers (reviewed in Feinsinger 1983a).

Unfortunately for the speculation outlined in the preceding two paragraphs, patterns in the flowering of coexisting plant species have proven to be somewhat illusory (Poole & Rathcke 1979, Gleeson 1981, Rathcke 1983, 1984, Fleming & Partridge 1984, Rathcke & Lacey 1985, Wheelwright 1985). Observed distributions of the flowering seasons of "competing" plant species should always be tested against the distributions to be expected were flowering seasons random with respect to one another, *i.e.*, those distributions generated by a "null model" (Harvey *et al.* 1983) of flowering phenologies. When performed properly, these tests usually reveal that purportedly "regularly dispersed" flowering seasons are displaced no farther from one another than would be expected by chance alone (Fleming & Partridge 1984).

As in the remainder of community ecology, most discussions of species interactions and phenotypic patterns within "pollination guilds" (coexisting plants using a common set of pollinators) rely on data either on the ecological interactions or on the patterns but not both. Recently, my colleagues (J. H. Beach, W. H. Busby, S. Kinsman, Y. B. Linhart, K. G. Murray, W. Z. Pounds, J. A. Wolfe) and I have spent several years studying both species interactions and community patterns in two guilds of plants in cloud forest at Monteverde, Costa Rica. One guild consists of plants pollinated by the short-billed hummingbird *Lampornis calolaema;* the other guild contains plants pollinated by long-billed hummingbirds, primarily *Phaethornis guy*. We documented flowering phenologies, monitored flower-visitation patterns, examined floral morphologies of the ca. 40 plant species concerned, and noted the patterns with which pollen grains were deposited on the beaks and feathers of hummingbirds. We evaluated interactions among plant species by detailing the effects of neighboring flowers on the pollen loads a plant's stigmas receive.

Results have revealed tremendous complexity in plant-pollinator and plant-plant relationships. Neighboring plants of different species sometimes have adverse affects on one another's pollination (as measured by the number of conspecific, compatible pollen grains that stigmas receive), but only in the guild with short-tubed flowers, and even there only during certain seasons (Feinsinger *et al.* 1986). Long-tubed flowers of different species actually enhance one another's pollination on occasion. The species composition of neighboring plants does not have consistent effects on the number of heterospecific pollen grains a stigma receives; furthermore, S. Kinsman (unpublished manuscript) has failed to find any significant detrimental effects of heterospecific grains even when they do arrive on stigmas (see also Kohn & Waser 1985). Thus, competition sometimes occurs, but only through mechanism 2b.iv above and only in one of the two guilds examined.

Even short-tubed flower species at Monteverde do not exhibit the pattern expected from the process of competition in a stable environment (Murray *et al.* 1987). In a "null model" analysis of data collected between July 1981 and June 1983, none of the 12 short-tubed species we examined, and only 2 of the 19 long-tubed species of flowers we examined, had blooming seasons that overlapped with the remainder of their guild significantly less than expected by chance alone. On the other hand, 3 of 19 long-flowered species actually experienced greater phenological overlap from other species than expected by chance. Furthermore, in neither guild did species flowering simultaneously exhibit significantly greater morphological displacement than expected by chance (Murray *et al.* 1987).

A number of explanations exist for the absence of community-level pattern we discovered. For example, (1) the variable environment of the Monteverde cloud forest, like most other habitats, produces considerable year-to-year variation in flowering phenologies and interspecific overlaps, thus permitting the coexistence of species (or phenotypes) having traits that would be maladaptive in a stable environment (cf. Chesson 1986, Chesson & Case 1986, Hubbell & Foster 1986). (2) The cloud-forest community, like other communities, is in long-term climatic disequilibrium (cf. Davis 1986); plant species may be migrating independently, and at different speeds, over the landscape. (3) Other selective forces that affect flowering phenology and flower morphology, such as those related to fruit production, may override the forces generated by interspecific pollen loss (Rathcke & Lacey 1985); the consequences of flowering at the "wrong" time may have little consistent effect on eventual reproductive output.

The complexity we discovered is undoubtedly not unique to the Monteverde cloud forest. This complexity suggests that it may be far too simplistic to expect plants sharing pollinators always to compete intensely or to flower in patterns that minimize overlap, just as analogous expectations for other "competing" species have often been shown to be unrealistic (Wiens 1977, Simberloff & Boecklen 1981, Strong 1983, Strong *et al.* 1984, Diamond & Case 1986). Convergence among plants to utilize the same effective pollinators seems to be much more likely than divergence to avoid competition (Brown & Kodric-Brown 1979). Furthermore, the complexity of interactions in the Monteverde cloud forest suggests that simultaneous investigation into processes of species interactions and into phenotypic patterns of those species are more valuable than investigation into one or the other in isolation. We hope that other investigators, whether primarily "pollination ecologists" or primarily community ecologists, will undertake similar investigations.

COMPARISONS OF ANIMAL-FLOWER INTERACTIONS AMONG COMMUNITIES

Two sites that differ in a major ecological feature may exhibit pronounced differences in animal-flower interactions as well as in other community components. For example, a change in elevation can alter the relative effectiveness of different pollinator taxa, leading to a shift in the frequency of plants relying on these taxa and profoundly affecting the dynamics of each plant or flower-visitor guild (Cruden 1972, Kalin-Arroyo *et al.* 1983, 1985, in press). Community-level patterns in flowering phenology may also vary with elevation (Kalin-Arroyo *et al.* 1981). Likewise, comparisons between wet and seasonally dry forest sites in Costa Rica have revealed profound differences in community phenology of plants (Frankie *et al.* 1974, Opler *et al.* 1980a). Nectar-feeding birds on different continents may be resource-limited to very different extents, affecting greatly the ecology and evolution of their relations with bird-pollinated flowers (Carpenter 1978).

Islands typically have fewer species of flower-visiting animals (and plants) than equivalent sites on the mainland; this decline in species richness can affect the ecology of the nectarivore species that remain (as compared with their conspecifics on the species-rich mainland) and the pollination of the plants they visit (Feinsinger *et al.* 1979a, 1982, 1985, Linhart & Feinsinger 1980, Feinsinger & Swarm 1982, Spears 1987.

Finally, species identities of plants and pollinators, and the nature of species interactions, may change as a disturbed patch of landscape goes through secondary succession (Parrish & Bazzaz 1979, Opler *et al.* 1980b). Most studies taking this approach utilize anthropogenic disturbances. Recently, we completed a study comparing natural disturbances (treefall gaps and larger, landslide-like gaps) with the intact understory of the Monteverde (Costa Rica) cloud forest, but found only subtle differences in species identities and species interactions among these habitats (Feinsinger *et al.* 1987, in press, Linhart *et al.* in press).

APPLIED POLLINATION ECOLOGY

Pollination ecology and agriculture

A vast literature exists on pollination of crop plants (see reviews by Free 1970, McGregor 1976, Caron 1979, Crane & Walker 1983, Erickson 1983, Estes *et al.* 1983). Many techniques used to assess the pollination event itself, and its consequences in terms of seed or fruit output of the plant, are very sophisticated (except for the practice of determining effective pollinators simply by tallying insect flower-visitors). Yet surprisingly few "post-revolutionary" concepts of animal-flower interactions have filtered back into the applied literature. The fact that many temperate-zone crop plants are wind pollinated may partly explain this paradox, but neither have most concepts dealt with in this review been applied to the many animal-pollinated tropical crops.

Pollination ecology and conservation

Although Kevan (1975) proposed that pollination be examined in the context of environmental conservation, I know of only two papers that clearly relate conservation and animal-flower interactions: a popular article (Janzen 1974) and a short speculative essay (McClanahan 1986; although see Howe 1984b concerning plant-frugivore interactions and conservation). Fragmentation of natural habitats and the spread not only of sterile lands (such as pastures) but also of species-rich successional vegetation must have profound effects on nearly every aspect of animal-flower interactions mentioned in this review. Habitat fragmentation cannot help but affect population structure and, eventually, microevolution of the surviving plant populations. Direct or indirect effects of habitat fragmention on the pollinator milieu may act as a broad community-level "selective filter" on recruitment in plant populations: recruitment in some plant populations, because of their breeding systems and pollinators, may be affected scarcely at all by habitat fragmentation, but recruitment in others may decline dramatically or cease altogether as a result of inadequate pollination. Habitat fragmentation undoubtedly has profound effects on guilds of nectarivores that normally migrate among several different patches, distributed broadly over the landscape. Such long-term effects on the community ecology of conserved habitat fragments, effects more subtle but perhaps more profound than the loss of conspicuous carnivore species from these fragments, need to be investigated carefully.

SUGGESTIONS FOR FUTURE RESEARCH

Although a continuation of "pre-revolutionary" pollination ecology is certainly valuable, other areas of research may be more productive. For example:

(1) A few particular pollination syndromes are virtually uninvestigated from a "post-revolutionary", quantitative standpoint, and offer many intriguing possibilities for future research. Chief among these, despite problems associated with its crepuscular or nocturnal nature and the fabled unpredictability of its animal participants (see Martínez del Rio & Burquez 1986), is the interaction between hawkmoths and moth-pollinated flowers.

(2) Research on the relationship between the foraging energetics of flower-visitors and nectar availability in flowers has only been rigorously examined by a relatively few researchers and in a very few groups. Techniques are available for quantifying precisely the energetic expenditures of small animals, and for quantifying precisely the nectar output of plants.

(3) Other than gaps in knowledge pointed out earlier, the determinants of foraging choices in nectarivores have been investigated quite exhaustively. Further details on, for example, the movement of bees within or between inflorescences may not add much to extant knowledge. Aside from Heinrich's (1979b) and Laverty's (1980) work on bumblebees, though, we know next to nothing about the *ontogeny* of foraging. How does a hummingbird fledgling, leaving the nest for the first time, learn to forage? learn which flowers are rewarding, which unrewarding? learn the spatial locations of flowers before starving to death? set up a trapline, a territory, or even a haphazard foraging route in a community where all resources are apt to be consumed by older individuals?

(4) With the exception of studies mentioned above and a few others, very little is known about the short-term (an annual cycle or less) and long-term (over several years) dynamics of nectarivore guilds. As is true for the remainder of community ecology long-term studies are tremendously more valuable than short-term studies that might, unbeknownst to the investigator, be taking place under unrepresentative conditions or, just as serious, might miss the unusual events crucial to shaping the animal and plant assemblages under study.

(5) Likewise, instead of fragmentary studies concerning interspecific pattern alone, or concerning competitive interactions alone, integrated studies are needed that deal simultaneously with pattern and process in plant species interactions as mediated by pollinators.

(6) Comparisons of animal-flower systems between the subalpine/alpine meadows of temperate North America and those of the southern Andes have begun and hopefully will expand. The large body of research performed at Rocky Mountain Biological Laboratories provides an excellent comparison for Andean investigations.

(7) Perhaps most crucial, considering the recent awakening of the world's conscience in regard to tropical deforestation, is the infusion of new ideas (and new researchers) into applied pollination ecology. The scarcity of up-to-date, quantitative, carefully designed and interpreted research on the role of pollination ecology in agriculture, or in the conservation of fragmented habitats, is inexcusable. Good studies can yield information useful in an applied sense while testing general hypotheses in rigorous enough fashion to provide the requisite publications in non-applied scientific journals.

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