POLLINATION: A PLINTH, PEDESTAL AND PILLAR FOR TERRESTRIAL PRODUCTIVITY. ... THE WHY, HOW, AND WHERE OF POLLINATION PROTECTION, CONSERVATION, AND PROMOTION

by

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INTRODUCTION

There are a few, crucial ecosystemic processes that sustain terretrial life on planet Earth. They embrace biophysical interactions in the soil and atmosphere; some comprise quite specific co-evolved relationships, others are more general in scope. The association of plants' roots with fungi through mycorrhizae and microbes in Nitrogen fixation permit, or at least stimulate, plant nutrition and growth. The dispersal of plant propagules (fruits, seeds etc.) by animals is basic to the evolution and maintenance of biodiversity in flowering plants (Angiospermae) (Janzen 1983). The interactive roles of herbivores, predators, parasitoids, parasites, and pathogens are ecologically understood as often being crucial to sustaining ecosystems and their diversity (Andrewartha and Birch, 1984). Similarly, pollination is a pivotal, keystone process in almost all productive terrestrial ecosystems. Nevertheless, pollination has been generally overlooked in that regard until very recently (Buchmann and Nabhan, 1996). That is a surprising oversight given that the biodiversity of world's dominant flora, flowering plants, and dominant fauna, insects, are so intimately and co-evolutionarily enmeshed through insect and flower relationships. The co-evolutionary time spans over 400 million years. The vital roles of pollinators and flowers are no less important in remote wildernesses of the Arctic and deserts than in highly managed farming systems, e. g., in greenhouse hydroponics. Thus, pollination is the hub of a multi-spoked wheel which has all - consumers, human beings, livestock, and wildlife - at the rim (Fig. 1). Moreover, the ecological roles of non-pollinating flower visitors in the web of life provide benefits, and sometimes problems, which are essential to other aspects of ecosystemic function.
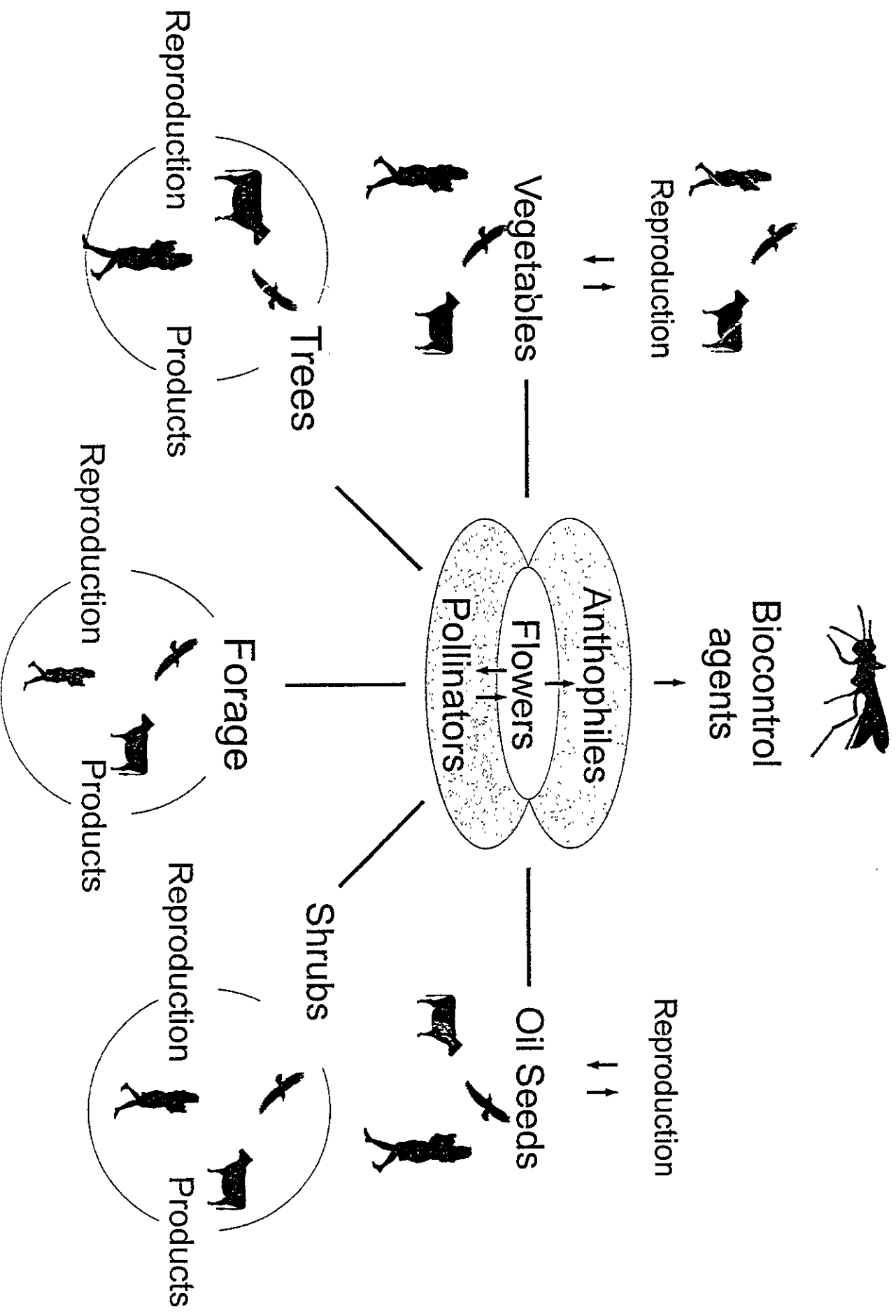
Figure 1 near here
Caption: Figure 1. The central place of pollination and animal-flower relationships in global terrestrial productivity for human beings and wildlife through provision of foods, other products, and continued reproduction of crop and wild plant.

Because many scientists have appreciations of only components of pollination biology, and because it is such a crucial ecosystemic process, I have attempted to be quite thorough, but from a zoological perspective. I present my view in two parts. Part I, drawn largely from Kevan and Baker (1998), is a general overview of pollination and especially the diversity of organisms and processes involved. Thus, the huge range of pollinating animals is introduced before the co-evolved natures of animals' sensory physiology (vision and olfaction), nutrition and metabolism, foraging energetics and behavior are related to botanical facets of the systems and to the structure of ecological communities. It is becoming more generally agreed that ecosystemic integrity and diversity is central to sustained productivity in all systems. Hence, and understanding of the basics of pollination ecology are important. Part II, drawn largely from Kevan *et al.* (in press) and Kevan (in press) is about managed ecosystems and the special importance of pollination to agricultural production. Conservation, protection, and promotion of pollinators concerns honeybees, other managed pollinators, beekeeping, and native pollinators in agricultural and other managed settings. Managed ecosystems range from those in highly artificial environments, such as greenhouses through to semi-wilderness forests. Throughout, pollinator problems are widespread. The diversity of pollinators ranges from honeybees to lesser known managed bees and to wild pollinators. It is becoming apparent that assemblages of pollinators provide the best assurances for crop production, and other flower visitors are important in crop protection. I also address the roles of other anthophiles (flower visitors) in agricultural and natural ecosystems, particularly with regard to pest management and natural regulation of animal and plant populations. I end the review with a discussion of the value of pollinators in assessing environmental pollution and stress. Thus, I hope that I have convinced my readership that the importance of pollinators and other anthophiles extends far beyond plant reproduction, crop productivity, and pest management into aesthetic and ethical aspects of the quality of human life.

PART I. POLLINATION, POLLINATORS, & ANTHOPHILES: DIVERSITY IN BIOTA AND PROCESSES

Pollination is simply the transfer of pollen from the anther of one flower to the stigma of another or the same flower. After production of the sexual organs and associated structures, pollination is the first step in the reproductive process of higher plants. It is achieved by biotic and abiotic means. Abiotic pollination occurs by wind, water, or gravity. Biotic pollination is effected by animals. There is an entire and specialized vocabulary concerned with plant breeding

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Reproduction

Vegetables

Reproduction

Trees

Products

Reproduction

Products

Forage

Reproduction

Pollinators   Flowers   Anthophiles

Biocontrol
agents

Reproduction

Oil Seeds

Shrubs

Reproduction

Products

systems (Richards, 1986) and pollination mechanisms (Faegri and van der Pijl, 1979) which need not be invoked in this view. The most important concepts and terminology in reference to agriculture are presented in Roubik (ed.) (1995) and Free's (1993) book is an encyclopedic treatise on crop pollination by insects.

Anthophiles, or flower visitors, are animals which feed at flowers. They may seek pollen, nectar, oil, or floral tissue to satisfy their nutritional needs (see Kevan and Baker, 1983, 1998; Barth 1985). Pollen provides protein, lipid, carbohydrate, vitamins and minerals in various amounts depending on the plant species. Nectar is mostly a sugary solution and provides energy for locomotion, mostly flight. It also contains other compounds, some probably involved in nutrition, in trace amounts. Oil is provided by some specialized flowers as the reward for their specialized pollinators. Floral tissue is thought to have been the original resource sought by primitive, herbivorous anthophiles, the beetles (Coleoptera) (Bernhardt and Thein 1987) although nectar feeding Diptera may have been also among the earliest of pollinators (Ren 1998). Pollinators are anthophiles which bring about pollination. Not all anthophiles are effective pollinators: some are floral larcenists that remove the resources sought by pollinators or eat pollen needed in abiotic pollination (Inouye, 1980); others may be innocuous and merely rest in flowers or glean residual resources after pollination is over. Although pollinators are vital to plant reproduction, non-pollinating (or poorly pollinating) anthophiles may also be important in ecosystemic function. For example, many insects that are useful in biocontrol of pests, require florally derived food to mate, find hosts, oviposit and complete their life cycles (Jervis et al., 1993; Ruppert, 1993). There are also anthophiles that use floral sites for capturing prey (Kevan and Baker, 1983; Greco and Kevan, 1994)

Biodiversity of Anthophiles, Pollinators & Pollination
General

Demonstrating that an anthophile is a pollinator requires care. First it is necessary to establish that the plant in question requires a pollinating agent; some plants set fruit and seed without the intervention of pollinators, and some can do so even without fertilization (Richards, 1986). Then, it is not enough that the anthophile is commonly encountered on flowers of the plant: the particular anthophile may be a floral larcenist on some plant species but the true pollinator of another. A pollinator must visit the flower in such a way, and within such a period, that viable pollen is transferred from anther to stigma. Associated with these requirements are the anatomical and behavioural fit of the pollinator and the flower, the appropriateness of the floral advertisement to the pollinator's sensory capabilities, and the floral resources d the pollinators' needs. Taken together, floral characteristics can be combined into "syndromes" that suggest the nature of the pollinator, and the characteristics of the pollinator may suggest what sorts of flowers they are best suited to pollinate (see Faegri and van der Pijl, 1979; Whitehead et al., 1987). The harmonies between floral and pollinator characteristics can be taken as evidence for the long period of co-evolution between flowering plants and pollinators. Nevertheless, there are many flowers that are effectively pollinated by a wide diversity of animals (Waser et al., 1996) along with many that are special, with restricted assemblages of potential pollinators (e.g., Grant and Grant, 1965, 1968; Hurd et al., 1975; Faegri and van der Pijl, 1979; Vogel, 1990; Proctor et al., 1996). Very few species of plants appear to be pollinated by single species of pollinators.

The diversity of anthophiles probably numbers in the millions of species. Most species of bees and wasps, and many ants (Hymenoptera), true flies (Diptera), moths and butterflies (Lepidoptera), and some families of beetles (Coleoptera) visit flowers. There are other insect orders in which anthophily is common, as in thrips (Thysanoptera), and others where it is quite specialized, as in the Zaprochilidae (Orthoptera) or sporadic, as in the springtails (Collembola).

Proctor et al. (1996) present an extensive discussion of the most important orders of insects which visit flowers. The characteristics of the flowers they visit (i.e., color, shape, scent, and rewards) function as a unit and can be used to typify the flowers according to their pollinators. These suites of floral characters, or floral syndromes, are discussed by Faegri & van der Pijl (1978) and, although not intended to be precise, are useful as generalizations which become evident throughout this review, the misgivings of some pollination biologists not withstanding (see Herrera 1996, Waser et al. 1996).

Coleoptera

The most primitive pollinators are often thought to be, and to have been, beetles. By the time flowering plants became important in late-Jurassic and Cretaceous time, beetles were well differentiated. They were probably destructive in flowers, chewing on the ovaries, anthers, and other floral parts, as well as eating pollen and floral secretions. The flowers they visited are conceived as heavily constructed and bowl shaped, perhaps with the scent of aminoids or fermenting fruit. Pollination was accomplished in a "mess-and-soil" manner. *Magnolia* is often tendered as a model. Many flower-visiting beetles loosely fit the above description. However, the syndrome of cantharophily as described is

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not evident in many flowers that are also visited and pollinated by beetles. Some specialized relationships exist as in the pollination of some orchids by beetles and, as in the neotropical beetle, *Nemognatha*, which has highly elongate maxilla used to reach deep into long tubular flowers, such as those of *Ipomoea*.

Most of the predatory Adephaga are not flower visitors, but among the Polyphaga there are many flower visitors. Some families (e.g., Mordellidae, Oedemeridae, and Melyridae) may be exclusively anthophilous as adults in search of food. Some show clear adaptations to floral feeding such as forward projection and elongation of mouthparts, uptilting of the head, and elongation of the prothorax.

Curculionidae are known to be associated with many palm inflorescences, and recently *Elaeidobius kamerunicus* has been introduced from Africa to Malaysia to pollinate the oil palm *Elaeis guineenis*, also of African origin (Syed *et al.* 1982, Kevan *et al.* 1986). Palm inflorescences (form and unisexuality) are reminiscent of strobili of Cycadaceae, some of which are also pollinated by beetles, including weevils.

Diptera
Diptera have also been suggested as pollinators early in the evolution of flowering plants (see references in Larson *et al.* in press). The Nematocera are the most primitive. In most families the proboscis is short, although variable in form. Sciaridae have been recorded from the flowers of *Drimys* (Winteraceae), a primitive flowering tree of the tropics. Its flowers, like those visited by other Nematocera, have readily accessible nectar, exposed or partially exposed in short tubes (e.g., *Achillea, Senecio, Polygonum,* various Brassicaceae, and Apiaceae) or even somewhat hidden (e.g. *Salix*). Most Nematocera are small (Mycetophilidae, Cecidomyidae, Simuliidae, Chironomidae, Ceratopogonidae, etc.). For the most part, these insects seek nectar, although some feed on pollen [e.g., *Bibo, Scatopse, Sciara,* and *Atrichopogon* (Downes 1971)]. The larger Tipulidae are restricted to the same sorts of flowers, as they too have short mouthparts. The Nematocera with longer proboscides (e.g., Culicidae and Bibionidae) also visit such flowers, but included are some with deeper tubular corollas (e.g., Asteraceae and Scrophulariaceae). Hocking (1953) has detailed the nectar relations of biting flies, but in general the relations of Nematocera and flowers are poorly known except that nectar is important in nutrition, fuel for flight, and longevity (Yuval 1992; Smith & Gadawski 1994). Fungus gnats have been shown to be important in the pollination of flowers on the floor of Californian redwood forests (Mesler *et al.* 1980).

Although most flower visiting by Nematocera seems rather general, specialized relationships exist as in mosquito pollination of *Habenaria* orchids and various Nematocera in pollinating Araceae. In the latter the inflorescenc and associated structures rely on heat, mimetic scents, and colors to attract the pollinators (below). Cocoa is pollinated by specialized Ceratopogonidae (cf. Winder 1978, Free 1993, Roubik 1995).

The Brachycera present a wide diversity of flower visitors. The recent report of Ren (1998) of Late Jurassic fossils of these flies concludes that they were pollinators of angiosperms even then. There are numerous records of Stratiomyidae, Dolichopodidae, Lonchopteridae, Phoridae, and especially Empididae and Bombyliidae as flower visitors. Probably, most adult Brachycera feed at flowers. Those with short mouthparts visit many kinds of flowers with easily accessible nectar. Those with longer mouthparts, especially the Bombyliidae, also visit more deeply formed and tubular flowers. The bombyliids are among the most specialized of dipteran flower visitors. Most have long sucking mouthparts (Jervis and Gilbert 1998). *Bombylius major* has a proboscis about 10 mm long; in *B. discolor* it is about 12 mm. This genus has been recorded on *Viola, Primula, Cardamine, Vaccinium,* and *Muscari*. The Empididae, although not as specialized for flower feeding as many bombyliids, are common flower visitors throughout their almost ubiquitous range. These flies use their tubular piercing mouthparts for killing and feeding on prey as well as for extracting nectar from open to short tubular flowers.

The Cyclorrhapha, the largest suborder of Diptera, is split into the Aschiza and Schizophora. In the Aschiza, Syrphidae (hover or flower flies) is the most important family of anthophiles. These flies feed on nectar and pollen. Their mouthparts are variable, allowing different species to feed from the open-flowered Apiaceae to the deep flowers of Asteraceae, Labiatae, Scrophulariaceae, Violaceae, Primulaceae, Polemoniaceae, and so on. The hover flies with short mouthparts may be found on deep tubular flowers from which they feed on pollen; they are unable to reach the nectar. Pollen is the protein staple of many Syrphidae (Gilbert 1981). Little is known of the anthophilous habits of other Aschiza; some families are flower visitors, others are not.

In the Schizophora, the Acalypterae contain one noteworthy flower-visiting family, the Conopidae. These insects have long proboscides, and about 6 mm in *Sicus* spp. And 4 mm in *Conops* spp. They seem to be restrictive in their floral preferences, the Asteraceae being favored. They are recorded from other flowers. Their possible role in pollination is not well understood. Most families of the Acalypterae have been recorded on flowers. Many Tephrididae oviposit on the heads of Asteraceae. Some Drosophilidae and Sphaeroceridae are sometimes found feeding and

breeding in spathes of Araceae and in other flowers.

The Calypterae are an important group of anthophiles. The parasitic Tachinidae have elongate mouthparts (Jervis and Gilbert 1998) and are frequently found on flowers , especially of Asteraceae. Calliphoridae have shorter mouthparts and may visit flowers when preferred food (e.g., dung and carrion) is not available. The Muscidae is a huge family with many well-known anthophiles. Many have short mouthparts and are not specialized anthophiles. Their importance in pollination is often discounted although they are abundant, frequently visit flowers, and effectively transport pollen. They are especially important pollinators in the Arctic (Kevan 1993). *Scathophaga* spp. feeds at flowers for nectar and for prey. The Anthomyiidae are well-known flower visitors; some have quite long mouthparts. They feed on nectar; some also feed on pollen which may be the protein staple for adult nutrition and ovarian maturation.

The syndrome of myophily is rather broad and indefinite (Larson *et al.* in press) but the sapromyophilous pollination syndrome is characterized by flowers which attract a variety of dung and carrion flies. The flowers are mimetically colored to resemble dung or carrion and release skatoles or aminoids to be appropriately smelly. *Rafflesia* (with flowers up to 1 m across), desert *Stapelias*, Aristolocheaceae, some Araceae, and orchids serve as examples. Some (e.g., *Ceropegia*) have light windows towards which the pollinators crawl, passing the sexual parts of the inflorescences in attempting escape.

Lepidoptera

Most adult Lepidoptera feed extensively on floral nectar. Some feed on a variety of other liquids, as in puddling, or on fruit juice, excrement, animal secretions, and even blood. A few do not feed at all, especially in the females. The Micropterigidae may feed directly on pollen. The characteristic long, sucking proboscis shows its epitome in *Xanthopan morgani* f. *praedicta* (Sphingidae) which feeds on nectar of, and pollinates, *Angraecum sesquipedale*, an orchid of Madagascar with a nectariferous spur 25-30 cm long. Generally, Lepidoptera imbibe only less viscous nectars, but some (e.g., *Plusia gamma*) may secrete saliva to dilute syrupy or crystallized nectars for imbibing, as do many Diptera.

The flowers visited by the diurnal butterflies are often colorful and may or may not be scented. Typically, they have long tubular corollas with extended petal lobes which form a platform on which the butterflies land to feed (e.g., *Phlox, Primula, Dianthus*). The heads of many Asteraceae form similar platforms. The flowers visited by nocturnal moths are typically pale and strongly scented. The scent acts as a long-distance attractant, and the color, contrasting with dark vegetation at night, may be enhanced by the floral parts being long and divided. Some flowers provide landing tforms, but those pollinated by hovering moths, such as Sphingidae, open more horizontally and are more trumpet shaped. Recently, *Gnetum* (in the bizarre order Gnetales of the gymnosperms) despite its lacking petals has been shown to be pollinated by moths (Kato & Inoue 1994) in Malaysia.

Hymenoptera

Bees are recognized as the most important pollinators, yet other groups of Hymenoptera are frequent visitors to flowers. The Symphyta have short mouthparts and no special adaptations to anthophily. Many visit the flowers of their larval host plants and flowers with easily accessible nectar. There they may feed on nectar, pollen, or floral parts. Their relations with flowers are nearly all unspecialized and little studied. In the Apocrita the Parasitica are also mostly unspecialized anthophiles, but some, especially in Braconidae, Ichneumonidae, Leucospidae, and Chrysididae, have elongate mouthparts apparently adapted for feeding on nectar from tubular flowers (Jervis 1998) White flowers seem to be frequently visited. Nevertheless, some may be restricted in the range of flowers they will visit. Studies of the floral relationships of Parasitica are needed because of their potential as biocontrol organisms and the importance of nectar in their nutrition (Patt *et al.* 1997). Some highly specialized relationships are noteworthy, such as the pollination of *Cryptostylis*, an Australian orchid, by *Lissopimpla semipunctata* (Ichneumonidae) by pseudocopulation in which the males pollinate the flowers while attempting to copulate with them. The remarkable story of fig pollination by *Blastophaga* is described by Wiebes (1979) and Janzen (1979) and the keystone place of figs in tropical forest ecology pointed out by McKey (1989). The Chrysididae are the most specialized of the Parasitica for flower visiting, some having long proboscides, yet their role in anthecology is unknown.

Among the Aculeata, only the bees have elongated proboscides. The adults of many families of wasps visit flowers extensively (Spradbury 1973), mostly for their own nutrition. Some social Vespidae (e.g., *Vespula*) also gather sugary liquids to feed their larvae. "Wasp-flowers" have been characterized as dull, pinkish to brown in color, with easily accessible nectar and sometimes unpleasant smell (e.g., *Scrophularia, Cotoneaster, Epipactis*). Some Formicidae are frequent visitors to flowers, but their importance in pollination is probably mostly little. Nevertheless, for some plants the ant pollination syndrome is for low sprawling plants with flowers of different individuals being intermixed and with easily accessible nectar. The ants can walk between flowers of different plants carrying pollen. *Diamorpha smallii*

(Crassulaceae) is a convincingly described example (Wyatt 1981). Other relations between ants and flowers involve the protective function of ants feeding at extrafloral nectaries and repelling other more destructive herbivores from developing flowers, as in *Helianthella* (Inouye & Taylor 1979) and in various crop plants on which extrafloral nectaries support a complex of biocontrol agents (Bentley 1983).

The Apoidea are the most important and highly adapted anthophiles. Their mouthparts are especially adapted for imbibing nectar and their bodies, with characteristic plumose hairs, for carrying pollen. They are highly diverse structurally, behaviorally, and taxonomically. Bumblebees and honeybees are quick at learning floral intricacies and behaviorally adept at manipulating complex flowers (von Frisch 1967, Menzel 1985, Laverty 1994). The syndrome of bee pollination is characterized by flowers which are zygomorphic (i.e., bilaterally symmetrical) with hidden rewards (usually nectar or pollen, but sometimes oils). Familiar examples are Lamiaceae, Violaceae, Fabaceae, Scrophulariaceae, Orchidaceae, *Aconitum*, and *Delphinium*. Broadly tubular flowers such as those of Ericaceae, Boraginaceae, and Campanulaceae and more narrowly tubular Caryophyllaceae, Primulaceae, and Brassicaeae which are radially symmetrical are also bee flowers. Complex and highly specialized relationships exist in the brazil-nut (Lecythidaceae), in pseudocopulatory pollination in *Ophrys* (Kullenberg 1961), and in essential oil gathering and pollinating by male bees at orchid flowers as part of their mating behavior (Williams & Dodson 1972, Buchmann 1987, Roubik 1989, Vogel 1990). The diversity of bees on flowers and their pollinating habits are given in broader studies on Onagraceae (cf. Linsley *et al.* 1963), creosote bush (Hurd & Linsley 1975), sunflower (Hurd *et al.* 1980), and squash (Hurd *et al.* 1974). Eickwort and Ginsburg (1980) thoroughly reviewed foraging behavior in Apoidea. Roubik's (1989) encyclopedic book on tropical bees discusses their flower relations and Plowright and Laverty (1984) provide details for bumblebees.

Minor Groups of Arthropods
Although most anthophilous insects are Holometabola, lower orders are also found (cf. Porsch 1958, Kevan & Baker 1983). Collembola ingest pollen, and sometimes nectar, from flowers all over the world (Kevan & Kevan 1970). Plecoptera and orthopteroids also visit flowers (Porsch 1958, Kevan & Baker 1983). In the latter, floral mimicking predators (mantids) and herbivores (phasmids) are known. Blattids are known to visit flowers but are infrequently recorded. They may be pollinators. Tettigoniids, especially *Conocephalus*, may be frequent and destructive flower visitors. The peculiar Australian Zaprochilinae are adapted for anthophily, having narrowly prognathous heads (Rentz Clyne 1983). Acrididae are frequently encountered on flowers, but discounted as incidental visitors. Earwigs (Dermaptera) hide in flowers where they are generally destructive.

Thrips are notorious flower visitors, and some have mouthparts especially adapted for piercing and sucking out pollen grains (Lewis 1973, Kirk 1985). Their role in pollination has been investigated in only a few plants, e.g. in European Ericaceae (Hasterud 1974) and in Malaysian Dipterocarpaceae (Appanah & Chan 1981)

Heteroptera are conspicuous and common anthophiles. Nabidae, Miridae, Lygaeidae, Coreidae, and Pentatomidae are the most frequently found anthophilous families; they frequent flowers with easily accessible nectar (e.g., Asteraceae and Apiaceae). Some Phymatidae use flowers as places to prey upon other insects (Balduf 1941, Greco and Kevan 1994). There is little information on the importance of the anthophilous habits of these insects to either the insects or the plants. There are occasional records of Neuroptera, Mecoptera, and Trichoptera as flower visitors feeding on nectar, or pollen, or both (Porsch 1958).

Vertebrates
Among the vertebrates, some groups of birds (e.g. hummingbirds (Trochilidae), flowerpeckers (Dicaeidae), honeyeaters (Meliphagidae), honeycreepers (Coerebidae), sunbirds (Nectariniidae), and lories (Loriinae)) are specialized pollinators that service flowers illustrating the syndrome of ornithophily. The flowes are mostly red and tubular with orientations on the plants for hovering or perching birds. Bats (fruit bats or flying foxes (Pteropidae) of the old world Tropics and leafnosed bats (Phyllostomatidae) of the Neotropics) are notorious as anthophiles and pollinators (see Arita and Martinez del Rio, 1990). In the South Pacific, conservation issues loom for flying foxes and the plants they pollinate (Cox et al., 1991). The syndrome of chiropterophily includes nocturnally blooming, pale, large, robust flowers with strong scents, numerous anthers and abundant nectar. There are even a few other specialized gliding and scansorial mammals that are important pollinators, especially in Australia and Africa (see Proctor et al., 1996). Even primates are important as pollinators in some places. e.g., Madagascar (Kress et al., 1994).

The co-evolved system of attractants and rewards for pollination.
lor and Color Vision

The visual spectrum of insects is shifted approximately 100 nm to the shorter wavelengths of the spectrum as compared with humans: their vision extends from about 300 (UV) to 650 nm (yellow-orange). The extensive review by Menzel (1985) shows that most insects so far tested have peaks of sensitivity in UV, blue-green, green (or yellow). In *Apis* and *Bombus*, color vision has been shown to be trichromatic, that is, using those three primary colors. Some flies appear to be deuteranopic (color blind, analogous to red-green color blindness in humans) and confuse blue through yellow but distinguish UV. Some insects may have only tonal, or black and white, vision. A few insects seem to include red as a fourth color. The neural mechanisms of color vision in insects are known to be very different from those of human beings and rather than using color mixing, work by color opponency coding (Backhaus 1991), the details of which are beyond the scope of this chapter. Kevan (1978, 1983) and Kevan and Backhaus (1998) have placed insect color vision, as represented by the European honeybee, *Apis mellifera*, into an ecological context, especially in anthecology, by considering the properties of daylight and the spectral reflectance of flowers, and their backgrounds across the insect visual spectrum. Kevan's original method of colorimetry and color naming by adapting techniques used in the trichromatic color-naming scheme used for human color vision has shortcomings, but it provided a method whereby human beings may start to have an appreciation of the diversity of color patterns in the insect world. The scientifically rigorous approach through color opponency coding (Backhaus 1991) now allows for precise measurements of color differences of objects and lights as they are perceived by insects. Nevertheless, Kevan's (1972a, 1983) ecological generalizations hold and Kevan and Backhaus (1998) suggest new directions for research. Particularly important is that UV is no more important to insects than the other primary colors and that all wavebands of concern to insects must be considered when attempting to understand floral colors as insects may see them (Kevan & Backhaus 1998).

Kevan (1983) examined whole floras of particular habitats–the Canadian high arctic and Canadian weeds–and showed that the colors of the flowers are more diverse and more discrete to insects than to humans. More recently Menzel & Shmida (1993), by examining some of the flora of Israel and Chittka *et al.* (1994), using a general data base of spectral reflectances of flowers, arrived at similar conclusions which they expanded into floral phenology, habitats, and growth form. Recently, Pielot (1998) has used computer simulations of floral colors and insect color vision systems to
ive at the conclusion that evolutionary processes quickly produce a more or less stabilized array of discrete floral colors and the sort of trichromacy usually found in insect pollinators.

Color patterns within flowers are more diverse and contrasting when looked at in the insect visual spectrum. These color patterns, or nectar guides, assist insects in obtaining rewards on complex or large flowers. Some of these are bulls-eye patterns as in *Myosotis* spp. with its blue coloration and yellow center, or in many Asteraceae with yellow centers and yellow + UV peripheries. Others are patterns of stripes and spots such as can be seen on *Viola* spp, *Digitalis* spp, many lilies, and so on. In general, butterfly flowers show the highest incidence (83%) of nectar guides, followed by zygomorphic flowers and then capitulate ones. Even about half of the bowl-shaped flowers examined have nectar guides. These patterns may change with age, telling the informed visitor the state of the flowers (Weiss and Lamont 1997). In *Aesculus* spp. the yellow-spot nectar guides turn red as the flowers age and cease nectar production; they are then ignored by bumblebees. The capitula of *Senecio* spp. become brown in the center as they age, cease producing nectar and pollen, and are then ignored by hoverflies. The flowers of numerous genera of legumes change the colors of their banner petals as they age (e.g., *Lupinus, Lotus, Oxytropis, Caesalpinia, Parkinsonia*). They often also change their shape, some by wilting, after pollination. Post-pollination changes are often rapid as in orchids (cf. Gori 1983).

Some generalizations on the color preferences of insect groups for flowers can be made cautiously. Flowers reflecting blue are frequented by bees, but these flowers are often structurally adapted to bee pollination (e.g. , Fabaceae, Scrophulariaceae, Boraginaceae, Lamiaceae). Nocturnally pollinated flowers are pale, as are flowers of the deep forest, and contrast against dark or ill-lit backgrounds. Yellow flowers attract an almost unlimited diversity of visitors. Some unspecialized Coleoptera, Diptera, and Lepidoptera seem to show preference for yellow. Red flowers are mostly associated with bird pollination, but others have butterfly and beetle pollinators (Kevan and Backhaus 1998, Dafni 1997). Some butterflies have been shown to have red-sensitive vision. There are almost no UV flowers: *Papaver rhoeas* is one, being red (invisible as a color to most insects) and UV. The UV reflective patterns on *Ophrys* flowers pollinated by pseudocopulation by male *Gorytes* wasps offer a "supernormal" visual image in mimicking the female

wasp: the flowers have more UV insect reflectance than the model (Kullenberg 1961).

Floral Size, Shape and Other Visual Attributes

From the foregoing, it is obvious that flower color is important to anthophiles in their recognition of plant species and the potential for reward offered by the flowers. Other visual attractants also play a part in attraction. The size of flowers, inflorescences, or the corporate image of floral groups have been shown to be positively related to attractiveness over distance (Dafni *et al.* 1997). However, size and color combine in fascinating interplay. Giurfa *et al.* (1996) showed that the distance from which an object is detected by an approaching honeybee depends on the angle the object subtends at the bee's eye, but that distance is influenced greatly by the color of the object and the contrast it makes with its background. For example, an 8 cm disc that has colour contrast, which includes contrast in the green part of the spectrum, with its background is visible from about 90 cm (an angle of about 5 °) but that if green contrast is lacking, the distance of detection is much less at about 15 cm when the angle is about 15°.

Floral shapes are also recognizable by insects. The ratio of the length of the perimeter of a given shape to its area is termed contour density and is important in attraction and recognition. Many insects appear to have innate preference for objects with high contour densities (see Dafni *et al.* 1997).The orientation of floral shapes are also recognizable. Moreover, bees can distinguish between symmetrical an asymmetrical ones (Giurfa and Eichman 1997). It is generally thought that honeybees, at least, remember idetic (i.e. photgraphic or template like) images for use in recognition and discrimination (Dafni *et al.* 1997). Dafni and Kevan (1996, 1997) have related flower's shapes and nectar guides to their presentations to foraging activities of foraging insects, the positions of densest areas of ommatidia on the compound eye (fovea) and habitat. In short, they propose that bees that forage on vertical arrays of flowers should have forward-upward directed fovea as they forage upwards on downwardly oreinted flowers of inflorescences; but bees that forage on meadow plants with single flowers or tight inflorescneces (Asteraceae, Apiaceae) should have forward-downward directed fovea as they forage over the plants and descend to land and feed.

Flicker fusion, that is, the speed at which flickering images blur together and appear to cease to flicker, is very much faster in insects than in humans. Thus, floral movement and the outlines of flowers where they contrast against the background, do not blur-out as the insect moves towards and about the flowers and the ommatidia of the compound eye are repeatedly and sequentially stimulated. Dafni *et al.* (1997) discuss what little is known about this aspect of flower visiting by insects. In general, flowers with broken outlines and patterns of coloration or with moving parts are more attractive than plane or stationary objects, but these phenomena have been little studied.

The contour following behavior of insects (Lehrer *et al.* 1985) as they hover momentarily before they land on flowers indicates that they scan the object for general orientation, detection of shape and floral orientation, and perception of nectar guides or floral parts, or both. Certainly edge detection is very important to landing by insects (see Dafni *et al.* 1997) and many flower visiting insects orient to the edges of flowers or floral parts.

Odor & olfaction

It is more difficult to generalize about floral odors than about colors. Odors are rather more difficult to analyze despite modern techniques (Dobson 1994; Knudsen *et al.* 1993). Nevertheless, some generalizations can be made. Floral fragrances are generally blends of chemicals of different classes. These include isoprenoids, derivatives of fatty acids, benzenoids, and aminoids which, in turn, are represented by compounds with different functional groups such as alcohols, esters, ketones, acids, and hydrocarbons (Dobson 1994). These compounds serve mostly to attract pollinators (Williams 1983, Dobson 1994). Indeed, insects' powers of olfaction are more diverse than their powers of vision. Many floral odors have no counterparts outside blossoms: we associate the scents with flowers. In diurnal flowers, it seems that floral odors mostly act as a close-in attractant to entice landing after relatively long-distance attraction by general coloration and at closer distances by color patterns. However, the corporate scent of large stands may act over long distances as has been noted in pollinator attraction to orchards. The olfactory sense of bees seems quite similar to that of humans, although bees are more sensitive to floral scents and pollen volatiles (see Dobson 1994) and their own pheromones (von Frisch 1967). Butterfly-pollinated flowers are mostly weakly scented, possibly reflecting a poorly developed olfactory sense in these insects. Nevertheless, butterflies can and do orient strongly to olefactory cues (Dobson 1994). Diptera are diverse. Some appear not use olefactory cues in oriented to flowers, others learn to associate floral rewards with scents, and others apparently have innate responses to various kinds of aromas (Dobson 1994). Flowers pollinated by nocturnal Lepidoptera (moths) are notorious for their heavy-sweet, noctrnally emitted, scents. These contain acyclic terpenes, benzenoid, and often indolic compounds (Dobson 1994) which are detected from long distances by foraging moths. The compounds may also function as feeding and oviposition stimulants. We

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have already noted plants with mimetic scents that attract pollinators. These include skatoles and aminoids which are emitted from various Araceae, Aristolocheaceae, *Stapelia*, *Rafflesia*, and so on, and attract dung and carrion-seeking flies and beetles (Dobson 1994). Musky scent from *Arum conophalloides* attracts biting flies and fungal scents of some Aristolochiaceae and Araceae entice Mycetophilidae to enter and pollinate (Vogel 1978). The bee-orchids, *Ophrys*, are remarkable in producing a chemical mimic of the mating pheromones of bees and wasps; they resemble farnesol, hydroxycitronellal, and γ-cadinene (Priesner 1973) and induce copulatory behavior by the male insects on the flowers to bring about pollination. At other orchids, male euglossine bees collect chemically complex perfume droplets (Williams and Dodson 1972; Roubik 1989). The perfume is used by the bees in mating behavior, and the specific relations between species of euglossine bees and *Catasetum* act as isolating mechanisms in both the plants and insects (cf. Dodson 1975, Buchmann 1987).

Some floral scents, such as phenylacetaldehyde, which smells of lilac, has been tried to bait black-light traps for moths. This compound is also emitted by the bladders of *Araujia sericifera* (Asclepiadaceae) flowers. The flowers are complex and only strong moths bring about pollination; the weaker ones are held by the tongue in the flower (Cantelo & Jacobson 1979). Different scent morphs in alfalfa have been shown to be preferentially pollinated. Galen and Kevan (1983) investigated this sort of phenomenon in the Rocky Mountain alpine plant, *Polemonium viscosum*, which may have either sweet or skunky flowers. The former are most visited by bumblebees and are more frequent at higher altitudes, as are bumblebees. At lower altitudes, but still above timberline, bumblebees are less common, skunky plants more common, and the flies which visit the flowers have fewer open bowl-shaped flowers from which to feed than they do on higher slopes and disruptive selection has been invoked (Galen 1996). Some insect pests, e.g. seed chalcids (Eurytomidae) respond positively to floral volatiles of their host plants, but some floral volatiles also have deterrent properties and may function in protection or in reducing the size of the guild of pollinators (see Dobson 1994 for discussion).

THE REWARDS OF VISITING FLOWERS

As shown in Fig. 2 the insect rewards of visiting flowers are mostly nutritional, in nectar or pollen or both, or other floral tissue, but they also include havens from predation, for warmth and sex. The chemical nature of nectar and pollen can be placed in the context of the foraging energetics of insects. Baker & Baker (1975, 1983) and Kevan & Baker (1983) have reviewed the significance of nectar chemistry to pollinators, and Baker & Baker (1983) and Kevan & Baker (1983) have discussed pollen. Foraging energetics has been well reviewed by Heinrich in respect to bumblebees (1979) and in general (1983). Through the following discussion, the coadaptations of floral rewards and insect foraging and energetics will be seen to be as precise as the coadaptations for floral attractants and insect senses.
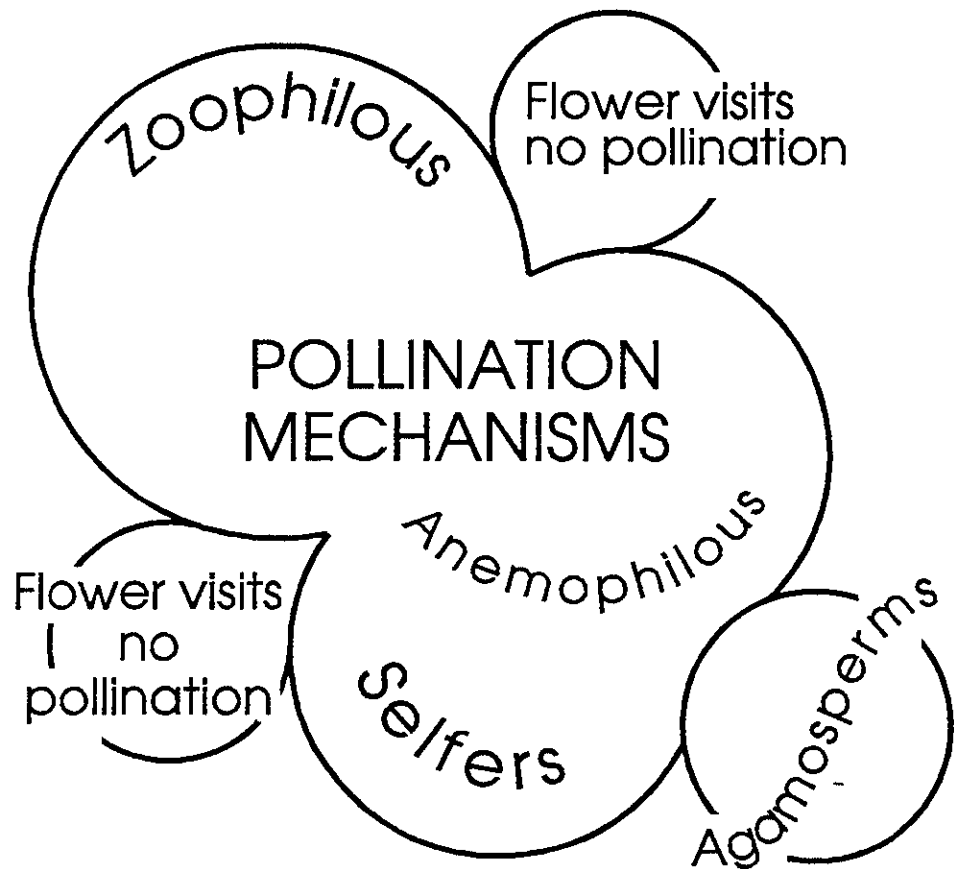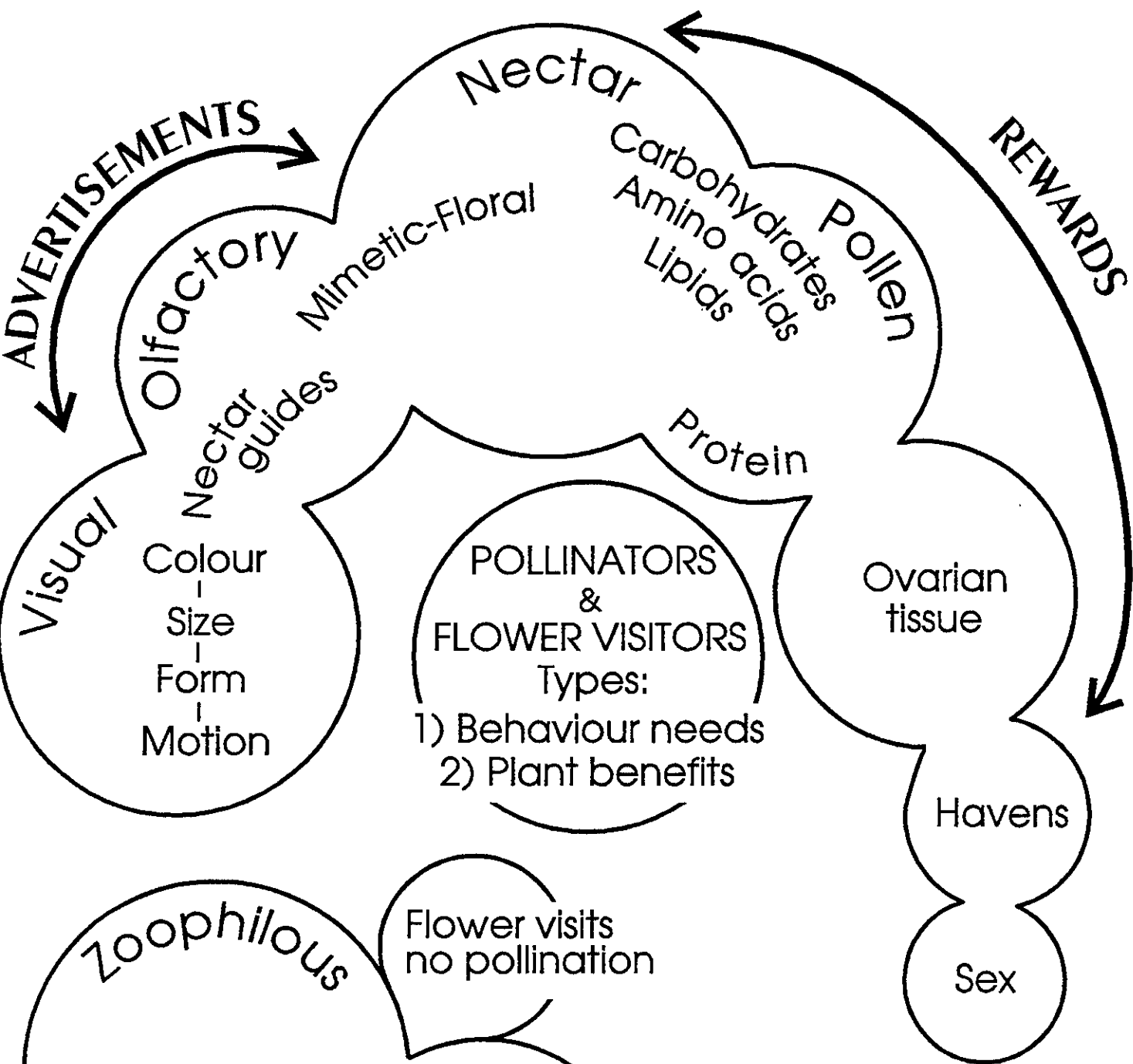
Figure 2 near here
Caption: Figure 2. The interplay between floral attractants or advertisements, and floral rewards for pollinators and other anthophiles as they relate to pollination mechanisms and co-evolutionary relationships (see Fig. 3). (from Baker and Kevan 1984)

Nectar & Other Liquid Secretions

Nectar is a plant secretion derived from phloem sap. Its secretion is a complex physiological process of special glands (nectaries) that are not restricted to flowers. Autonomous rhythms in the plant, together with the plant's nutritional state, water balance, and responses to the physical environment, all affect secretion. After secretion, nectar may evaporate or absorb water, depending on atmospheric humidity, to become more or less concentrated (Corbet *et al.* 1979), or it may be resorbed (Búrquez and Corbet 1991). Thus, generalizations about sugar concentrations of nectar must be made cautiously (see Kearns and Inouye 1993).

Nectar is a complex mixture of chemicals, of which sugars are the major constituents. Amino acids, proteins, lipids, antioxidants, alkaloids, vitamins, organic acids, allantoin and allantoic acids, dextrins, and inorganic materials such as minerals may be present and have some role in pollination.

The three major sugars of nectar are glucose, fructose, and sucrose. These occur in different proportions in different plant families (e.g., Ranunculaceae tend to be sucrose-rich, whereas Asteraceae and Brassicaceae tend to be hexose-rich). Open bowl-shaped flowers tend to be hexose-rich, have concentrated nectar because of evaporation, and are visited by generalist anthophiles with short lapping mouthparts. Flowers pollinated by long-tongued bees, butterflies, and moths tend to be sucrose-rich. Those pollinated by short-tongued bees may be either. The amount of sugar and nectar secreted also follows the same ranking of least in generalist flowers to more with increasing specialization. The

least amounts are found in open bowl flowers and the most in the zygomorphic and stereomorphic flowers. Not all nectar sugars have the same nutritive value (Haydak 1970). Several are toxic to honeybees, but not to other insects (e.g., galactose, lactose, and raffinose). Although the various uses that insect groups put different sugars to may be different, the main outcomes of sugar ingestion are energy for locomotion (Hocking 1953, Heinrich 1983), development, maintenance, and progeny production (Chapter X), and sometimes in thermoregulation (Heinrich 1993; Barth 1985). Sugars may be converted into fat, as in migratory insects (Johnson 1969, Kevan & Kendall 1997), and stored for long-distance flight and ovarian maturation (Kevan & Kendall 1997). Sugar solutions fed to otherwise starved insects prolong their lives although they slowly lose nitrogen.

The presence of protein-building amino acids in nectar may important in the nutrition of nectarivorous insects. However, there are few experimental studies which test this. Baker & Baker (1982, 1983) have surveyed floral nectars for the amounts of amino acids and found that those with the most amino acids are taken by insects which do not ingest pollen, for example, flowers pollinated by butterflies, settling moths, bees, and wasps. These nectars had 1.15-0.91 µmole/ml of amino acids, whereas those pollinated by insects which may also ingest pollen (flies and bees) had less than 0.56-0.62 µmole/ml. Exceptions occur on either end of the scale with dung and carrion-mimicking flowers at 12.5 µmole/ml and hawkmoth pollinated flowers at 0.54 µmole/ml. In the latter, huge amounts of nectar are imbibed, as much as 1 ml without satiation, and this would contain amounts of amino acids which could be toxic if they were not weakly represented. All 20 protein amino acids can be found in nectars, but all are not equally available. Alanine, aarginine, serine, proline, and glycine are the most commonly available, whereas tryptophan, histidine, and methionine are scarcest. Nonprotein amino acids may also be present. Apart from the nutritive function they probably have, amino acids may be feeding stimulants and taste modifiers.

Proteins in nectars probably have enzymatic roles and are present in small amounts. Lipids and oils are also present in many nectars [34% of those tested by Baker & Baker (1983)], most commonly in those imbibed by Hymenoptera and Diptera. Polyunsaturated fatty acids and sterols are two classes of lipids important to insects, as are fat-soluble vitamins. The exact nutrition roles of these compounds as nectar constituents for insects is unknown, but the lipids must be regarded as beneficial. They may form a waterproofing monolayer on some nectars and thus retard evaporation of water (Corbet et al. 1979). Ascorbic acid and other antioxidants tend to be found together in nectars, elaiophores, and stigmatic exudates where they may prevent rancidity of the lipoidal compounds.

Oil droplets are secreted by some flowers, especially in central and south America in lieu of nectar [e.g., ocrophulariaceae, Malpighiaceae, and Melastomataceae (Vogel 1974, Buchmann 1987)]. The secretory organs, elaiophores, may or may not be part of the nectary. Some Anthophoridae (Centris) have specialized tarsal brushes for handling this oil, which may be mixed with pollen to form food pellets for progeny (Neff and Simpson 1981, Buchmann 1987, Roubik 1989).

Potentially toxic or distasteful compounds such as nonprotein amino acids, glycosides, alkaloids, and phenolics are well known in some nectars and may find their way into honey. Minerals may be important nectar constituents but are not well studied. Potassium at 1500 ppm deters bees from taking onion nectar (Waller et al. 1972). The water in nectar may be important in electrolyte and water balance in insects, so that in hot dry environments watery nectar may be imbibed (Willmer 1986).

Pollen
Although pollen is often suggested to have been the original reward sought by insects visiting the reproductive organs of plants as they started their coevolution with flowering plants (Kevan et al. 1975), it is now mostly secondary to nectar. Nevertheless, it is a vital food for many insects such as springtails, orthopteroids, thrips, beetles, flies, and larval bees. Pollen is highly nutritive (cf. Stanley & Linskens 1974, Harborne 1993), being rich in protein, peptides, and amino acids. Free sugars are less important in pollen than in nectar. Starch may or may not be present and may be an alternative to lipids in other pollens as stored energy reserves for pollen development (Baker & Baker 1979). Lipid-rich pollen tends to be found in plant species which offer pollen as the only floral reward. Wind- and self-pollinated plants tend to produce starch-containing pollen. There is also a correlation with size of pollen grains; the smaller the grains the more the tendency to lipid storage. Lipids in pollen include sterols, which may provide consumer insects with the building blocks of hormones and pheromones. Vitamins are also present, along with pigments, enzymes, and occasional toxic substances.

There has been little experimentation on pollenivorous insects. Pollen is important in honeybee nutrition (Haydak 1970), and in some Diptera it is ingested more frequently by females than by males (by the former at the time of

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yolk deposition in ovarian maturation) (see Larson *et al.* in press)

Other Rewards

Apart from nectar and pollen, some flowers offer special food bodies, sometimes staminodes (non-pollen-producing stamenlike structures), to pollinating insects. However, little is known about these. Flower-destructive insects, especially beetles, must gain much nutriment from eating floral parts such as ovaries and maturing anthers.

Perfume collecting (see Vogel 1990) is mentioned above for euglossine bees. It is not restricted to *Catasetum* orchids, being recorded for *Spathiphyllum, Anthurium,* and *Gloxinia.*

Insects may find protection in blossoms. Certainly thrips, anthocorids, small beetles, and flies may spend extended periods in flowers and may be pollinators (above). The use of flowers, and later fruits, as protected brood chambers is evident in the extraordinary mutualisms of *Tegiticula* moths and *Yucca* (Powell & Mackie 1966), agaonid wasps and *Ficus* (Wiebes 1979, *Hadena bicruris* and *Silene alba* (Brantjes 1978) and in the pollination of oil palm by *Elaeidobius* weevils (Syed *et al.* 1982). Some plants, such as Araceae, generate heat which may drive off volatile chemicals attractive to pollinators. The interesting diaheliotropic responses of parabolic flowers, especially in the Arctic, are known to attract pollinators and positively influence seed production (Kevan 1989). *Serapias vomeracea,* a Mediterranean orchid, has flowers which entice solitary male bee pollinators to spend the night sleeping in them: the morning sun awakens them as temperatures rise to 3°C (Dafni *et al.* 1981).

Some bees and other insects mate in flowers, but the importance of this in pollination is not well known (cf. Kevan & Baker 1983). Insects using flowers as sites for ambushing prey are mentioned above (e.g., flower-mimicking mantids, *Scatophaga*, and Phymatidae). Balduf (1941) noted that the ambush bugs, *Phymata americana*, were most abundant on flowers with the most pollen and nectar, which were well visited by prey species. Crab spiders (Thomisidae) are notorious and cryptic predators in flowers. Greco and Kevan (1994) have studied the ways in which spiders and ambush bugs choose and use flowers for ambushing their prey and concluded that cost of changing ambush site (flower) is related to fastidiousness in choice: highly fastidious adult female crab spiders expend much energy and time in changing site by crawling down from one stem, across the ground, and ascending the next one chosen, but flying ambush bugs are far less choosy. Some mites also use flowers for finding prey or hosts and notorious among these are the nostril mites of hummingbirds (Colwell 1985).
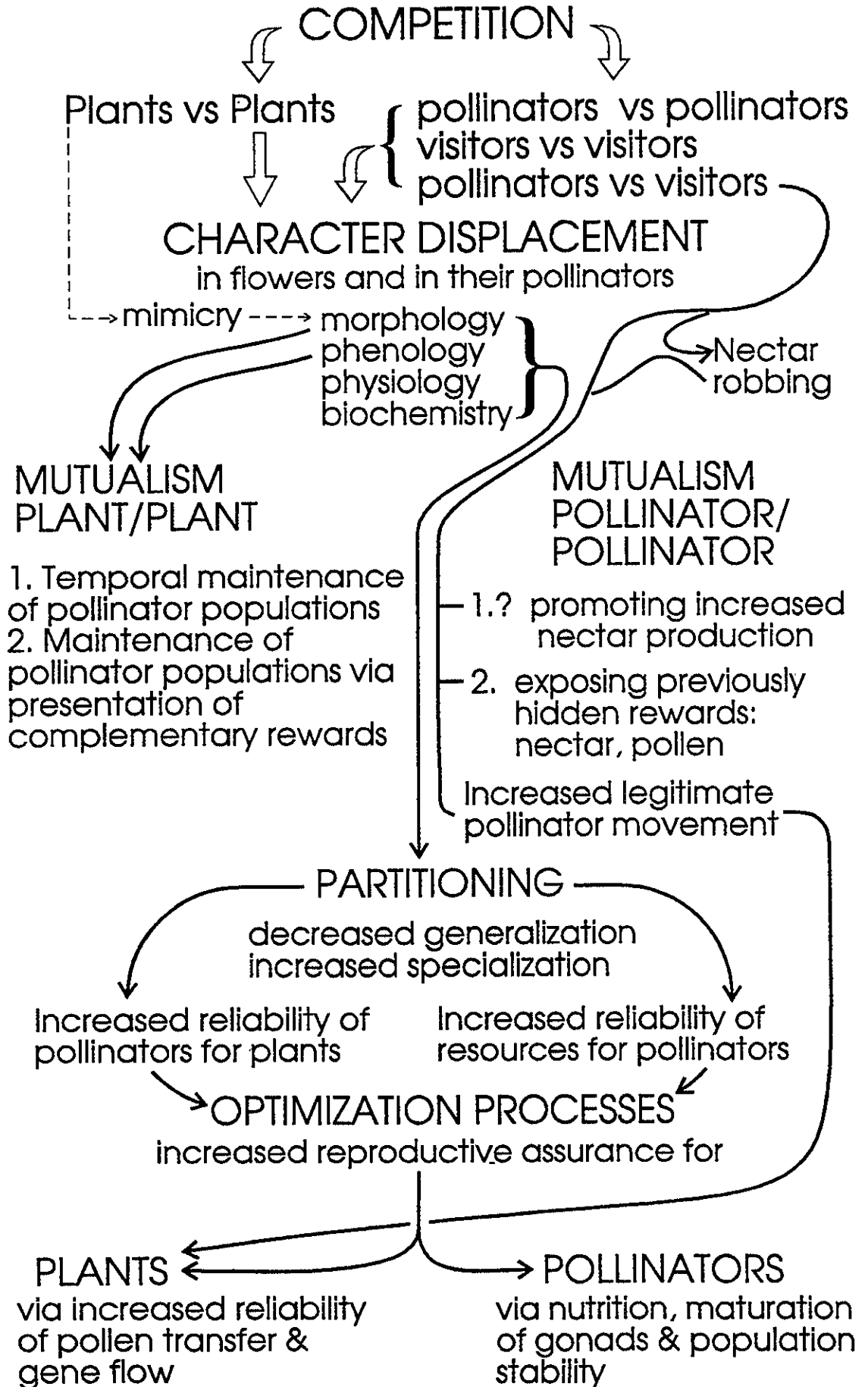

Foraging, Physiology, and Behavior

From the foregoing one can appreciate that the rewards provided by a flower are in accord with the nutritional needs of the pollinator. Most research has been centered on nectar rewards and energy needs of the pollinators. Thus, individual flowers must provide adequate reward to maintain the interest of the pollinators, but not so much as to satiate them before they make the required number of visits to neighboring flowers to bring about pollination (Heinrich 1983). The effectiveness of pollination is determined by floral structure, nectar characteristics (above), resource partitioning and competition between visitors (pollinating or not), and inter- and intraspecific competition between plants for pollinators The pollinators interact in the same sorts of ways but must make optimal use of time and energy in foraging effectively. Figure 3 shows this dynamic interplay of mutualism and competition. One can see how selective pressures for excluding inefficient pollinators can promote a complex pattern of interrelationships in plant–pollinator communities. These pressures result in a frugal energy balance between the plant donor and its pollinators. Concomitantly, coadaptive floral characters increasingly heighten the precision of visitation and pollination through coevolution with pollinator anatomy, preferences, and behavior (Kevan 1984). At the same time, there is room for reversal of specialization, and its not having special adaptive value, thus the favoring of less specialized relationships (Kevan 1984, Kevan and Baker 1984, Waser *et al.* 1996).

Figure 3 near here

Caption: Figure 3. The dymanic interplay of ecological and evolutionary processes through competition and mutualism that can lead to specialization and highly co-evolved systems. It is important to note that the processes depicted may vary in importance, and even result in effects that may become maladaptive. Thus, the processes may run in reverse as precision and specialization decline (from Kevan and Baker 1984).

Physiology

DYNAMICS of POLLINATION ECOLOGY

COMPETITION

Plants vs Plants

pollinators vs pollinators
visitors vs visitors
pollinators vs visitors

CHARACTER DISPLACEMENT
in flowers and in their pollinators

mimicry ----> morphology
phenology
physiology
biochemistry

→Nectar robbing

MUTUALISM PLANT/PLANT

1. Temporal maintenance of pollinator populations
2. Maintenance of pollinator populations via presentation of complementary rewards

MUTUALISM POLLINATOR/ POLLINATOR

1.? promoting increased nectar production

2. exposing previously hidden rewards: nectar, pollen

Increased legitimate pollinator movement

PARTITIONING
decreased generalization
increased specialization

Increased reliability of pollinators for plants

Increased reliability of resources for pollinators

OPTIMIZATION PROCESSES
increased reproductive assurance for

PLANTS
via increased reliability of pollen transfer & gene flow

POLLINATORS
via nutrition, maturation of gonads & population stability

The energy balance in pollination has botanical and zoological components. The amount of absorbed solar energy plants devote to nectar remains almost unstudied. Measuring energy consumption in insects is difficult and mostly done under the artificial conditions of respirometry, using restrained insects so that the readings O_2 consumed o. CO_2 emitted are unnatural. Insects may change their metabolic rate 10-fold over a few minutes, with little outward sign but thier body temperatures are reliable indicators of energy expenditure because most (80%) of their energy is released as heat (Heinrich 1993).

Compared to other animals, flying insects consume vast amounts of energy relative to their weight. During flight, honeybees and bumblebees consume about 10-11 mg of sugar/hr. Sphinx moths have slightly lower metabolic rates yet their weight range, from about 100 mg to 6 g, makes for sugar consumption between 8 and 840 mg/hr. Hovering flight of bumblebees, moths, and hoverflies is most expensive. Small flies (e.g., *Drosophila*) and butterflies (with large wings) have lower metabolic rates in flight.

Another energy expense for foraging is preparation for flight: they must warm up. Some insects, such as flies, butterflies, and some bees, bask in the sun, sometimes in flowers, others regulate their body temperature metabolically and may have metabolic rates of 1000-2000 times as great when thermoregulating than when torpid at 0°C (Heinrich 1993).

Once an anthophile (insect, bird, or bat) has arrived at a patch of floral resources, it may forage by hovering in front of flowers (the most expensive way), flying between flowers and landing on them to feed, or walking between them. Sphinx moths, bombyliid flies, and humming birds do the first, butterflies, flies, and perching birds do the second, ants and scansorial mammals do the last, and many anthophiles including bumblebees and some bats may do all three. On the patch, energy expenditure is determined by the spacing of plants with flowers, and of the flowers on each plant, and by the time it takes the visitor to extract the reward (handling time). Thus, one can see that walking, although energy-efficient, may become costly if the visitor spends too long at it and could be feeding more frequently by flying. Greco and Kevan (1994) found that crab spiders, which must walk from plant to plant to change ambush sites are deliberate in their initial choice of flowers, but adult ambush bugs choose quickly but then often move by flight from their initial floral station to a more preferred one. Both time and energy are expenses in foraging.

With the ideas of foraging physiology, insect size, and anatomy in mind, one can understand the close correlation between the diversity of pollinators, their different energy needs, and the variety of flowers they visit and their rewards, according to composition, concentration, and caloric content. Some flowers pollinated by flies may have as little as 10 μg of sugar in them, which may be highly concentrated by evaporation to as much as 163 mg in *Acanthus mollis*. Hawkmoth pollinated flowers produce the most nectar and the most sugar; however, this sugar is relatively dilute and so not viscous and easily imbibed through the long tubular proboscis of the moths. Honeybee sucking rates decline markedly when syrup concentrations exceed 50-60% sugars. Flies and some butterflies spit on crystallized nectar to liquefy it. Honeybees have a taste threshold of about 10% sugars in syrup; below that they do not taste the sugar. This is a built-in safeguard against net energy loss as the bees ignore too dilute nectars. Insects with lower metabolic requirement (e.g., Lepidoptera) show lower thresholds for tasting sugar solutions. Anthophilous predators choose flowers by some means that indicate liklihood of prey capture.

Behavior

Heinrich (1975, 1979) reviewed the energetics of foraging, especially by bees, and provided details on how nectar resources and foraging energetics are related. A pound of white clover honey represents the production of 8.7×10^6 flowers, which bees visit at a rate 500 per trip of 25 min. Thus, 17,330 bee-foraging bouts are required, taking 7221 bee hours of labor. *Bombus fervidus* forages at 40 flowers/min on red clover, which contains 0.05 mg sugar/flower; this is unavailable to shorter-tongued honeybees and bumblebees as it is out of reach. *B. terricola*, a short-tongued bumblebee, forages faster (110 flowers/min) on *Hieracium*, which has minute amounts of nectar in each floret. On the other hand, bumblebees foraging on *Chelone glabra*, with large complex zygomorphic flowers with an average of 3.3 mg of sugar each, visit for 2-8 min and spend up to 30 sec entering the flower. The time is well invested. In bumblebees, tongue length is an important anatomical feature, partitioning different species among flowers with corresponding corolla tube lengths (Harder 1982, 1983). Learning is also important, as bees invest nonproductive time in learning how to forage from complex flowers, which in turn should offer greater rewards (Laverty 1994). The distance to patches of resources is important to insects which provision nests and must take food home. In honeybees, the waggle dance, signifying the direction and distance to food, is more intense the nearer the source (von Frisch 1967). If food for honeybees is 2-3 km distant, they can make 20 trips/hr whereas if it is 14 km away, only 1. For bumblebees on red clover, flying to a patch 1 km away costs $6.7n$ min or 267 blossoms.

The efficiency of pollinator foraging benefits both plant and insects. Theoretically, a flower visitor should move in ʌch a way as to be optimally efficient in both foraging and dispersing pollen. Hence, the forager should travel short distances and not double back. Both features of optimal foraging have been demonstrated (Pyke *et al.* 1977, Pyke 1978, Waddington 1983). Interplant flight distances are generally short. Turning during foraging has also been quantified, and bees foraging in rich patches of plants with abundant nectar turn more frequently and with sharper angles than they do on less rewarding patches. This activity keeps the forager on the patch for a greater number of more frequent visits. Nevertheless, the mean angle of directional change is 0°, that is, the bees turn left or right but on average move ahead. Wind is an important factor because of the aerodynamics of upwind flight or downwind movement of floral odor or direction of wind over the flowers (Woodell 1978). Foraging at flowers on trees can be likened to collecting materiel from the storeys of a tower, by which it is most efficient to start collecting at the top of the tower and carry in increasingly heavy load down (see Kevan 1990).

Part of this efficiency must also be in the forager's ability to recognize flowers and to learn how to manipulate them. As already mentioned, this requires an investment on the part of the forager so that, once having successfully probed a flower type and obtained a reward, it should continue to forage from those flowers as handling efficiency increases (Laverty 1994). So, floral constancy is developed. Honeybee foragers become recruited to patches of flowers through the waggle dance in the hive but will change to other flowers if resources decline. Bumblebees are less rigid and at any one time have specialty flowers (a "major"), secondary specialties ("minors"), and a testing behavior by which other flowers are investigated (Heinrich 1978). Real (1981) found that if rewards are variable, foragers avoid the flowers, apparently eschewing uncertainty or averting risk.

As well as learning about flowers, foragers also learn their locations. Honeybees are unique in that they can communicate that information to each other. Particularly remarkable are trap-lining insects, such as euglossine bees, butterflies, and perhaps sphinx moths, which forage along extended routes linking isolated patches of resources. Clearly, these activities increase foraging efficiency, as the forager spends less time in site exploration.

So far we gave examined the movements of foragers between plants. Most plants produce more than one flower at a time, some have many thousands in bloom at once. Foragers tend to advance from one flower to the next by moving more or less ahead to the nearest flower. On vertical inflorescences, they tend to start at the bottom and move up (see Kevan 1990). Generally, the nectar is more dilute below, so gustatory saturation may be controlled. Also, the ʌvermost flowers are in the female stage and the uppermost int he male so that pollen flow is between plants. ʌxamples are *Epilobium angustifolium, Delphinium, Aconitum,* many Scrophulariaceae, Fabaceae, and Lamiacae. Highly linear arrangements of flowers, as in *Chamaedaphne calyculata, Polygonatum, Lotus,* and secund inflorescences, make forager movements even more predictable. Circular arrangements, as in Asteraeceae, *Trifolium,* and *Allium,* require foragers to move around the inflorescence until they revisit the first flower visited. Plowright and Hartling (1981) have shown the precision of the relationship between optimal foraging by bumblebees and the optimal number of florets in bloom on inflorescences of red clover for optimal seed-set by outcrossed pollen.

The problems of pollination of massively flowering plants such as trees have been even less investigated from the viewpoint of pollinator movement. It is difficult to see why foragers should not state themselves on one tree and thus not effect cross-pollination. Clearly, large pollinator forces are needed. In Costa Rica Frankie et al. (1983) found that bees follow the opening of flowers on individual trees and move between trees (Frankie & Haber 1983), and Kevan (1990) showed that foragers tend to start foraging on flowers higher in trees, and work their ways down. Thus, they may move in an optimal pattern, and not cross their own paths before departing. On the other hand, Zimmerman (1979) has argued for random movement and optimal foraging together, whereby foragers on dense arrays of flowers on bushy plants eventually cross their own paths and may then depart to the next plant.

Not all insects which visit flowers are potentially pollinating. Some illegitimately remove resources, especially nectar. Inouye (1980) has categorized nectar robbing as involving the destruction of floral tissue and nectar theft as the removal of nectar without destruction or pollination. Some bees are frequent nectar robbers and chew holes in the corollas of flowers to get deeply hidden nectar which would be otherwise unavailable to them. A variety of small insects are commonly thieves, merely entering the flowers or feeding at the bases of the petals or sepals from outside. Pollen larceny also takes place in the same sorts of ways.

Communities of Plants & Pollinators

Pollination ecology at the community level is a new field, even though information about the plants and pollinators of discrete areas has been collected since the late 1800s. Particularly thorough are works reporting on the European alpine community, the arctic, and various geographic areas of Europe and North America. Kevan and Baker

(1983) brought some of this information together, linking it to modern works.

In pollination in alpine and arctic regions Diptera seem to be most important, but bumblebees and Lepidoptera are also well represented. In the Chilean Andes butterflies are important at the highest altitudes. On islands, flowers are often less showy and pollination syndromes less specialized than elsewhere. The same is true on remote and isolated mountain tops. Woodell (1979) points out that plants dispersed to isolated localities may leave their pollinators behind. Kevan and Baker (1983) refer to studies that point out special circumstances and peculiar pollinator assemblages from the Arctic, New Zealand, the Galapágos, East African mountains, Australian alps, Aldabra in the Indian Ocean, and Norderney off the coast of northern Europe. Extreme environments may change pollination systems: sensitive pollinators may be replaced by less sensitive ones (cf. Cruden 1972); the periods of flowering and pollinator activity may be modified to coincide with relatively benign conditions; plants may adapt to abiotic pollination by wind or rain or may become adapted structurally to their environment, along with their pollinators (as discussed for wind and heat above); pollinators may change their habits from flying to walking in cold environments; and plants may avoid insect pollination by becoming self-pollinating or being apomictic.

Although it appears that more generalist pollination systems become more frequent as latitude or altitude increase, close inspection suggests this may not be the case. But even in the arctic there is a significant proportion of specialization (e.g., *Bombus* and Syrphidae on Scrophulariaceae and Fabaceae) (Kevan 1972b). In the boreal forests numerous instances of specialized pollination inter-realtionships exist, along with a variety of plant breeding systems that rivals that of the tropics (Kevan *et al.* 1993). Furthermore, Heithaus (1979) concluded that in tropical forests of Costa Rica there does not appear to be a high degree of specialized relationships. Appanah and Kevan (1995) discuss the diversity of tropical bees and their roles in Southeast Asian forests and again note that relationships range from highly specialized to general. Studies from California, Colorado, Yorkshire, British Columbia, Canadian bogs, South American deserts, the Andes, and the Alps all support these observation (see Kevan & Baker 1983). Different plant communities in a given area are likely to show differences, as Proctor (1978) showed in Ireland. There, in more stable and species-rich communities, the incidence of entomophily increases over anemophily, and entomophily is more specialized in the most stable and rich communities.

To maintain anthecological communities through the optimization processes of pollination energetics for both pollinators and plants, floral and pollinator population densities must be in some sort of fluctuating equilibrium. When floral resources are heterogeneously dispersed, pollinators show less floral constancy, and as the rewards in a particul-patch diminish to below a critical level, suggested to be that of the habitat in genera, foragers should depart from the patch (Charnov *et al.* 1976). Thus, there are fluctuating pressures to select for specialization and generalization which require that genetic and behavioral flexibility be maintained. It is important to realize that factors which favor specialists or generalist pollinators are not necessarily the same as those which favor specialist or generalist flowers (Waser *et al.* 1996, Herrera 1996).

Pollination communities are highly dynamic, being based on the mutualism between plants and pollinators and on competitive relations of plants for pollinators and visitors for plants. Figure 2 shows the evolutionary and ecological pathways this mixed interplay of mutualism and competition may generate.

Competition between plants for pollinators is not well documented. Some weeds, such as dandelions and other "cornucopian" flowers, offer copious rewards and may draw pollinators from other plants and thus affect their reproductive success. Losers in such situations may respond by minimizing competition or its effects. They may become more specialized and reduce the spectrum of their pollinators but assure rewards to those they use. They may remove themselves temporally from competition by shifting their flowering time. On the other hand, they may avoid competition by becoming self-pollinating, at least in part. These ideas are interesting but, as Kevan and Baker (1983) discuss, they are not sufficiently established as fact to be unequivocally accepted. Some phenological patterns in flowering probably have evolutionary significance, possibly reflecting character displacement and even mutualistic effects between temporally spaced blooming plants do fuction: sequential blooms by different species maintain populations of long-lived pollinators such as hummingbirds or nests of social bees (Waser & Real 1979). These ideas lead to consideration of floral mimics of other flowers, another area wide open for research (Dafni 1984). A recent book (Lloyd and Barrett 1996) on floral biology, plant reproductive systems and mostly botanical aspects of pollination provides many interesting evolutionary and ecological insights, but it should be read with considerable care for some of the rather biased views it presents.

Competition between flower visitors is better documented but still little studied. Interspecific dominance rankings place bumblebees as the dominant insects, followed by syrphids and butterflies (Kikuchi 1962 - 1964). Robust body form seems to be an important factor, although small *Trigona* have been documented to drive off larger bees from

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artificial feeding dishes (Koeniger & Vorwohl 1979). The spread of the Africanized honey bee from Brazil is affecting populations of native pollinators as they come into competition (Roubik 1989). The influence of European honeybees on displacing native pollinators in Australia has evoked concern among conservationists as the former are also nectar theives and do not effect pollination (Paton 1993). The potential outcomes of such competitive interactions are shown in Figure 2 and are similar to those for interflower competition, that is, character displacement. Some examples of this may be represented by bumblebees in their differing tongue lengths and body sizes (above) and by similarities of features in species comprising pollinator assemblages of particular plants (cf. Kevan & Baker 1983). These phenomena are difficult to study experimentally but Laverty and Plowright (1985) documented the negative effect of hummingbirds on bumblebees when both were foraging together on *Impatiens*: the bumblebees restricted their activities in the shelter of the stems of the plants when hummingbirds were present, but foraged more widely when the latter were absent.

At a more general level, the natural relationship between the diversity of organisms and their abundance in a taxocene (e.g. pollinators, bees, butterflies) is predicted to be log-normal as an outcome of niche hierarchy, i.e. overlapping but incomplete competition (Sugihara 1980). Indeed, there are examples from bees and butterflies (Kevan et al. 1997) in agricultural and natural ecosystems which appear to support that theory. Log-normality of diversity and abundance in pollinator guilds (taxocenes) seems to provide the greatest levels of pollination activity and plant reproductive success as measured by fruiting and seed-set in various ecosystems from agricultural (Melendez 1997) to less managed and natural ones (Kevan et al. 1997). The possibility of such an indicator of ecosystemic health hasw huge implications for global terrestrial productivity and conservation.

PART II. POLLINATION, POLLINATORS & ANTHOPHILES IN MANAGED AND WILD ECOSYSTEMS: PROTECTION, PROMOTION & CONSERVATION
The Systems: Agroecosystems, Urban Areas, Forests & Wilderness
General

Pollinators are important is all but a few terrestrial ecosystems. In this part of my review, I have arranged the ecosystems from the most contrived (Greenhouses) through Annual and Perennial Cropping Systems, the Urban environment, to Forests and Wilderness.

It must be conceded that honeybees are the most valuable of pollinators in agriculture. They can be managed in easily transportable boxes for pollination of many agricultural crops. Their biology is well known and the technology for using them effectively as pollinators well established (Free, 1993). Nevertheless, they are not the be-all and end-all of crop pollination (Bohart, 1972; Westerkamp 1991; Batra 1995; Williams 1996). They are not the only commercially used pollinator, and cannot be relied upon to consistently pollinate all crops (Martin and McGregor, 1973; Kevan, 1989e, Richards, 1993; Torchio, 1994; Williams 1996). This should be no surprise given the huge diversity of flower and pollinator types. For example, bumblebees (*Bombus* spp.) are the pollinators of choice for red clover, which has corolla tubes that are usually too deep to allow honeybees access to nectar (Free, 1993). Willmer et al. (1994) have noted the superiority of bumble bees as pollinators of raspberry, vis à vis honey bees which service the crop well, because of several desirable foraging habits they show. For pome fruits pollination, orchard bees (*Osmia* spp.) show greater efficiencies and start foraging at lower temperatures than do honeybees (Torchio, 1987, 1991). Alfalfa leaf-cutting bees (*Megachile* spp.) are the primary pollinator for alfalfa and other leguminous crops (Richards, 1993). Bumblebees are now used for pollination of tomatoes and other solanaceous crops in greenhouses (Banda and Paxton, 1991; Kevan et al., 1991c) and of some leguminous crops. The use of the blueberry bee (*Habropoda laboriosa*) is being encouraged for blueberries (Cane and Payne, 1988, 1990), and the hoary squash bee (*Peponapis pruinosa*) has similar potential for use on squash and pumpkin (Willis and Kevan, 1995). Recently, in Malaysia, carpenter bees (*Xylocopa* spp.) have been managed by providing nesting material for pollination of passion fruit with flowers too large to be pollinated by honeybees (Mardan 1991, 1993).

Pollination of some crops is not effected at all by bees but by other pollinators. Oil palm is now effectively pollinated in Malaysia by the recently introduced weevil, *Elaeidobius kamerunicus* Faust (Curculionidae). It is the natural pollinator of oil palm and was introduced from West Africa, the original home of the oil palm, to Malaysia for pollination (Syed et al., 1982; Kevan et al., 1986). The results have been startlingly successful and were evaluated at (USA) $115 x 10^6 per annum in increased oil crops in 1982. Since then economic returns have remained similarly high as the weevils have become established.Various annonaceous fruit crops are pollinated by beetles, but relatively little information is

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available on the pollinators most adapted to these plants (see Roubik (ed.) 1995). Cacao is pollinated by midges (Diptera:Ceratopogonidae) (Free, 1993; Roubik, 1995) and mango mostly by an assemblage of flies and other insects (Free, 1993; Roubik, 1995). Durian, an important fruit crop of tropical Asia, is bat-pollinated (Roubik, 1995) and makes an even more extreme example of the need to consider alternative pollinators for many crops. In the Tropics, issues regarding pollination are especially important because the natural pollination mechanisms of many plants (crops and others) are not known (Kevan, 1984, 1995; Mbaya and Kevan, 1995; Roubik, 1995).

The importance of the forage, pollen or nectar, sought by pollinators, in relation to pollination success is beginning to be recognized. Yet, in many crop plants, especially those with specialized floral forms (e.g. blueberry, cranberry), bees foraging for pollen are more effective than nectar foragers (Cane and Payne, 1988; MacKenzie, 1994). On these crops, honeybees are often poor pollinators because of the small proportion of pollen foragers in their colonies and their inability to "buzz-pollinate" to obtain the pollen they seek (Buchmann, 1983). Some crop plants that require or benefit from insect pollination do not produce nectar and rely on pollen foraging insects. Among these are kiwi-fruit, tomato, and perhaps pomegranate. Lupine also produces only pollen but is automatically self-pollinating. Pollen-foraging honeybees are thought to be better pollinators than nectar foragers even for apples and other such crops that produce relatively open flowers (Free, 1993).

Expanded and continued evaluation and development of management practices for non-honeybee pollinators will ensure adequate and economical pollination for a diversity of crops and other plant species. The value of "pollinating bees in a box" cannot be discounted wherever agriculture is practiced (Free, 1993; Roubik, 1995; Kevan, 1995) but, as Roubik (1995: p.1) points out, the age of "designer pollination" is beginning, as pollination technology diversifies.

Recently, conservation concerns for pollination have started to take on a greater profile than ever before (Kevan, 1974, 1975a, b, 1986, 1989d, 1990b, 1993; Kevan et al., 1990a, b, 1991a; Parker et al., 1987; Torchio, 1990, 1991, 1994; Corbet et al., 1991; Osborne et al., 1991; Williams et al., 1991; Richards, 1993; Ellis and Ellis-Adam, 1993; Kingsmill, 1993; Watanabe, 1994; Banaszak, 1995a, b; Batra, 1995; Buchmann and Nabhan, 1996; Matheson et al. (eds) 1996; Kearns and Inouye, 1997; Allen-Wardell et al. 1998). Some of this concern has resulted from the recognized value of pollination to agriculture. Figures calculated for the U.S.A., Canada, and Australia, mostly in regard to honeybees, show that the value of pollination far exceeds that of hive products (Southwick and Southwick, 1992). The European Economic Community commissioned the study by Corbet and coworkers (noted above) as a result of its recognition of the international scope of the problem. Nevertheless, the economics of animal pollination in agriculture in any one country are complex and difficult to assess (Southwick and Southwick, 1992). That notwithstanding, agriculture cannot do without a variety of pollinators, including the most important, honeybees. The total value of animal pollination to world agriculture has not been estimated, and the value to world ecosystemic health, including that in the gardens of cities, towns and suburbs, is beyond measure!

Other flower visiting insects are also invaluable, especially predators and parasitoids which are important in controlling populations of otherwise pestiferous insects in all environments. Although new and more environmentally sensitive approaches to agriculture and forestry recognize and encourage these biocontrol agents (Altieri, 1987), the crucial place of floral resources in their livelihoods is often not considered (for examples, below).

Most of the foregoing has concerned pollinators, but the plants' side of the equation should not be ignored. The huge diversity of crop plants that are pollinated by insects is well explored in Free's (1993) account of insect pollination of crops, and recently Roubik (1995) has edited a treatise on tropical plants alone. These books list literally hundreds of crop plants and their pollination requirements so far as they are known. The value of non-crop forage plants, often regarded as weeds, to pollinators of crops and other anthophiles is also high. In situations where such alternative forage, which would normally be available before, during, or after the bloom of the crop, has been eliminated or reduced in abundance, the natural assemblages of pollinators have suffered and so have crop yields. This situation has arisen in blueberry heaths in eastern Canada and Maine, U.S.A. (Kevan et al., 1997). In Europe there is growing awareness of the need to maintain or create flower-rich field borders to stimulate populations of beneficial insects like aphidophagous hoverflies (Syrphidae) and ladybird beetles (Coccinellidae) and parasitoid Hymenoptera (e.g., Molthan and Ruppert, 1988; Weiss and Stettmer, 1991; Schmidt, 1992) and pollinators (Lagerlöf, et al. 1992; O'Toole, 1993).

Greenhouses

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Greenhouses represent the most artificial of all agricultural environments. Nevertheless, pollination is an
)ortant feature of some productivity of some greenhouse crops. Honeybees have been used extensively in pollination
ʋɪ greenhouse crops, including strawberries, various tender fruits, cucumbers and melons. Honeybees do not forage well
under greenhouse conditions and their services are expensive and troublesome. Recently, however, bumblebees have
become commercially available and are used widely in Europe and North America especially for tomato pollination
(Kevan et al. 1991c). In Canada, only native species of *Bombus* are allowed, and these differ from East to West coast.
The lesson of irresponsible introductions of exotic species has been given all too often, yet, knowingly, some venal
commercial interests have flaunted biological sense, e.g. in the case of the introduction of European bumblebees into
Japan. The success of bombiculture has its roots in the researches of conscientious scientists in Canada and Europe. It
has been suggested that bumblebee collectors working for commercial houses in Europe have caused regional declines
in populations (Özbek, 1995 for Turkey).
    Within greenhouses, the agents of biotic control of pests (Hussey and Scopes 1985) must find nutrition. Flowers
and plant sap are no doubt important.

Annual Crops

    Landscapes dominated by annual crops (e.g. grains and oil-seeds) tend to be the most intensively managed and
most highly disturbed. The fields are monocultures which are replaced annually with either the same crop or a different
one, depending on the status of rotational practices. Such high levels of disturbance by annual cultivation and other
management techniques do not allow for the establishment of pollinator populations and the vegetation of perennial
native plants they need (Ellis and Ellis-Adam 1995). Pollinator populations are generally low in such areas
(Schwenninger 1992), but field margins offer small patches for nesting sites and forage (Kevan et al. 1990a, Lagerlöf et
al. 1992) Furthermore, most of the crops grown annually do not depend on insects for pollination. Cereal grains are
wind-pollinated or set seed asexually, the various species of beans are self-pollinating, and many vegetable crops do not
require pollination in farmers' fields because the end-product, the crop, is roots, stems, leaves, and immature flowers.
Oil-seed crops, such as canola, flax, safflower, and sunflower require, or at least benefit from insect pollination (Free,
1993). Fruit vegetables such as tomatoes and peppers and some strawberry varieties pollinate adequately without insect
pollen-vectors. Nevertheless, when cross-pollination takes place the crop is often of higher quality. Only field cucurbit
 ɔs (melons, cucumbers, squash, gourds, and pumpkins), some cole crops (some canola varieties, mustard, and oil-
ьɛɛd radish), and some annual forage legumes require insect pollination in Canada (see Kevan, 1989c, e). A tabular
summary of pollination requirements for Canadian crop plants is given by Kevan (1994). For most, honeybees are
usually considered adequate and the pollinator of choice. However, for squash, gourds, and pumpkins the specialized
bee, *Peponapis pruinosa* (Say), is more efficient and can become well established where these crops are grown year
after year in the same general area (Kevan et al., 1988; Willis and Kevan, 1995). For some annual forage legumes,
native bees and the alfalfa leafcutter bee can be adequate substitutes for honeybees (Richards, submitted).

    From the view point of wildlife biodiversity, field margins, headlands or turn-rows, fence-lines, road, rail, and utility
rights of way, public lands, and so forth are important refuges for a wide variety of pollinators. The value of these areas
to agricultural productivity is unknown, denigrated, and not researched. Certainly there is almost no appreciation of their
biodiversity and general ecological importance in Canada. However, suffice it to say that much of the rural wildlife of
mammals and birds in intensively farmed parts of Canada probably depends on the activities of these insects in
pollinating wild plants which provide sustenance, especially in winter and spring, to semenivores, frugivores and more
generalist herbivores.

Perennial Crops

    Many perennial crops are dependent on insects for pollination to greater or lesser extents. It is in association with
these crops that the demise of native pollinators is best documented.

    Alfalfa is best pollinated by leaf cutting bees (Megachilidae), of which one, introduced species, *Megachile rotundata*,
has been developed commercially (Richards, 1984, 1987). However, there are many other species of leaf-cutting bee
known in Canada, many of which have not been investigated, but may have economic potential (see Salt, 1940; Hobbs
and Lilly, 1954; Ivanochko, 1979). The demise of populations of native leaf-cutting bees in Manitoba was attributed to
habitat destruction in the 1930s and early 1950s (Salt, 1940; Stephen, 1955). Stephen also noted a drop in alfalfa seed
production from 1000 kg/ha to 150 kg/ha as field sizes increased and leaf-cutting bee habitat was removed. The drastic

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decline in alfalfa seed production in Ontario in the 1940s may have had a similar cause, coupled with use of pesticides. Benedek (1972) attributes declines in alfalfa pollinators in Hungary to weed (alternative bee forage) control.

Red-clover (*Trifolium pratense* L.) seed production appears to be well below potential in most parts of Canada (e.g. Peace River, Alberta and British Columbia; Rainy River, Ontario) apparently because of shortages of bumblebees in those regions (Kevan and Hughson, 1992). The same is true for seed production in cicer milkvetch in southern Alberta, where supplemental populations of bumblebees have been shown to increase seed yields (Richards, 1993). Insufficient nesting habitat and alternative forage for the right species of bumblebees (those with appropriately long proboscides to reach the nectar at the base of the flowers) on overly large fields may partially explain the problem and, in combination, exacerbate the effects of long-term use of pesticides and irrigation which drowns nests of soil- inhabiting bees.

The decline of biodiversity and abundance of pollinators of lowbush blueberries (*Vaccinium angustifolium* and *V. myrtilloides*) in Maritime Canada provides the best and most well documented example of a pollination tragedy. Finnamore and Neary (1978) note about 190 species of Canadian native bees associated with flowers of this crop, which requires pollination by insects. Some bees are more important pollinators than others, and some blueberry fields support different suites (guilds) of pollinators from others (Kevan et al., 1997). The reasons for those specificities are not understood. Nevertheless, the use of fenitrothion in New Brunswick for spruce budworm control in forests adjacent to blueberry farms caused such drastic reductions on pollinator abundance and diversity (Kevan, 1975b; Kevan and LaBerge, 1979) that blueberry yields fell statistically below the levels expected (Kevan and Oppermann, 1980). Subsequent recovery seems to have taken place over periods of 1 or 2 to over 7 years, depending on the severity of damage (Kevan and LaBerge, 1979; Kevan and Plowright, 1995; Kevan et al., 1997). Analyses and publication of the details of recovery must await funding. More recently, the diversity and reproductive potential of blueberry pollinators are being reduced by use of herbicides which kill alternative forage for the pollinators when blueberries are not in bloom (Osgoode, pers. comm.). The overall situation, the ramifications in the forest communities, and the influence of other pesticides on pollinators, their abundance and biodiversity and importance in pollination of crops and native vegetation have been examined (Kevan and Plowright, 1989, 1995).

More recently, alternative, managed pollinators for lowbush blueberries have been studied. In particular, the alfalfa leafcuttting bee has been shown to be an excellent pollinator of this crop in Nova Scotia and Maine (Fisher et al 1993; Javorek and MacKenzie, 1994). In addition, growers are enthusiastic because the bees remain on the fields whe. they are placed. Commercially produced colonies of bumblebees also have potential on this crop. In the near future, it is hoped that integrated use of native bees, leafcutting bees, bumblebees, and honeybees will provide flexible and assured pollination.

MacKenzie and Winston (1984) measured the diversity and abundance of native pollinators of various berry crops (highbush blueberry (*V. corymbosum* L.), raspberry (*Rubus idaeus* L.), and cranberry (*V. macrocarpon* Ait.)) grown in the Lower Fraser Valley of British Columbia. They noted that both abundance and diversity were lower on the crop plants than on the surrounding native vegetation (Shannon-Wiener indices in the natural areas ranged from 1.18 to 0.61 versus 0.75 to 0.29 on the crops). They ascribed a combination of effects to explain their findings, i.e. impact of pesticides, competition with managed pollinators, and habitat destruction. More recently, MacKenzie (1994) found somewhat different results from studies on cranberry bogs in Massachusetts and highbush blueberry fields in New York. Diversity was much greater in those loactions than in British Columbia (Shannon-Wiener indices for cranberry bogs were 1.00 to 2.00 on cultivated bogs and 1.62 to 2.25 on natural and abandoned bogs; on cultivated and natural fields of highbush blueberry they were 2.33 to 2.67). Although the abundances of the bees are most difficult to compare because of differences in methods, it appears that similar or greater numbers of bees were foraging on the crops in British Columbia than in the northeastern U. S. A.. These differences may reflect field sizes, type and amount of surrounding vegetation, and pesticide uses. In addition, because blueberries and cranberries originated in northeastern North America, the diversity of pollinators would be expected to be greater there than in an area of recent introduction and cultivation, such as British Columbia.

Most orchard crops require insect pollination. Particularly important in temperate countries are apples (*Pyrus malus* L.), pears (*P. communis* L.), and tart cherries (*Prunus cerasus* L.). Little information is available on the diversity and abundance of native pollinators on these crops in Canada. Brittain (1933) recorded 0.66 to 3.51 wild bees per 10 minutes on apple flowers under conditions allowing for pollinator flights (except as noted when and where populations

were weakened by chemical use) involving at least 27 species (listed insects, other than Hymenoptera, included 20 species of Diptera). To my knowledge, no recent counterpart for that information is available for the Annapolis Valley, Nova Scotia. More recently, from orchards and surrounding areas in the Okanagan Valley, Scott-Dupree and Winston (1987) provide figures on the comparative diversity and abundance of wild bee pollinators in orchards and surrrounding areas in the Okanagan Valley of British Columbia (100 species recorded). They recorded the highest capture rates of wild bees from flowers in uncultivated areas far from and near orchards from approximately 10.4 to 17.5 bees/hour, similar to the rates observed by Brittain (1933), compared to within orchards at 5.8 to 2.5 bees/hour. Their lowest figures came from orchards far from uncultivated areas. Shannon-Wiener diversity indices followed the same trend, but are less clear-cut. Studies made in the Niagara region of Ontario recorded 106 species of insects from the flowers of apple trees with the maximum numbers of bees observed per hour being similar to those recorded in Nova Scotia and British Columbia (Boyle and Philogène, 1983; Boyle-Makowski and Philogène, 1985, Boyle-Makowski, 1987). Bumblebees were rare. It has been suggested that the reduction in numbers of bumblebees in the region has resulted from use of insecticides and habitat destruction (Plowright and Laverty, 1987), as has been also suggested for pollinator assemblages in European orchards (Jacob-Remacle, 1989). Verma (1990) also discusses the role of non-*Apis* pollinators in apple production in northern India. Some orchard crops probably do not depend on insects for fruit-set, e.g. peaches (*Pr. persica* (L.) Batsch.) and nectarines (*Prunus* sp.), and some cherries (*Prunus* spp.) (Kevan, 1988a; Free, 1993) but for these and others the requirements have not been rigorously worked out. Vineyard grapes (*Vitis vinifera*) are wind pollinated.

Urban Environments

Many people value flower visiting insects in urban and suburban environments and various publications are avaibale for encouraging butterflies in gardens. In Europe, several studies have been made on bees in cities (e.g. Haeseler 1982; Jacob-Remacle, 1984; Kratchowil and Klatt, 1989; Tores et al., 1989; Saure 1996) and other highly anthropogenic environoments (Haeseler 1972). Jacob-Remacle (1976) studied the effects of artificial domiciles in encouraging urban populations of bumblebees in Liège, Belgium. Those studies exemplify the amazing adaptability of some species of pollinators to persist and thrive in small enclaves of highly disturbed vegetation and to contribute to nan well-being by their mere presence and through pollinating various ruderal, ecouraged, and cultivated plants.

Pastures & Rangelands

Although much of the pastureland of the world has been created by deforestation, in some extensive areas natural prairie grasslands are the basis of rangelands. The ecological and economic importance of pollinators that inhabit pasturelands has not been assessed.

Overstocking, overgrazing, lowering the groundwater table, and introduced animals have changed the face of grasslands everywhere. Although dominated by grasses, these habitats are home to many showy, insect-pollinated plants. Botanists and ecologists have recognized that the slow demise of many native plants has mostly has come about through herbivore (cattle) preference, grazing pressure, and terrain disruption (Johnston et al., 1971). Associated with the above has been a recently recognized decline in populations of some species of bees. In th Karoo of South Africa, populations of various Aculeata (wasps and bees) are threatened by cattle grazing (Gess and Gess 1993), on North American prairies it is primarily bumblebees that have been adversely affected (Richards and Myers, 1995b). The decline in floral resources may be primarily responsible, but habitat destruction cannot be ruled out as an equally important factor (cf. demise of the prairie locust in North America). In Central America, deforestation for creation of grazing lands has caused declines in populations of oil-collecting (*Centris*), and other, bees (Janzen, 1974; Vinson et al., 1993). Data are lacking to assess the extent of damage in terms of how landscape rehabilitation of plants and pollinators should be approached. In North America efforts by Ducks Unlimited, an organization supported by waterfowl hunters, have aimed to increase the areas of native grasslands and associated wetlands. Their programmes are laudable and are leading to some recovery of grass and forb biodiversity through general habitat restoration is occurring (see Trottier, 1992).

The pastures in many parts of the world are not just grasslands, but are managed to include nutritive plants, especially forage legumes. They may be used for grazing or hay production. In British Columbia, where clearcuts are planted with forage legumes to accelerate succession to rapid reforestation, pollination poses a challenge which has not been properly addressed. Pastures offer relatively undisturbed habitat for native pollinators, but management practices, such as stocking rates, may reduce the diversity of showy-flowered plants available to pollinators (Richards and Myers,

1995b). In England, pastures are less intensively managed and may lack forage legume plantings. Nevertheless, land use practices on them seem to have caused the conspicuous *Primula veris* and *Ranunculus acris* to have declined and bee numbers and diversity are expected to follow (Corbet et al., 1991). The fate of inconspicuous flowers of importance to pollinators has not been monitored. Rasmont (1988) attributes declines in French and Belgian populations of bumblebees to early cutting of hay and use of herbicides against broadleaved weeds (including Asteraceae and Lamiaceae, which are important sources of food for bumblebees and other pollinators). Although data are generally lacking, simultaneous mowing and baling of alfalfa for hay when it is flowering but before fruit-set (i.e. when the plants are at their nutritional zenith) result in large numbers of dead bumblebees incorporated in the bales and smashed by the machinery (Kevan, personal observations)

Agroforestry, Forestry, & Wilderness
In agriculture, agroforestry, and forestry, beekeeping can and does contribute to the livelihoods of many people. The ancillary, and greater benefit than the hive products is pollination. A particularly interesting publication by Svensson (1991), **"Bees and Trees"**, explores these ideas more fully and presents the reasons why well-rounded programmes aimed at diversification of rural economies and opportunities embrace apiculture and pollination (Kevan 1995).

Apart from the socio-economic benefits of beekeeping in semi-wilderness to natural areas, are conservation concerns. These include issues of pollinator introductions and their potential for displacing natural pollinators (Pyke and Balzer 1983, Paton 1983, Dafni and Shmida 1996) and diminishing the reproductive potential of native plants (Paton 1983, Dafni and Shmida 1996). However, as Roubik (1996a, b), Thorp (1996), and Buchmann (1996) discuss, even the introduction of *Apis mellifera* into South, Central, and North America seems not to have caused any extirpations of indigenous bees or plants. The problems are complex in that the particular introduced pollinators have not been present in the areas under study for only a short time and the areas themselves are under various other stresses, habitat fragmentation, agriculturalization, urbanization, and chemical pollution, which would be expected to affect native pollinators adversely.

Habitat fragmentation, sometimes induced chemically rather than physically, has been shown to adversely affect the reproductive capacity of some plants in floras as diverse as from Canada to Argentina (Abrose and Kevan 1990, LaMont et al. 1993; Rathke and Jules 1993, Aizen and Feinsinger 1994, Nabhan and Buchmann 1996) as a result of paucity of pollinators to extreme distances between obligately outcrossing plants. The adverse effects of insecticidal spraying on pollinators and associated reductions in plant fecundity in forests has been reviewed and documented by Kevan and Plowright (1995). By and large, though, community level studies linking pollinator assemblages with plant reproductive ecology in more or less natural environments are wanting. Nevertheless, the messages in Janzen's (1974) and Kevan's (1975a et seq.) papers are all too likely to prove out as more an more specific data accumulate.

The Pollinators & Anthophiles.
Managed Pollinators
General
From all of the foregoing, the importance of pollination in global sustainable productivity in agriculture and nature is clear. However, agriculture is changing rapidly all over the world. In North America and Europe some lands are being retired from farming (Corbet 1995) while other land is being more intensively cultivated. In other instances, more environmentally sensitive, low-input practices, such as organic methods, low and no till cultivation, are being used. These trends, coupled with reductions in the use of pesticides, generally bode well for pollinators and pollination. However, ecologically appropriate planning for these changes in land use are not being instituted and the crucial place of pollinators is largely ignored (but see e.g. Rasmont, 1995; Corbet 1995; Klemm, 1996; Edwards 1996).

In the developing world, expanding agriculture, increasing monoculture, intensification of cropping systems, growing use of agrochemicals, and the rapid deterioration of natural areas are all serious problems. Lack of adequate information about the roles and biodiversity of pollinators, and their decline in natural and agricultural systems is alarming. Although the situation in these countries is dire, recent publications (Roubik,1995; Kevan, 1993a, b, 1995; Krell, 1995, 1996; FAO, 1986) and the efforts of the International Bee Research Institute through their continuing series of Conferences in Tropical Apiculture, are making some impact. Nevertheless, pollination continues to be a neglected area which must be considered in modern and traditional agriculture worldwide.

Figure 2 near here

ʼeybees & Beekeeping

The diversity of beekeeping practices goes beyond that represented by hives of European races and hybrids of honeybees (*Apis mellifera* sspp. *ligustica, caucasica,* and *carnica* or the Italian, Caucasian, and Carniolan honeybees). Nevertheless, those bees are the best understood and easily managed for pollination and hive products. There are numerous books on beekeeping with those bees, but the most encyclopedic is the most recent edition of **The Hive and the Honey Bee** (Graham (ed.), 1992). For a global perspective, Crane's magnificent treatise (1990) is indispensable.

Throughout the African and Middle Eastern parts of the range of *A. mellifera,* indigenous races are kept in various types of hives and by various management techniques. Many of these races are rather defensive and prone to abscond from their hives, whether artificial or natural. Thus, they are difficult to keep. The so-called "killer bee", better referred to as the Africanized bee (a hybrid between European and African races), has spread from Brazil throughout the tropical and subtropical Americas since the introduction there of the African parent stock of *A. m. scutellata* from southeastern Africa in 1956. It is notoriously defensive and easily provoked to attack intruders, be they beekeepers or innocent passers-by (Espina, 1986). These bees are genetically and behaviourally diverse (FAO, 1986; Ruttner, 1988)

In Asia, other species of honeybees are kept or encouraged for human exploitation. The most important of those is the Asiatic hive bee (*Apis cerana*) which probably comprises as much racial biodiversity as does *A. mellifera* (see Ruttner, 1988, Verma, 1995). Although the Asiatic hive bee has been much maligned as a manageable species, recently more attention has been paid to its potential (see Kevan (ed.), 1995; Verma, 1990; Punchihewa, 1994) and the wisdom of transplanting European honeybees beyond their natural range has been seriously questioned (Kevan ed. 1995). In tropical and subtropical Asia, other species of honeybees are used commercially. The honey of *A. dorsata,* the giant or rock honeybee, is harvested in India, Bangladesh, Sri Lanka, Malaysia, Thailand, Viet Nam, Kumpuchea, and Laos, and as is honey of its races or sister species, *A. laboriosa* in the Himalayan foothills and *A. d. binghami* in parts of the Southeast Asian Archipelago. The presence of the huge, single-comb, open colonies of this species on one's property or nearby is considered to be an omen of good luck. The smallest honeybee, *A. florea,* is also exploited commercially. Its small, single-comb, open nests are harvested and sold whole in various parts of Southeast Asia, especially Thailand (see Crane, 1990).

In the tropical and subtropical Americas, where there are no indigenous species of *Apis,* stingless bees ʼliponinae) have been traditionally kept since pre-Columbian times. This agricultural practice, called meliponiculture, is enjoying some resurgence with the encouragement and recognition of non-European cultural values. Meliponine bees occur throughout the world's tropics and present immense potential for managed pollination in agriculture. However, little attention has been paid to their biology as pollinators (see Roubik, 1988, 1995).

Parasites, Pathgogens, Predators, & Pesticides

Mites as parasites of honeybees have evoked major concern world-wide as tracheal mites (*Acarapis woodi*) and *Varroa jacobsoni* have spread at alarming rates (Needham et al., (eds) 1988; Connor et al., (eds) 1993). The impact of these parasites on colonies of honeybees is well documented, but little information is available on their effects on pollination. It has been suggested that many amateur and small-scale beekeepers have abandoned their activities because of the additional complexities of bee management associated with monitoring for mites and controlling them once detected. The numbers of feral colonies of honey bees has decreased significantly as mite infestations have become common throughout the U. S. A. (Watanabe, 1994). The combined effects of losses of hobby beekeepers and feral colonies are already adversely affecting pollination in rural and urban settings, as predicted nearly 10 years ago (Kevan, 1988b, 1989a, b). Furthermore, chemical control of mites may not be acceptable to producers of pure honey because of the issue of potential contamination of human food and other hive products used by the general public.

The expected changes in the practice of beekeeping, which is mostly in the hands of small-scale operators widely dispersed over the agricultural landscape, seem to be resulting in fewer beekeepers and lesser dispersion and dispersal of free pollination from honeybees in managed hives. Already there are complaints, concerns and pressures in are of the U. S. A. about inadequate numbers of honeybees for pollination of pome, stone, and small, soft fruit crops (e.g. Maine, Florida, California, Michigan, and New York) (Watanabe, 1994). Pollination services may come to be provided by commercial beekeepers at an additional cost to the grower and consumer. Encouraging natural or managed populations of non-honeybee pollinators would buffer the adverse effects of fewer honeybees, and in the long run would be economically beneficial (Sherman, 1987; Kevan et al., 1990a)

That scenario also would apply to beekeeping operations in other parts of the world where non-native diseases have invaded the native stocks of honeybees. In India, the possible transfer of diseases from European honeybees to the Asiatic hive bee (*A. cerana*) was suggested to have caused the demise of the latter to the detriment of honey

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production (see Verma, 1990; Ahmad, 1995).

Great care must be taken when honeybees are being considered for introduction from one part of the world to another. The spread of honeybee parasites from place to place and between species is mostly attributable to human activities (e.g. *Varroa* in North and South America, Europe and western Asia; tracheal mites in North America; etc.) (Needham et al., (eds) 1988; Kevan et al., 1991b). Quarantine protocols are well established in some countries (e.g., Kwang, 1995 for Malaysia) but unfortunately lacking in others. The closure of the Canadian border to the importation of honeybees from the U. S. A. in 1987 successfully slowed the spread of mites in Canada. This has bought time for Canadian beekeepers and researchers to prepare for these problems and for new control and detection methods to be developed.

Bailey and Ball (1991) provide up-to-date information on honeybee pathology worldwide. Diseases can cause serious losses if not properly controlled through monitoring and treatment. For beekeeping with European honeybees, American foulbrood, a bacterial disease of the larvae, is the most serious. Other brood diseases, such as European foulbrood (bacterial), chalkbrood (fungal), and sacbrood (viral) are less problematic. The only disease of adult European honeybees that is of concern is dysentry (protozoan *Nosema*) which occurs in sporadic outbreaks. For the Asiatic hive bee the viral disease, Thai sacbrood, has caused widespread losses (Anderson, 1995) as epidemics have swept parts of Asia to be followed by resistance and recovery of populations (Verma, 1990).

Honeybees throughout their native ranges are prey to a variety of predators, ranging from those as large as bears, through smaller mammals, birds, reptiles and amphibia, to other insects. Some predators occasionally cause serious losses to beekeepers, but are generally not considered to be serious (Morse (ed.) 1978).

The dangers of pesticides, especially insecticides, to pollinators are well documented and understood, especially with regard to the European honeybee. Less understood, and often overlooked, is the problem of sublethal effects which reduce longevity and adversely affect foraging, memory and navigational abilities of some bees (see MacKenzie, 1993; Kevan and Plowright, 1995). Johansen and Mayer (1990) have recently written a highly informative book on the subject, with the main emphasis on the U.S.A. There is published information on the toxicity of most pesticides used worldwide to European races of honeybees, and sometimes other bees. Nevertheless, more effort needs to be directed to understand the effects of pesticides on other species of pollinators. From the few comparative studies available, it is evident that the toxicities of pesticides to honeybees are poor predictors of the hazards posed to other species (NRCC, 1981; Johansen and Mayer, 1990; Kevan and Plowright, 1995).

Mosquito control programmes have been associated with major losses of honeybees in Canada and the U. S. A. In Manitoba, efforts to combat serious outbreaks of western equine encephalitis by controlling its mosquito vectors resulted in damage to colonies of honeybees totalling $90,000 in 1981 and $850,000 in 1983 (Dixon and Fingler, 1982, 1984). Although not measured, the effects of these programmes on populations of native pollinators would have been expected to be extremely severe (see below). The adverse effects of extensive applications of pesticides against major pests, such as other forest defoliators, locusts, and grass land herbivores have received little scientific attention (see below).

Recent trends in many parts of the world towards reducing the use of pesticides in agriculture and forestry have made great strides in lessening the incidence of pollinator poisonings. Nevertheless, in developing countries, the problems are still severe (Adey et al., 1986; Sihag, 1995). Also, it must be remembered that pesticides are an integral part of integrated pest management practices (IPM) for crop protection in modern agriculture and forestry. Many pesticide containers bear labels with cautions about dangers to pollinators. When such cautions are heeded, poisonings can be reduced. The dangers of pesticide poisonings of pollinators still must be kept in mind and constant vigilance exercised.

Most pesticide problems stem from accidents, carelessness in application, and deliberate misuse despite label warnings and recommendations (Johansen and Mayer, 1990). As pesticide applications become more and more regulated and applicators are required to take courses in safety and use before certification, the problem should diminish. However, in many countries regulations are wanting, lax, or ignored. When they are enforced, the penalties are generally not harsh enough to encourage changes in practices (Adey et al. 1986). Methods, such as not spraying blooming plants or spraying when pollinators are not foraging are common sense approaches to reducing problems associated with pesticide applications, even when regulation is poor (Adey et al., 1986; Johansen and Mayer, 1990; MacKenzie, 1993).

In agricultural settings, pesticide use can easily be monitored and controlled by a) responsible agents of the agrochemical industries manufacturing and selling pesticides, b) diligent applicators who pay heed to labels, recommended application rates, and warnings about pollinator poisonings and human health, c)and government

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extension agents. Through those personnel, other interested people in agriculture, pollination services, and the general public can become informed about proper use of pesticides.

Future Potential & Needs

Honeybeekeeping stands at the threshold of major changes. The incidence of mite parasitism in Europe, the Americas and Asia has stimulated intensive research efforts in bee breeding for resistance and tolerance, in honeybee protection by synthetic and natural biocides, and in sophisticated management. Much remains to be done in order to understand how honeybees and their parasites interact at the ecological, physiological, and biochemical levels so that the genetic diversity of the species within *Apis* can be exploited. Certainly, agriculture cannot function without honeybees. The potential for diversifying stocks within the genus is great (Rinderer, 1995, Sylvester, 1995). At the same time, the value of alternative pollinators must be recognized in agricultural research priorities (Parker et al., 1987; Torchio, 1990; Williams et al., 1991; Kevan et al., 1990a; Kevan, 1991, 1993; Roubik, 1995).

Other Managed Pollinators

Other bees that do not produce harvestable quantities of honey, if any at all, which are managed, or have potential for management as pollinators include leafcutting bees, alkali bees, orchard bees, squash bees, blueberry bees, and carpenter bees. Those bees have been mentioned above with respect to particular crops. Crane (1990) lists about 50 species of bees that have been managed either commercially (very few) or experimentally for pollination.

Parasites, Pathogens, & Pesticides.

Leaf-cutting bees also suffer from diseases. The most important is the chalkbrood fungal disease (caused by *Ascosphaera aggregata*) of the alfalfa leaf-cutting bee, *Megachile rotundata* (Vandenberg and Stephen, 1982). This disease has a major impact on the culture of alfalfa leaf-cutting bees. Diagnosis facilities have been established in some areas (e.g., western Canada) where these bees are the most important pollinators of alfalfa. Control of this disease involves careful and sanitary management, and fumigation of pathogen-infested nesting material (Goettel and Richards, 1991; Goettel et al., 1993). Research on diseases of other managed pollinators, such as orchard bees (*Osmia* spp.) (Rust and Torchio, 1991) and bumblebees (*Bombus* spp.) (Palm, 1948; Lipa and Triggiani, 1992) has intensified as these pollinators take on an increasingly important role in agricultural crop production.

The importance of diseases and other associated organisms in the regulation of populations of native pollinators is unknown. However, a wide variety of pathogens, parasites, parasitoids, and predators are known to be associated with native bees and other pollinators, in nature (Alford 1975). The little evidence available suggests that they have a minor to moderate influence in population regulation of the pollinators affected, but more research is needed to test this hypothesis. The incidence of preimaginal mortality factors have been estimated as ranging from about 7 to 92% in a few species, e.g. *Diadasia* (Linsley and McSwain, 1957), *Halictus ligatus* (Packer, 1986), and even from fossil bees (Ellis and Ellis-Adam, 1993)

The problem of pesticide poisonings of other managed pollinators is serious wherever pesticides are used. In general, guidelines borrowed from the literature on honeybees are used to assess the effects of pesticides, but as has been pointed out by Kevan and Plowright (1995 and references therein), those are not reliable. There are records of evaluated losses of alfalfa leafcutting bees caused by pesticides in the western USA (Johansen, 1977), but by and large there is little information relating specifically to the effects of pesticides on non-honeybee pollinators.

Native Pollinators

Another issue in pollinator conservation is the increasing recognition by scientists of the importance of non-honeybees as crop pollinators (Bohart, 1972; Kevan, 1987, 1990b; Parker et al., 1987; Torchio, 1987, 1990, 1991, 1994; Kevan et al., 1990a, Richards, 1987, 1993). In all likelihood, much of the credit given to honeybees for pollination in reality belongs to other species. Nevertheless, the lack of general acceptance of the greater efficiency of other pollinators for certain crops and failure to recognize that some crops are poorly, if at all, pollinated by honeybees has hampered appropriate developments towards pollinator conservation for agricultural productivity (see Kevan, 1989e). This problem is further exacerbated by the paucity of resources directed to research and development for management of other species of bees.

The demise of pollinators, as illustrated in the body of this chapter, has come about through four major human

activities: 1) pesticide use; 2) habitat destruction; 3) spread of diseases and parasites; and 4) competition from introduced flower visitors. Most information comes from temperate regions, but the same problems can be assumed to be equally or more severe in the Tropics (see Kevan, 1986, 1993; Mbaya and Kevan in press). The aim of this section of my paper is to review briefly the information available on each factor and to place into perspective the potential seriousness of continued failure to consider their effects.

Pesticides, Parasites, and Pathogens.
        Issues of pesticides in non-agricultural settings and agroforestry are more complex because of the importance of a wider diversity of pollinators. The most well understood situation is in eastern Canada, where fenitrothion, sprayed against spruce budworms (*Choristoneura fumiferana*) defoliating forest trees, had devastating side effects on wild, native pollinators of commercial blueberry fields and on the pollinators servicing the sexual reproductive needs of some of the native flora. A number of plant species of the forest and forest margins suffered reduced fruit and seed set, which in turn would be expected to impact wildlife by depriving them of natural quantities of food (Kevan and Plowright, 1989, 1995). Other instances in which native pollinators must have been seriously affected by pesticide applications are noted above in reference to honeybees.

Habitat Destruction
        There are three ways in which habitat destruction affects pollinator populations, as with populations of any organism: 1) destruction of food sources; 2) destruction of nesting or oviposition sites; and 3) destruction of resting or mating sites. The most common means of habitat destruction are through the establishment of monocultures, overgrazing, land clearing, and irrigation.

        The destruction of food sources in agricultural areas is best illustrated by examples of the removal of vegetation (mechanically or by herbicides), that provides the pollinators' food when crops are not in bloom (Kevan, 1974, 1986, 1991, 1993; Kevan et al., 1990a, b, 1991a). Very often the vegetation which is removed is regarded as unwanted, as weeds or competition for the crop plants, yet is invaluable to pollinators and other beneficial insects. A discussion of these problems with respect to biological control, IPM, and pollination in the Tropics is provided in Kevan (1986). Documentations of the negative effects of the removal of "unwanted" vegetation on pollinator populations in agricultural areas come from Europe and North America (see below). Road-side and right-of-way sprayings of herbicides can reduce the diversity and abundance of alternative food supplies for pollinators.
        The destruction of nesting and oviposition sites has been documented in Manitoba for the demise of populations of leaf-cutting bees (Megachildae) which were left without nesting sites in stumps and logs as fields of alfalfa for seed production expanded (Stephen, 1955), in Europe for bumblebees as the amount of relatively undisturbed land in hedgerows and other non-cultivated areas declined (Corbet et al., 1991), and in the Tropics for the inadequate pollination of cacao by midges in plantations from which oviposition substrates, i.e., rotting vegetation, had been too fastidiously removed (Winder, 1977). By contrast, in Malaysia, additional substrate of rotting palm trunks is provided to increase pollinator populations (Ismail and Ibrahim, 1986).
        Habitat manipulations associated with agriculture often adversely affect availability of both food sources and nest sites, creating a double problem for native pollinators, especially those that are long-lived, such as colonies of bumble bees. Most native bees foraging on commercial cranberry bogs are bumble bees (Kevan et al., 1983; MacKenzie and Winston, 1984; MacKenzie, 1994). The diversity and abundance of these, and other bees, on bogs were much greater on bogs in Massachusetts than in bogs in Wisconsin, British Columbia, and Ontario. Bumble bees were particularly abundant, and often exceeded the numbers of honeybees, even though colonies of the latter had been placed there specially for pollination (MacKenzie, 1994). The success of bumble bees on Massachussets' bogs may be attributable the great expanses of natural areas surrounding them and their irregular shape, often with long fingers and corners jutting into the natural vegetation. More recently developed cranberry growing areas, such as in Wisconsin and British Columbia, have large, square bogs with little natural vegetation nearby. They are more typical of modern agriculture and tend to have low diversity and abundance of bees (Cane, personal communication)
        Examples of the destruction of special mating or resting sites pertain to pollinators with rather special requirements and to those associated with rare plants. Although this problem is suspected to be real, documentation is not available and would require special study (Torchio, personal communication).
        The general issue of habitat destruction for pollinators has evoked concern on a broad scale. Daniel Janzen's (1974) article "The deflowering of America" exemplifies the problem. He points to a vicious cycle of reduced vegetation

for pollinators' resources, reduced pollination in the vegetation, the demise of the plant's reproductive success and reductions in seed and fruit set, resulting in the failure of revegetation with the equivalent level of biodiversity as would have otherwise existed. This cycle applies to all parts of the world because pollination by animals is an integral part of almost all terrestrial ecosystems (see also Kevan and Collins, 1974; Ambrose and Kevan, 1990; Haack, 1994). Nevertheless, recent books and reviews on conservation of insects and their habitats give short shrift to pollinators and all but ignore the consequences of their demise (e.g. Collins and Thomas (eds), 1991; Hawksworth (ed.), 1991; but see LaSalle and Gauld (eds), 1993).

Competitive Interactions

The most studied of the competitive interactions between pollinators as they relate to pollination is that of the effect of the Africanized honeybee on native pollinators and European races of honeybees in South and Central America. Roubik (1978) first pointed out the apparent reductions in populations of native bees in Central America after the invasion of Africanized bees. Subsequently he placed the phenomenon in a broader context (1989), but the whole issue of the competitive interactions of Africanized bees with native pollinators in South and Central America is complex (see Pedro and Camargo, 1991; Roubik 1996). It appears that no indigenous species have become extinct through competitive interactions with the exotic honey bee.

In Australia there has been recent debate on the effects of the introduced European races of honeybees on the native flora and fauna of pollinators. Paton (1993) concluded that there is justification for the concern that European honeybees have caused reductions in the pollination of some native plants, especially of those that are bird-pollinated, by removing the nectar sought by the birds and causing changes in their populations and foraging habits. Sugden and Pyke (1991) concluded that competition with honey bees adversely affected the populations of native bees, e.g., *Exoneura asimillima*. The issue of the effects of European honeybees on native pollinating insects is not so clear from the botanical side, but the same trends are evident in respect to the native bees. The sequence of events is as follows: Honeybees displace native pollinators by removing floral resources; honeybees may not be able to pollinate the flowers from which they remove the resources; the plants then fail to reproduce sexually or at all and their populations dwindle; remaining and reduced populations of native pollinators dwindle further; and so on. In Europe there is concern that intensively managed honeybees may deplete the already depauperate floral resources required by native bees and other anthophiles and so depress their populations further. This problem is especially urgent where honeybees are shifted to areas where honey production can be high and profitable for beekeepers (Evertz, 1995; Petanidou and Ellis, 1996; Sugden 1996)

There are similar concerns related to the movement of other managed pollinators into areas where, previously they have not been present. Commercially reared bumblebees are an important component of greenhouse tomato production (Kevan et al., 1991c; Kevan, 1994). At least three regionally native species are being used, *Bombus terrestris* L. in Europe, *B. impatiens* Cresson in eastern North America, and *B. occidentalis* Greene in western North America. Protection of native populations is the primary concern and thus sensible constraints are applied mainly in the geographical areas of their use. Planned introductions of non-native bee species should be treated with great care, with all due attention paid to quarantine, and more important, to the possible ecological ramifications of escapes, which are inevitable. Already, European bumble bees have been taken to New Zealand (Dunning, 1886), Chile (Arretz and MacFarlane, 1986), Tasmania (Semmens et al., 1993; Donovan, 1994), Japan (Kato 1993; Ikeda and Tadauchi, 1995), and possibly Argentina (in 1993 or 1994) mostly without appropriate consideration. Stephen and Thorpe have both expressed grave concern about the irresponsible transport of eastern North American bumblebees to the west coast of the U. S. A. by commercial operations (in Bumblebee Quest, 1994). Dafni and Shmida (1996) also express misgivings about the impact of *Bombus terrestris* on the anthophilous fauna and pollination of the flora of Mount Carmel in Israel. The disastrous introduction of Africanized honeybees (*Apis mellifera scutellata*) into South America, and its consequences, are quite well known (Roubik, 1978, 1988, 1989). In Indonesia, the introduction of the Asiatic hive bee, *Apis cerana* from west of Wallace's and Wegener's Lines into Irian Jaya has resulted in the spread of this bee to neighbouring Papua New Guinea, where it now threatens to spread to Australia. The consequences of such introductions to the natural diversity and abundance of native pollinators, and consequently to the native flora, were not assessed. Despite repeated warnings (Crane, 1982; Kevan, 1986) and excellent examples of appropriate procedures from recent introductions of biocontrol agents and pollinators (eg. *Elaeidobius kamerunicus* (Curculionidea)) from West Africa to Malaysia for oil palm) (Kang and Karim, 1982), ill-considered introductions still occur.

Protection and Promotion.

The protection of native pollinators is critical to global sustainable productivity (Kevan, 1991, 1993; Krell, 1995). The situation in Europe has been reviewed by Corbet et al. (1991), Osborne et al. (1991), Williams et al. (1991), Banaszak (1995a, b), in Belgium by Rasmont (1995), and tropical Asia by Appanah and Kevan (1995). Habitat destruction, from nesting sites (above) to forage (Janzen, 1974 and above) is a major issue. Introduced diseases are threatening the health of the native honeybee races and their pollinating activities in Africa (Mbaya and Kevan, 1995). Although the impact of pesticides is declining in importance in North American and European agriculture as the use of insecticides declines, it remains very important elsewhere (Sihag, 1995). Competitive interactions between flower visitors (above) seem important in tropical and subtropical Americas and in Australia. Clearly, and contrary to the views of some, human intervention in natural systems in some places has exceeded the tolerance of those systems to sustain themselves (Kevan et al., 1997), even within pollination systems. Unfortunately, in many instances, human beings are jeopardizing their own existence, and the demise of pollination and its biodiversity is one subtle, but crucial, example of the insidious process.

Surely, it would be prudent to set-aside areas for native pollinators in agroecosystems and to encourage their populations by providing forage and nesting sites for their conservation (Corbet 1995). Krell (1995) and Corbet (1995) discuss the importance of hedges, field margins, riparian forests, rights of way, road-sides, copses, successional growth, and home gardens as places where native pollinators can thrive. Several recent publications (e.g., Banaszak 1995a, b; Kevan 1995; Buchmann and Nabhan, 1996; Matheson et al. (eds) 1996; Kearns and Inouye, 1997) should go far in sensitizing the general public, policy makers and planners, and politicians to the importance of pollination and pollinators, the seriousness of their demise, and the urgency for their conservation.

Other Anthophiles

Many anthophiles are unimportant as pollinators, but floral resources are important in their lives. Biocontrol agents represent a particularly valuable group of insects in agroecosystems. Leius (1960, 1967) showed that the incidence of ichneumonoid parasitism of codling moth in apple orchards was greater if floral resources, such as those of weeds, were available in the orchards. Syme (1975) noted the importance of floral resources to biocontrol agents in forests as well. In fact, long ago it was suggested that the failure to establish of potentially useful biocontrol agents against Japanese beetles was caused, at least partially, by lack of floral resources (King and Holloway, 1930). Certainly some of the successes reported in the high incidence of natural biocontrol agents of pestiferous insects in low-input agricultural systems (Altieri and Whitcomb, 1979; Altieri, 1987) should be ascribed to the availability of floral resources (see Kevan, 1986).

PART III. POLLINATION & POLLINATORS AS BIOINDICATORS

Bioindicators are organisms which provide indication, by their presence (abundance) or absence, of on-going activities in the ecosystem. Bioindicator species are usually used to diagnose problems. There are indicators of anaerobic waters, rapid eutrophication, pollution, and pesticides. On the other hand, they can also indicate amelioration of problems, or even suggest that the activities in an ecosystem are performing according to expectations within normal bounds. In the latter cases, the species used may be indicators of some aspect of ecosystemic health. In this section, I explore pollinators and anthophiles as bioindicators of agrochemical stresses and of pollution in the manner described above. Finally, I explore the use of community ecology in measuring ecosystemic health by way of pollinators and the stress of insecticides. The approach has broad, general applicability to help diagnose ecosystemic dysfunction and health, even if the nature of the environmental stressor is not known or only partially understood (Kevan et al., 1997).

Agrichemicals & Pollutants

Pollinators, especially honeybees, are often killed in large numbers by insecticides. They may also accumulate other pesticides in their bodies and hives. Analytical techniques for pesticide residue detection are well worked out so that bees and hive products can be used to monitor for pesticides in the environment. Most often toxic residues are assayed to determine the likely cause of bees' deaths and the hazard posed by pesticides to pollinators rather than for purposes of environmental monitoring. As in use of residue analysis of bioindicator organisms, the nature of the suspected residue must be at least somewhat known.

Honeybees have been investigated quite often to monitor pollutants. Honey or pollen or both may become taminated with various industrial pollutants. The release of arsenic and cadmium may cause mass killings of honeybees and contaminate pollen, but not nectar (Krunic' et al., 1989). The accumulation of radioisotopes in honey and pollen following the Chernobyl disaster in April 1986 illustrates the value of honeybee colonies as samplers of local, regional, and global environmental quality (Bunzl et al., 1988, Ford et al., 1988). They also sample fluorides (Dewey, 1973), heavy metals (Stein and Umland, 1987) and organic compounds (e.g. PCB's and pesticides) (Anderson and Wojtas, 1986; Morse et al., 1987) through floral nectar, pollen, and their own bodies. They have been advocated as bioindicators in natural, agricultural, industrial and urban milieus (Rousseau, 1972; Drescher, 1982; Celli et al., 1983; Bromenshenk et al., 1985; Stein and Umland 1987), yet, despite their proven worth, programmes for their use as biomonitors do not seem to have been instituted.

Bromenshenk et al. (1991) addressed the problem of population dynamics in honeybees with respect to pollution and so expanded concern for the health of pollinators beyond pesticide hazards. Little information is available on the effects of pollutants on other pollinators. Dewey's (1973) data show that the highest levels of fluoride, associated with an aluminium reduction plant, were found in flower-visiting insects (from bumblebees to butterflies and hoverflies). Sulphur dioxide reduces activity of pollinators, including honeybees and male sweat bees (*Lasioglossum zephrum*), but may not kill them (Ginevan et al., 1980).

Ecosystemic Stress and Health

The idea that concepts of health can be applied to ecosystems is not that new, but it has had difficulty in practicality and acceptance because there are problems as to how such a form of health might be measured. The measures of ecosystemic health that have been proposed are not satisfactory to scientific ecologists. Some have been based on natural processes which are not necessarily indicative of ill-health (e.g. eutrophication and succession), some suites of symptoms comprise different measures of the same ecosystemic processes, others are anthropocentrically derived and intrinsically laden with human values (Costanza, 1992; Rapport, 1992; Callicott, 1995; Jamieson, 1995). Nevertheless, the concepts of health and ecosystemic conditions can be juxtaposed through rigorously applied ecological principles. If ecology is defined as the study of the distribution, abundance, and activity of organisms, then these three facets of life on earth should be included in ecosystemic analyses, including those aimed at health. One of unifying concepts in ecology is that of competitive exclusion and niche hierarchies as arranged by degrees of overlap. Sugihara (1980) has argued that in complex communities of organisms, the species occupy a hierarchy of niches with partial overlaps. The theoretical outcome of such an arrangement, given also the physical constraints of an environment, is the well-known log-normal relationship between species' diversity and abundance. Although this relationship has been suggested to be merely a mathematical outcome of the arrangement of diversity and abundance of objects (e.g., size classes of grains of sand and their abundance) (May, 1975), I accept Sugihara's argument of the biological meaning behind the log-normal relationship. Thus, it has been incorporated into a measure of ecosystemic health which involves pollinators.

The study of quantitative community ecology is relatively new and complex. Animal and plant interactions in pollination have allowed for some generalizations to be ventured concerning the structure and dynamics of ecological communities (Rathke, 1983, 1988; Kevan and Baker, 1984; Jordano, 1987; Frankie et al., 1990; Vogel and Westerkamp, 1991; Ellis and Ellis-Adam, 1993). However, there are few studies of pollinator biodiversity and species' abundance and log-normality (but see MacKay and Knerer 1979, Tepedino and Stanton 1981; Melendez-Ramirez, 1997). We (Kevan et al. 1997) hypothesized that in the insecticide stressed environments of blueberry fields from 1970 to 1975 in south central New Brunswick, Canada, that the log-normal relationship of species' diversity and abundance of pollinating bees would be perturbed. We tested this hypothesis with data from east, central, and west southern New Brunswick and in two periods, the years when insecticide Fenitrothion was being applied in the central part of the area, and the years following the cessation of its application in the vicinity of blueberry fields. Alomost all our data sets were log-normal. The exceptions were those from central New Brunswick taken during the years of Fentitrothion applications. We surmised that lack of log-normality in the one data set was indicative of ill-health.

It cannot be denied that the deleterious effects of Fenitrothion on pollinators and pollination in forests of Canada resulted in ecosystemic dysfunction can not be denied (Kevan and Plowright, 1995; Kevan et al., 1997). That it also adversely affected a component of agricultural productivity also seems highly likely (Kevan and Oppermann, 1980), and so it must also have affected the incomes of the land-owners, blueberry-growers, and the casual labour force involved in harvesting the crop.

CONCLUSIONS

Conservation of honeybees, other domesticated bees, wild bees, and other pollinators is an important issue in the global context of agricultural and natural sustainable productivity. It is a curious fact that, although the major pollinators for many crops grown in the world's temperate zones are known, the quantitative relationships of pollinator populations, activities, and densities with plant and flower density and resultant seed-set are largely unknown. The pollinators of many tropical crops are misidentified, unknown, or assumed to be honeybees. Further, the breeding systems of many tropical crop plants are unknown or misunderstood. It is important that apiculturalists expand their horizons to embrace the culture of non-honeybees and grasp the importance of other pollinators in agriculture. In an era of heightened concern about global environmental sustainability and conservation of biodiversity, the importance of pollination and processes that are deleterious to it embrace a wide front of inter-related issues (Fig. 4). These range through habitat destruction, poisonings, parasitic mites, disease, and competitive interactions with alien species causing the demise of various pollinators. The need for conservation, imaginative approaches to management, and basic biological research, must be fully recognized by biologists, ecologists, agriculturalists, and the general citizenry in the new spirit of global, environmental sustainability and conservation of biodiversity.

Figure 4 near here

Caption: Figure 4. How pollination and pollinator ecology can be related though applied research to concerns for human well-being (adapted from Roubik 1995).

29
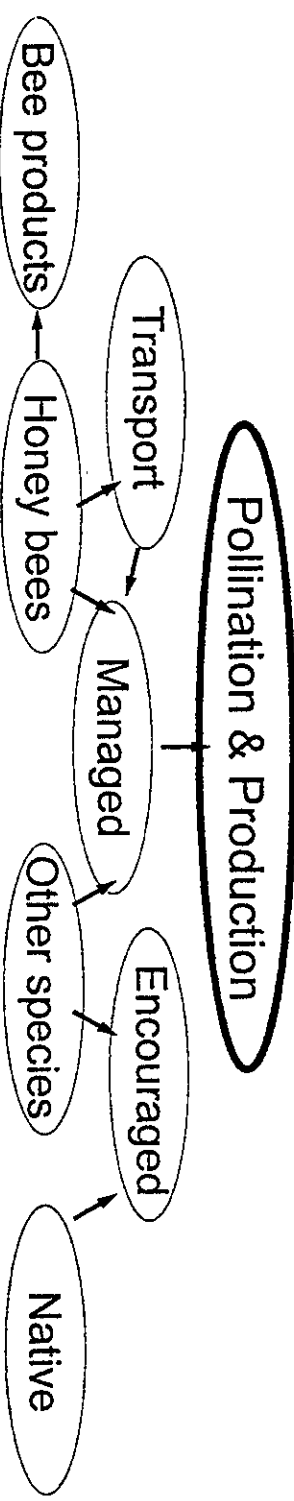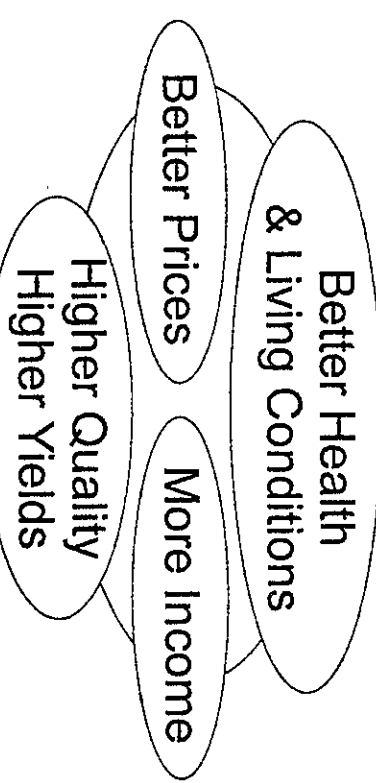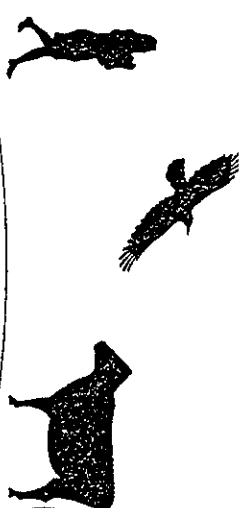
POLLINATION ECOLOGY

Crop Research

Breeding systems
Pollination needs
Selection
Biocontrol
Cropping systems

Pollination Research

Ecology
Biodiversity
Genetic, Species,
Community
Mutualism
Co-evolution,
co-dependenc

Ecological Research

Antecology
Synecology
Conservation
Biology
Pestology
Community,
mutualism
Landscape
Soil water
pollution

Bee products

Honey bees

Transport

Managed

Other species

Encouraged

Native

Pollination & Production

Higher Quality
Higher Yields

Better Prices

More Income

Better Health
& Living Conditions

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