

FLORAL RESOURCE UTILIZATION BY SOLITARY BEES (HYMENOPTERA: APOIDEA) AND EXPLOITATION OF THEIR STORED FOODS BY NATURAL ENEMIES¹

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ABSTRACT

Bees are phytophagous insects that exhibit recurrent ecological specializations related to factors generally different from those discussed for other phytophagous insects. Pollen specialists have undergone extensive radiations, and specialization is not always a derived state. Floral host associations are conserved in some bee lineages. In others, various species specialize on different host plants that are phenotypically similar in presenting predictably abundant floral resources. The nesting of solitary bees in localized areas influences the intensity of interactions with enemies and competitors. Abiotic factors do not always explain the intraspecific variation in the spatial distribution of solitary bees. Foods stored by bees attract many natural enemies, which may shape diverse facets of nesting and foraging behavior. Parasitism has evolved repeatedly in some, but not all,

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bee lineages. Available evidence suggests that cleptoparasitic lineages are most speciose in temperate zones. Female parasites frequently have a suite of characters that can be described as a masculinized feminine form. The evolution of resource specialization (including parasitism) in bees presents excellent opportunities to investigate phenotypic mechanisms responsible for evolutionary change.

PERSPECTIVES AND OVERVIEW

The >20,000 species of bees are allied to nest-building wasps and ants (Hymenoptera: Aculeata) (77). Bees arose within an assemblage of hunting wasps (sometimes known as Sphecoidea) that abandoned arthropods as the food source for their young in favor of using floral resources. Most bees are solitary (140, 160, 164, 167, 174, 202), although they may nest in aggregations. Unless indicated otherwise, when we refer to "bees," we mean solitary bees (for social species, see 140).

After a natural history overview, we focus on the following topics:

1. Some bees nest in isolation, while others nest gregariously. These spatial associations of conspecifics are likely to influence intraspecific competition and interactions with natural enemies (cf 232).
2. Many solitary bee species are resource specialists for pollen and oil, but rarely for nectar. The patterns and mechanisms of floral-host specialization by bees are governed by factors generally different from those affecting other insect specialists (see 14, 15). The interests of bees, unlike those of herbivores, are more congruent with those of the plant.
3. Numerous parasites attack adult bees, their offspring, or their stored food. Nest architecture, and foraging and nesting behavior, are hypothetically influenced by natural enemies, but this has not been tested critically. Major enemies of bees are other bees that are either facultative or obligate parasites. The great diversity of obligately parasitic bees, with their convergent morphology, allows us to study the evolutionary origins of behavioral flexibility and novel expression of condition-sensitive traits.

For brevity, we cite only more recent or comprehensive papers and recommend that interested readers use these bibliographies to find references to earlier works.

APOIDEA—WHAT ARE BEES?

Terminology

Solitary females store food in individual cells for their offspring. Most have no regular interactions with conspecifics, including offspring (for exceptions,

see e.g. 139). Cleptoparasites do not collect oil or pollen but rather invade nests of solitary bees and deposit eggs in the cells or on stored provisions (18, 224); the parasite's offspring consume the stored resources. Oligolecty describes persistent and apparently heritable provisioning behavior in which a bee species, throughout its range, restricts itself to gathering pollen from a few related plant genera (51, 118, 134, 170); these bees are specialists. Polylectic bees are generalists that collect pollen from plants of more than one family. Generalists usually are constant to a particular plant species over a short time, but the preference changes in response to past experience and perceived rewards (58, 65, 81, 221). Oligolects can also be flower constant, but they have a narrower range of acceptable hosts (51, 217). As with other classes of specialization, the dichotomy between oligolecty and polylecty is for classification purposes only.

Overview of Natural History

Some bees excavate nests in the soil, in living or rotting wood, or even in sandstone (13), whereas others construct nests from plant or earthen materials, usually in preexisting cavities, including snail shells or tunnels made by other boring insects (104, 135, 138, 160, 167, 174, 202). Representative illustrations of bees' nests appear elsewhere (104, 167, 174, 202). Nests contain one or more cells, either distributed throughout a branched tunnel system or clustered together. The mother usually coats the walls of each cell, or sometimes the pollen mass, with a hydrophobic secretion from her Dufour's gland (see section on antiparasite strategies). She provisions it with a mixture of pollen and nectar or oils collected from flowers in an area surrounding the nest (see 196), sometimes supplemented with glandular secretions (references in 59, 95). She lays an egg on, in, or, rarely, under the mass and seals the cell.

Life-history and diapause patterns are not well documented. Most temperate bees pass an unfavorable season as immatures, usually as postdefecating larvae (prepupae) (for exceptions, see 92, 139). Others diapause as adults (examples in 157). Frequently, species are typologically classified by the number of generations per season, and until recently, individual variability was neglected in these classifications. Facultative diapause (parsivoltinism) occurs (references in 157) and may be a bet-hedging strategy related to unpredictable resource availability (156) or to the abundance of natural enemies. Physiological mechanisms of apoid diapause are not well studied (see 133).

Classification of Apoidea

The superfamily Apoidea contains more than just bees. It includes some, though not all, of the carnivorous spheciforme wasps [= Sphecidae (sensu 22)], but which spheciforme lineage is the most closely related to bees is unknown

(reviewed in 5, 30). Bees constitute a monophyletic group, as evidenced by several shared derived characters (reviewed in 5, 147).

Origin and Evolutionary History

Michener (142) speculated that bees arose in the xeric interior of West Gondwanaland, presumably concurrent with, or soon after, the radiation of angiosperms (211). Early apoid history is speculative, because fossils older than those from the Cenozoic are rare or nonexistent (references in 168). Fossilized remains of bee activity include putative nest burrows or cells, as well as leaves with disc-like sections removed as if cut by megachilid bees (reviewed in 24).

Phylogeny and Classification of Apiformes

Two informal groups, referred to as short-tongued (S-T) and long-tongued (L-T), are used to classify bees (145). The phylogenetic relationships among S-T bees remain unresolved, but phylogenetic hypotheses for the major lineages of L-T bees have led to major changes in classification (171). Michener and coworkers (147, 171) provide higher taxonomic classifications for the genera mentioned here.

Diversity and Distribution

Faunal studies, though limited and idiosyncratic, show that bees abound in most habitats on all continents except Antarctica (see 142, 157, 174). Generic diversity is greatest in the Neotropical region, but bees are more speciose in xeric, temperate regions (8, 142, 175). Given that tropical angiosperms are diverse, especially in the Old World (207), the relatively depauperate tropical bee fauna is surprising. From a behavioral and ecological perspective, however, tropical bees may be more diverse relative to temperate-zone bees (175).

Several hypotheses may account for the less speciose tropical fauna, but none have been rigorously tested. All the surmised factors may play some role. The apparently lower diversity may relate to the following: competitive exclusion by honey bees (*Apis* spp.) and by the abundant and speciose social stingless bees (Meliponini) (90, 174); increased fungal attack and food spoilage, including the tendency of provisions to become hygroscopic (134); or increased predation and parasitism (cf 110).

DISTRIBUTION OF POLLEN SPECIALISTS AND CLEPTOPARASITES The relative diversity of oligolectic bees appears low in the tropics (see 89, 142, 174). Generalist species apparently predominate in most temperate biomes, except in xeric and Mediterranean-climate temperate regions (150). However, as most surveys do not examine pollen loads and as different authors use different definitions, conclusions are tentative.

Parasitic bees are also apparently rarer at lower latitudes (224; but see 90). A reported correlation (224) between the proportion of parasitic species in a given fauna and the latitude of the region surveyed may be biased because the analysis used species as independent data points. Analyses using higher taxonomic levels are currently unreliable, because at least some genera of parasitic bees are arbitrary rather than phylogenetically based. This geographic trend in parasitism is not a collecting artifact (224), and findings implicate seasonality and host synchrony in the evolution of parasitism (see 159, 224).

HOST LOCALIZATION IN TEMPORAL ENVIRONMENTS The apparent latitudinal decrease in relative abundance of both parasitic and oligolectic bees may be related to the common problem of localizing a specific resource in a spatially and temporally complex environment (see 15). Spatial or temporal unpredictability in flowering phenology can be substantial in tropical forests (see 12, 27). Unfortunately, long-term studies of spatial and temporal abundance of solitary tropical bees are uncommon (e.g. 219a). If synchronization with host activity is important for these specializations, then they should be relatively more common in tropical dry forests, where resource availability is more seasonal, than in wet forests (references in 12, 27). The greater percentage of oligolectic bees in Costa Rican dry forest (89), relative to bees in French Guiana (142), is consistent with these predictions. No pertinent data are available for parasitic species.

HABITAT PREFERENCE AND AGGREGATIONS OF NESTS

Many solitary bees have habitat preferences for nesting and often choose sites near flowers (e.g. 76, 118, 126, 164, 202). Insufficient information is available to assess any degree of preference: Few studies sample and describe suitable nesting habitats where floral resources occur but the bees do not. Numerous bees nest in aggregations (e.g. 62, 118, 164), which range in size from several to many nests per square meter (49). One aggregation contained an estimated 423,000 nests in 1300 m² (186). Aggregations can persist for more than 20 years (149, 176, 230) or die out a few years (126). Some bee species disperse from their natal sites and then form ephemeral aggregations at unpredictable locations (e.g. 64). Congeners exhibit different degrees of philopatry and the tendency to aggregate nests (compare 35 with 2 and 186).

Proximate Mechanisms for Gregarious Behavior

Nest aggregations might arise because of (a) limited suitable nesting habitats (e.g. 222), (b) a tendency for offspring to nest in natal areas (e.g. 146), or (c)

a tendency for individuals to nest near conspecifics (e.g. 64). The mechanisms responsible for gregarious behavior are poorly understood (see 38, 146, 223). Different species prefer different soil compositions, temperatures, or moisture levels (38, 146, 202). Moreover, some species favor vertical, and others horizontal, surfaces (references in 126, 138). However, in general, no obvious abiotic factors correlate with the locations of aggregations within a suitable habitat (38, 146).

For bees with persistent aggregations, an investigator can use genetic studies of population structure (e.g. 17) to determine whether hypothesis *b* or *c* applies. The mechanisms by which females learn the characteristics of their natal habitat upon emergence have not been studied, even though Fabre (71) long ago suggested they were important. Mandibular gland secretions may serve as aggregation pheromones (e.g. 59). Indeed, anecdotal observations suggest that, after initial colonization, ephemeral aggregations form via a self-organization process resulting from the increase in chemical attraction to a site as more females nest there (e.g. 64), analogous to the growth of urban populations (6a).

Evolutionary Benefits of Gregarious Behavior

The benefits associated with gregarious behavior are obscure and may differ for perennial and annual aggregations (for costs, see section on natural enemies of bees). One hypothesized benefit is that individuals form a so-called selfish-herd as cover from enemies (223). Available evidence is equivocal (reviewed in 172; also 54, 88). Whether bees gain information about foraging sites by following conspecifics from a central place, as known in some birds (e.g. 31), needs to be investigated.

RESOURCE SPECIALIZATION

Nonparasitic bees are prone to resource specialization. Factors associated with specialization in other phytophagous insects (e.g. detoxification) (reviewed in 14, 15, 84, 104a, 212) are less relevant for bees. Resource specialization by bees differs in its mechanisms, evolutionary causes, and ecological implications.

A few species specialize on a single species of pollen host (monolecty) (40, 66, 101, 152, 170, 187, 213). Because usually only one phenotypically similar plant congener is available locally (e.g. 170), these species may simply be without access to closely related hosts (also 118, 150). Where closely related pollen hosts bloom together, specialists typically use all of them (e.g. 217).

Specialist bees will occasionally provision nests with nonpreferred pollen if their host is temporarily unavailable (127, 161, 213). They then abandon

alternative plants when the host blooms (43, 148). We do not know whether emergency resources are nutritionally adequate for larval development.

Phylogenetic Origins of Oligolecty

Without an independently derived phylogeny, it is impossible to discern whether oligolectic or polylectic habits are primitive or derived within a given taxon. Like specialization in other insects and cleptoparasitism among bees, oligolecty has multiple independent evolutionary origins.

TAXONOMIC DISTRIBUTION OF OLIGOLEGES Pollen host specialization, which is unevenly distributed among higher bee taxa, is frequent in Rophitinae, Colletidae (other than Hylaeinae), Andrenidae, Melittidae, Megachilidae [including Fideliinae (236)], and nonsocial Apinae (118, 167). Most genera within these taxa contain both oligolectic and polylectic species (99). Polylecty is frequent in the Xylocopinae, Oxaeidae, Halictinae, presumably the Euglossini, and probably the Hylaeinae (118, 167). Pollen preferences of some colletids are not well known because these bees transport pollen internally; some euryglossines are oligolectic (96).

POLYLECTIC ANCESTRY Some oligoleges, including *Ceratina sequoiae* (52) and several halictines (e.g. 21, 69), occur in otherwise polylectic taxa. These oligolectic taxa are presumably not basal within their clades, and thus their classification supports the usual supposition that specialists descend from generalists.

OLIGOLECTIC ANCESTORS ON RELATED HOSTS Specialization on related hosts is sometimes conserved through multiple speciation events. Diverse genera exemplify evolutionarily conserved associations (Table 1), even across enormous geographic ranges (e.g. 166). Geographic ranges overlap for some species in these conservatively oligolectic genera (references in 102), an observation at odds with the tenets of competition exclusion.

OLIGOLECTY AND HOST SWITCHING Another pattern for entirely oligolectic lineages is that, as a group, related taxa may specialize on several unrelated plant families; however, any one species may be more restricted in its resource utilization. Oligolectic bee genera associated with multiple host families include *Diadasia* (5 plant families) (123, 124, 158), *Melitta* (8+ plant families) (41, 205, 235), *Dufourea* (17 plant families) (25, 60, 66, 127, 128, 217, 235; T Griswold, personal communication), *Micralictoides* (4 plant families) (19), *Conanthalictus* (2 plant families) (188; T Griswold, personal communication), *Andrena* (*Diandrena*) (3 plant families) (213), *Hesperapis* (including *Capi-*

Table 1 Oligolectic bee taxa whose species share a common genus of pollen host^a

Bee family	Genera	No. of species	Pollen host genera	Plant family	References
Colletidae	<i>Leioproctus</i> (<i>L. conospermij</i> sp. group)	3	<i>Conospermum</i>	Proteaceae	94
Andrenidae	<i>Andrena</i> (<i>Onagrandrena</i>)	24	<i>Oenothera</i> , <i>Camissonia</i>	Onagraceae	214
Halictidae	<i>Lasioglossum</i> (<i>Sphecodogaster</i>)	8	<i>Oenothera</i>	Onagraceae	21, 106a, 106b
Melittidae	<i>Rediviva</i>	~8	<i>Diascia</i>	Scrophulariaceae	33, 201
	<i>Macropis</i>	14	<i>Lysimachia</i>	Primulaceae	166, 220, 239
Megachilidae	<i>Lithurge</i> (<i>Lithurgopsis</i>)	9	<i>Opuntia</i> and other cacti	Cactaceae	144, 198
Apidae	<i>Peponapis</i> , <i>Xenoglossa</i>	17	<i>Cucurbita</i>	Cucurbitaceae	100, 148
	<i>Melitoma</i>	4	<i>Ipomoea</i>	Convolvulaceae	126

^a Several less-studied, small, and likely monophyletic genera of New World bees are likewise composed of oligolectes that share a common genus of pollen host. These include the rophitine bee genera *Sphecodosma* (*Nama*, Hydnophyllaceae) and *Xeralictus* (*Mentzelia*, Loasaceae); three subgenera of the panurgine genus *Calliopsis*, *Verbenapis* (*Verbena*, Verbenaceae), *Perissander* (*Euphorbia*, Euphorbiaceae), *Micronomadopsis* (*Trifolium*, Fabaceae); and several subgenera of *Perdita* (118). In addition, several Australian bee genera may be oligolectic for genera of the Myrtaceae (45).

cola) (4 plant families) (98, 128, 199, 205) and many subgenera of *Perdita* (99, 118). How did these disparate floral associations of oligolectic lineages originate?

Escape from competition is sometimes invoked as driving such radiations (references in 14, 212). Many oligolectes, however, belong to speciose pollen-collecting guilds with 75 or more bee species (e.g. 41, 100, 128, 235). Specialization has not opened empty niches but rather has channeled bees into bustling guilds. We hypothesize that the immediate ancestors to taxonomically diversified oligolectic bee lineages were themselves oligolectic. Mechanical factors such as pollen-grain size (e.g. 124) may underlie such switches, but chemical coevolution probably does not explain them (see below). Once established, new host associations may be enforced by two mechanisms: (a) the requisite match of phenology and habitat with the new host and (b) a tendency of male bees to search host flowers for receptive females (124). Both factors could promote fixation of the new host association once the switch occurred.

CONGRUENCE BETWEEN BEE AND PLANT PHYLOGENIES Probably few host associations among oligolectic bees result from reciprocal evolution or cospeciation (*sensu* 28), but relevant data are lacking. Cospeciation between bees and flowers may be disfavored for two reasons. First, most oligolectic bees do not discriminate among congeneric hosts, and so they should readily colonize

new sister taxa. Examples at the population level include a *Vaccinium* specialist that readily adopts another *Vaccinium* species outside its native range (44). Second, rates of host switching and evolutionary specialization by bees may outstrip speciation rates. In the >30,000 years since the progenitor of the desert shrub *Larrea tridentata* first appeared in the fossil record of North America (16), *L. tridentata* has come to dominate the warmer deserts. It now hosts 22 oligolectic bee species from 8 genera (100) that do not occur on South American *Larrea* species (142, 197) nor on any other member of the Zygophyllaceae (197a).

Adaptations for the Maintenance of Oligolecty

MORPHOLOGICAL SPECIALIZATIONS Morphological features used for pollen collection and transport, such as branched setae, distinguish all bees from wasps. At a course level, oligolectic bees are usually not recognizable by characters other than their limited floral niches. Body size, for instance, seems unimportant.

Pollen harvest The only known morphological innovations for pollen harvest by specialists consist of long hairs with modified tips. Such modifications, usually on the mouthparts or forelegs, have been reported for nine genera (19, 66, 94, 161, 170, 214). Sister taxa using other plants lack such hooked hairs (e.g. 161).

Pollen transport Hair density and pilosity may conform to extreme pollen sizes. Bees that carry tiny, dry pollen (<25 µm in diameter) often have dense scopae of plumose hairs (170, 214). Stout, unbranched, sometimes fluted hairs typify scopae of bees that carry large pollen (>100 µm in diameter), or onagraceous pollen webbed together with viscin threads (94, 118, 170, 214).

Gathering nectar Mouthparts of specialists may be differentially elongated or shortened to reach nectar concealed in tubular corollas or in shallow, open flowers (114, 195). Polylectic bees, however, also differ in proportional tongue lengths, as reflected in the informal divisions of short-tongued and long-tongued bees (see above) (for functional differences, see 85).

Gathering floral oils The use of floral oils has engendered a rich diversity of prominent morphological specializations in as many as ten genera (references in 33, 201, 220). Bees that collect oils often possess conspicuous setal brushes and combs on their tarsi and sometimes on abdominal sterna. Some *Rediviva* species use remarkably elongate forelegs to probe the twinned, oil-secreting, elongate spurs of *Diascia* flowers, which is one of the more persua-

sive cases supporting morphological coevolution among bees and flowers (201). Only two genera, *Rediviva* and *Macropsis*, are oil specialists (references in 33, 201).

BEHAVIORAL SPECIALIZATIONS Generalists, but usually not specialists, commonly visit flowers with complex corollas (231) that require prolonged trial-and-error learning for adept handling (e.g. 115). Conversely, specialists often utilize shallow flowers with easily accessible rewards (e.g. 60, 101, 154, 205, 235).

Floral sonication is a conspicuous and widespread behavioral adaptation used to harvest pollen from anthers that shed their pollen through terminal pores or slits (32, 214). Sonication can enhance pollen harvesting (JH Cane, in preparation). Many bees sonicate by shivering their flight muscles while contacting the stamens (32, 153, 214). Others drum, stroke, or milk anthers using their legs or mandibles (41; but see 153).

The propensity to sonicate anthers does not appear related to taxonomic classifications. However, there are a few patterns. For instance, tiny bees rarely sonicate anthers. Polyleges in diverse lineages do sonicate anthers using different mechanisms, but oligoleges rarely use novel means of sonication (39). We know little of the ontogeny and evolution of sonication, its mechanics (but see 109), or the advantages of different methods of floral sonication.

PHYSIOLOGICAL SPECIALIZATION Nectars are aqueous solutions of simple sugars that vary in concentration and are readily evaluated by bees (references in 177). Pollen also varies widely in nutritional composition, including the content of proteins (169; JH Cane, unpublished data), lipids (56), starches (9), and sterols (72). Melittophilous pollen is more protein rich than anemophilous pollen (JH Cane, unpublished data), but some plants (e.g. *Helianthus* spp.) that attract many oligoleges (e.g. 100, 101) do not produce especially proteinaceous pollen (JH Cane, unpublished data).

Bee larvae might be expected to develop best on pollen preferentially collected by their mothers. Some evidence supports a preference-performance relationship; larvae matured faster, grew larger, and survived better on pollen from their species' preferred pollen hosts than on other pollens (e.g. 83). Conversely, *Megachile rotundata* larvae grew normally on nonhost pollens such as carrot and cranberry (VJ Tepedino, unpublished data; JH Cane, unpublished data). Larvae of several oligolectic species fed and grew on nonhost pollen as well (21, 178). Even anemophilous pollen constitutes a marginally satisfactory bee diet (82). Limited evidence suggests that oligoleges do not generally specialize because of larval dietary requirements or pollen nutritional quality.

Floral oils Some bees incorporate floral oils into provision masses for larvae (references in 33, 220). Oils are calorically rich (175) and presumably less prone to spoilage than nectar. The physiological adaptations of bee larvae [including cleptoparasites (e.g. 186)] for diets of pollen or oil are unexplored.

Toxic pollen or nectar One hypothesis for food specialization in insects, namely evolved counter-adaptations to host chemical defenses (references in 14, 15, 84, 104a, 212), does not generally apply to the floral-host associations of oligolectic bees. Plants that chemically defend their tissues and seeds (e.g. *Solanum*, *Larrea*, *Curcubita*) usually do not defend their pollen or nectar (e.g. 56, 84, 200). Hundreds of generalist or specialist bee species collect pollen and nectar from these plants (80, 100, 101, 125, 235). Furthermore, chemically defended plants often host proportionately more species of specialized herbivores than specialized species of bees (compare 192 with 101).

Some plants have toxic nectar or pollen (7, 9, 56, 84, 200). In general, these plants (e.g. *Ranunculus* spp.) are infrequently visited by bees, and few host oligoleges (125, 209, 235). Most bees simply do not visit plants with toxic nectar or pollen.

PHENOLOGICAL SPECIALIZATION Bees are largely diurnal. Daily foraging activities, as for many insects, seem to be limited by temperature and illumination thresholds, as well as tolerance of wind and precipitation (50), but few experimental studies have tested these observations (117). Some taxa specialize in foraging at dawn, dusk, late afternoon (vespertine), or occasionally twice during the day (69, 119, 127, 128, 149, 155), and others forage at night (174, 238).

Diel patterns for provisioning often correspond with the daily initiation, cessation, or exhaustion of nectar or pollen production at preferred floral hosts (119, 149, 154, 155). A common pattern among plants is morning floral anthesis followed by the reduction of standing pollen crops, so early-arriving bees probably always do better than late comers. The first individual species of bee to arrive at a given pollen plant is called a matinal bee (119), and these bees can diminish the standing pollen crop by over a third by the time other bees arrive (JH Cane & SL Buchmann, unpublished data).

Diel foraging specializations have several anatomical and biogeographical correlates. Bees that fly at twilight or night have enlarged ocelli and somewhat paler coloration (references in 174). Matinal temperate bees are typically robust (119) with a thick pile of thoracic hair; both features are useful for thermoregulation (203). Bees of the lowland tropics (174) or warm deserts (118, 119) often exhibit matinal habits, and species of matinal genera retain their ancestral foraging habits in other biomes (102, 126).

Oligolectic species are mainly univoltine; brood production corresponds to

the annual bloom of their hosts (e.g. 170, 235). However, these species will still produce only one brood even if the host blooms twice annually (e.g. 101). Although date of first arrival at flowers is commonly used for evaluating phenological synchrony, a better measure is the yearly correspondence between the onset of bloom and bee emergence (149, 158). Oligoleges that emerge early may seek nectar at other plant species yet will delay nesting or provisioning until their preferred hosts bloom (44, 61, 149, 205).

In seasonal habitats, plants often do not bloom during a drought. Bees sometimes skip emergence under these conditions, and facultatively remain in diapause (see section on natural history). Conversely, a normally univoltine desert oligolege was observed to have a second annual generation after a freak summer rain induced its host plant to bloom (98). Unfortunately, abnormal emergence schedules of oligoleges have not been compared with those of univoltine polyleges. Detection of any special relationship between oligolecty and phenological tracking of flowers awaits additional, longer-term studies of emergence phenologies of univoltine oligoleges and polyleges at common floral hosts.

HOST RECOGNITION The conclusions regarding floral recognition and discrimination by bees have largely been drawn from the rich literature on nectar-gathering by social bees (see 58). In general, sensory systems do not differ substantially among bees, although a *Petunia* specialist has tetrachromatic photoreceptors rather than the trichromatic ones possessed by 26 other bee species, including another specialist (163). Spectral sensitivity functions of photoreceptors do not differ with respect to ecology (163), and the psychophysics of color coding may be universal in Hymenoptera (46). Specialists and generalists have similar densities of antennal chemosensilla (228).

Nevertheless, the relevance of generalizations from social bees to solitary bees is debatable, because the behavioral context is totally different: Foraging decisions of solitary bees are not influenced by the social needs of a colony. Many eusocial species stockpile food in their nests, so individual bees can temporally dissociate nectar and pollen foraging. Solitary bees, in contrast, usually do not stockpile food and must gather appropriate resources on a continual basis. The requisite discrimination capabilities of solitary bees are not well investigated. Only one study shows that solitary bees can recognize and respond to differences in the amount of pollen gained per flower (34). Diel foraging patterns (above) indicate that such capabilities may be more widespread.

Flower choice may be innate, or it might be learned from the scent of the bees' natal provision mass (119). Choice bioassays showed that inexperienced females of a local specialist (which is polylectic across its range) can discern the scent of their local floral host from others (55). Adult *M. rotundata* selected

flowers of their preferred host, even when reared on a diet of carrot pollen and nectar. This observation suggests that host recognition is heritable (VJ Tepedino, unpublished data). Field-foraging oligoleges may be constant to host petal-color morphs, but such constancy for visual cues is not universal (57, 130). Additional choice experiments are needed with naive foraging oligoleges before we can understand the origins and mechanisms of host recognition.

Pathways to Oligolecty

REPRODUCTIVE COSTS AND BENEFITS Oligolectic bees often forage at plants that have numerous other floral visitors. Observations that females complete fewer nest cells when resources are scarce, or when abundance fluctuates on daily or seasonal time scales, point to the costs of specialization (e.g. 20, 21, 34, 117, 149, 154, 158). Oligolectic bees are sometimes more proficient than competing polyleges in acquiring pollen from host flowers (43, 204). Oligoleges that use *Vaccinium* spp. (JH Cane, unpublished data) acquire as much pollen per flower as much larger polylectic bumble bees, as true for oligoleges on *Pontederia cordata* (86). Another *Vaccinium* spp. oligolege (*Habropoda laboriosa*) harvests as much pollen per flower as polylectic competitors, but it works faster (43).

Bee species evolve oligolecty via two non-mutually exclusive paths that relate to the relative abundance of floral resources. For convenience we name these the predictable-plethora and the restricted-resource pathways.

PREDICTABLE PLETHORA Many cases of oligolecty likely arose following this pathway. Plethoric plants are characterized by the following attributes: (a) production of large quantities of accessible pollen and nectar; (b) local patches that persist because either the plant is perennial or, if annual, it reseeds locally; (c) annual blooms that are reliable relative to nonhosts; and (d) blooms that coincide with local bee activity. Such plants (e.g. *Helianthus* spp.) are termed apparent (73). Their pollen is nutritionally adequate but may be unremarkable. These plants host taxonomically diverse guilds rich in polylectic and oligolectic bees, and such guilds may actually intensify competition among bees (170). Indeed, plants that produce a predictable plethora of pollen and nectar may act as evolutionary attractors for specialist bees. As bees are central-place foragers, if they must travel to sparse or widely spaced host patches, they will complete relatively few nest cells. Bees specialized for locally reliable flowers can devote more time to provisioning, especially when their emergence or activity coincides with peak bloom.

Bees are selective nectar foragers, but we do not know whether they recognize the nutritional qualities of pollen. Some social bees feed larvae progressively, such that hungry larvae fed deficient pollen solicit more food (219).

Most bees store a mass of provisions for their progeny and never receive direct larval feedback. Oligolectic females disregard interspecific heterogeneity in pollen quality, but we do not know whether bees that use nutritionally poor pollen compensate for the low quality by providing higher quantities, analogous to the way most bees match provision mass to sex of offspring (91). If adult bees cannot compare the nutritional value of different pollen, then taxonomic fidelity would help them gather resources adequate to support their own development, and polylecty becomes the strategy that requires evolutionary explanations.

RESTRICTED RESOURCES Some specialists seek out hosts that are minor elements of floral communities. Such bee guilds are more depauperate, with few generalists and perhaps less competition. These specialists are more likely to possess derived traits for harvesting or using host resources. Host associations are conserved (Table 1), and some may be relictual (166). This pathway mirrors the "biochemical arms race" (212) herbivory model, except that dietary restrictions are generally governed not by antagonistic host interactions, but rather by mutual benefits of host-pollinator relationships.

NATURAL ENEMIES OF BEES

Bees store floral resources for varying lengths of time. Animals that hoard food have many enemies, and bees are no exception (218). Although the amount of food stored in a given nest will be small, an aggregation can collectively contain large quantities (compare 149 with 237). While a solitary bee forages, her nest cells remain unprotected, unlike those of social bees (140).

The known enemies of bees are too numerous to list. However, an excellent survey of West German bees illustrates their diversity (235; also 99), which embodies the following parasitic, commensal, predatory, or scavenging associates: fungi, protozoa, nematodes, thomisid spiders, diverse mites, earwigs (Dermaptera), beetles (Coleoptera, 5 families), flies (Diptera, 6 families), wasps (11 families), bees (3 families), ants, birds, and mammals (for reviews of their biology, see 29, 48, 63, 68, 78, 79, 93, 97, 106, 108, 121, 132, 224). Parasites are hypothesized to regulate bee population size, but quantitative data are scarce (see 116, 122, 206, 222, 229).

Foraging Behavior, Habitat Preference, and Parasitism Rates

PROVISIONING SPECIALIZATION Modes of provisioning behavior influence bees' exposure to natural enemies, as does the foraging activity of other phytophagous insects (see 14). Polylectic behavior may increase mortality from natural enemies encountered on flowers [e.g. some meloid and rhipiphorid

beetles (121, 129)]. Conversely, specialization may allow such bees to forage in enemy-free space. Female meloids, for example, were placed in a greenhouse with nesting bees and plants from seven genera. Beetle larvae were recovered only from flowers of *Borago* spp., and the only parasitized bee nests contained *Borago* pollen (216). At this locality, pollen specialists restricted to other plants would be free of this parasite, while *Borago* visitors would be parasitized (see also 123).

NESTING PREFERENCE The choice of nesting location partially determines which suite of enemies will attack the nest. Some meloid beetles, for example, oviposit in cells or in nest tunnels. Their larvae attach themselves to bees active at those sites, restricting the beetles to gregariously nesting bees (68, 118, 120). Gregarious behavior presumably has the disadvantage of concentrating enemies in a local area (see 118, 223). Some anecdotal observations show that, on average, nests in aggregations are more heavily parasitized than isolated ones (e.g. 61, 226). Conversely, other studies show that 100% of the cells of isolated nests of several species can be parasitized (e.g. 111). Aggregations can be ephemeral or persistent (see section on overview of natural history), but we do not know whether persistent ones are more likely to support large parasite populations.

This frequently discussed relationship between tendency to aggregate nests and rates of parasitism is difficult to assess for several reasons. First, the number of taxa that obligately nest in aggregations relative to those that must nest in isolation is unknown. Aggregated nests are easier to locate and are probably more frequently reported. To address this problem, we need intraspecific comparisons among the many facultatively gregarious species (e.g. 61, 126, 230). Second, the spatial scale used to define an aggregation may not be relevant to the parasites (see 173). Third, many data on parasitism rates are point estimates, and the few long-term studies that have been done demonstrate how such data may not be representative. For a hole-nesting *Osmia* species, the rates of cell parasitism by a meloid beetle were usually less than 1% from 1974 to 1989, with a maximum of 3.7% in 1976. During a drought in 1990, however, parasitism rates increased to almost 33% (216). Within a season, rates can be equally variable (e.g. 189). Fourth, comparative studies often combine different host populations or taxa, which can have different numbers of specialized parasites (see 28).

Michener (143) hypothesized that nests distributed in two dimensions (those of ground-nesters) should be more heavily parasitized than those distributed in three dimensions (those of twig-nesters). The hypothesis incorporates considerations from foraging theory and makes two assumptions about information acquisition and processing (15): (a) Objects distributed in two dimensions are easier to locate than those distributed in three dimensions, and (b) parasites

search in both kinds of habitats. Assumption *b* is true for some parasites but not for others, including intraspecific parasites (summaries in 75, 135, 174, 224), and parasites presumably have sophisticated host-searching behaviors. Whether habitat specialists counterbalance each other in tallies of total rates of parasitism is unknown.

Available data do not support Michener's hypothesis: The mean rate of parasitized cells (x) for 27 ground-nesting species was 29.9% (SE = 4.6), which did not differ significantly from the rate for 25 twig- or mud-nesting species ($x = 29.2\%$) (WT Wcislo, submitted). Within one species, ground nests had 51.8% cells parasitized, while nests in twigs had approximately 36% cells parasitized, although these nests were at different localities (162). Many data on twig-nesting bees came from studies of trap nests, which artificially create aggregations (see 111), and parasitism rates may be lower under more natural nest densities. Proper tests should be based on comparisons within closely related taxa, such as twig- vs ground-nesting megachilids, xylocopines, or colletids (45, 67, 103), and should use data only from natural enemies that search in both habitats (e.g. some miltogrammine flies).

Strategies Against Natural Enemies

ACTIVE DEFENSE Most solitary bees do not aggressively attack natural enemies that wander too close to nest entrances (e.g. 95, 202), except for intraspecific parasites (see below). Active defenses are subtle and include opening cells for inspection and packing those containing fungi with soil (10). This behavior may decrease offspring mortality rates, as suggested for some sphecoform wasps (70).

PASSIVE DEFENSES Passive defenses involve physical and chemical features of nest architecture. Some solitary bees, especially those that do not nest in aggregations, often situate their nest entrances in concealed locations (e.g. under rocks, within clumps of plants). An *Osmia* species, for example, nests in a snail shell it drags to a depression and covers with debris (74). Constricted nest entrances and turrets may reduce parasitism (126, 138, 202). Nests of some solitary bees sometimes contain empty cells interspersed between provisioned cells (190, 230), which would theoretically reduce rates of parasitism (210).

The cells of most bees are lined with chemicals synthesized in the abdominal (metasomal) Dufour's gland (59, 87). The chemical composition of these secretions, which differs among taxa, includes macrocyclic lactones, terpenes, acetates, and alcohols. Chemical characterization of these compounds has greatly outpaced understanding of their functional significance. Allodapine and ceratinine bees have mandibular-gland compounds with repellent proper-

ties against ants and other enemies (references in 37, 59). Certain mandibular-gland compounds have germicidal properties (references in 42, 59), and they may help fumigate nests, because secretions can be released during biting motions of the kind made during nest excavations. Some megachilid, euglossine, and centridine bees incorporate plant resins into nest-cell linings. Resins physically defend plants and disinfect their wounds (113), and bees may gain similar benefits (136; JH Cane, unpublished data; G Gilbert, WS Armbruster & DW Roubik, unpublished data).

Parasitic Bees and Condition-Sensitive Behavior

Close neighbors are often a bee's worst enemy: Both opportunistic (facultative) parasitism (75, 224) and permanent (obligate) parasitic behavior (18, 224) are widespread. Thus, this array of parasitic specializations provides an excellent model to study the evolution of condition-sensitive behavior (cf 224, 233, 234).

PHYLETIC DISTRIBUTION Approximately 15% of bee genera or subgenera contain obligate parasites of other bees (167, 224). A conservative estimate would be that obligate parasitism has evolved independently at least 26 times (18, 167, 224). Parasitic bees are concentrated in the Apidae (and especially in the Nomadinae), Halictidae, and Megachilidae. The number of species in a taxon seems unrelated to the number of parasitic lineages generated by that taxon. For example, speciose families like Andrenidae lack parasitic bees, and a small taxon, Ctenoplectrini, contains a parasitic species.

Obligate parasitism is also phyletically biased within families. In Halictidae, for example, parasitic lineages occur in the Halictinae, but not in the Rophitinae or Nomiinae (141). Within Halictinae, in turn, the Nomioidini contain no known parasites, but parasitic behavior has evolved at least eight times in the cosmopolitan Halictini. Some lineages (e.g. *Sphecodes*) contain numerous parasitic species (141; WT Wcislo, in preparation). In the equally large but primarily neotropical tribe Augochlorini, parasitism has purportedly evolved at least three times (147; RW Brooks, personal communication), but no behavioral data confirm the parasitic status of these species.

HOST-PARASITE RELATIONSHIPS Lineages of parasitic bees have long been hypothesized to be related to, and derived from, their host lineages (18, 151, 224). This heuristic relationship is named Müller's Law (165), or Emery's Rule when applied to ants and wasps (e.g. 93). Phylogenetic studies are not yet numerous enough for statistical tests of this hypothesis, but it is valid in some cases, and certainly invalid for lineages with many host shifts (e.g. many nomadines) (references in 171).

Parasites differ in the degree of host specificity, even among congeners (e.g.

182; for other host associations, see 3, 4, 141, 167, 174, 184, 185, 202, 235). Apparent specificity may simply represent lack of information. Cladistic studies have demonstrated generic-level host shifts for various parasites (e.g. 3, 4, 182). Hosts shifts, like some parasite-host associations (e.g. 193), tend to be habitat specific. A few parasitic bees regularly associated with twig- or mason-nesting bees have shifted to ground-nesting bees, and vice versa (e.g. 11). L-T bees have expanded their host ranges to parasitize S-T bees, yet no S-T bee, not even the large, cosmopolitan genus *Sphecodes*, parasitizes L-T bees (WT Wcislo, unpublished data). The historical biogeography of bees (142) is not well-enough known to assess whether this pattern is related to the relative ages of these groups.

Some speciose taxa appear to be immune to bee parasites (167; WT Wcislo, unpublished data). No known hosts occur in Stenotritidae, Xeromelissinae, Euryglossinae, Diphaglossini, possibly Hylaeini [there is an unconfirmed report (241) of parasitic Hylaeini in Hawaii, which purportedly parasitize other hylaeines], Ceratinini, Xylocopini, Manuelini, Apini (excluding robber species—see 174, 224), Fideliinae, or Meganomiinae. Many of these taxa are abundant in Australia (45), which may partially account for their apparent immunity because the rich Australian bee fauna is curiously depauperate in parasites (except Allodapini) (224). A detailed comparative study of immune and susceptible taxa may lend insight into the evolution of parasitic bees.

HOST RECOGNITION, ASSESSMENT, AND NEST-ENTERING BEHAVIOR The mechanisms by which parasites recognize their host(s) have been studied in only one species, and this report showed the importance of olfactory evaluation (36). In addition, adult *Stelis montana* are known to ascertain whether a host cell is suitably provisioned (215), but most species have not been studied. The mechanisms for entry into a nest also are not well studied. Some parasites aggressively enter nests (194), while others avoid contact with a host (e.g. 1, 194, 215).

Parasitic *Nomada* spp. males have an odor bouquet similar to that of host females; hypothetically, these males transfer this odor to conspecific females during mating, thus enabling the parasitic female to more easily enter the host nest (references in 59). No behavioral data are available to support these hypotheses. No evidence supports chemical mimesis in other parasitic bees (see 194, 208).

Many parasites place their eggs in concealed locations within cells (representative illustrations are given in 167, 174, 202). Most nomadines oviposit in a cell wall before the cell is fully provisioned (183). This hiding is common in parasites. *Stelis* species oviposit within the host pollen mass, and *Coelioxys* species oviposit into the leaf mass that surrounds the cell of its megachilid host. When parasite larvae (e.g. Nomadinae) are in the same cell as living host

eggs or larvae, the parasites destroy the host larvae. For example, some parasite larvae undergo hypermetamorphosis to a "killer" instar, which actively crawls about the host cell and kills the host egg or larva, as well as other parasite larvae (180, 181). After dispatching its competitors, the killer larva molts to a typical grub-like bee larva. In other species, the adult parasite destroys the host egg or young larva. The parasite larvae of these taxa are not morphologically differentiated from host larvae (137) and are not active crawlers.

CONDITION-SENSITIVITY AND THE EVOLUTION OF PARASITISM Changes in context-dependent expression are increasingly recognized as a basic feature in the evolution of diversity (e.g. 225, 233, 234). The perceptual mechanisms that animals use to assess local conditions and implement alternative behaviors are poorly understood (see 15). The frequent evolution of obligate parasitism from facultative behavior in bees allows us to redress this situation.

Facultative parasitism Facultative parasitic behavior is generally thought to represent an evolutionary precursor to obligate parasitism (e.g. 18, 75, 224, 233). Kaitala et al (105) argue the two phenomena are unrelated, presupposing that pollen-collecting structures are lost concomitant with the origin of parasitic behavior. This presupposition is inconsistent with facts. Among parasitic *Paralictus*, for example, different species have lost pollen-collecting structures to differing degrees (141; WT Wcislo, in preparation), which shows that behavioral and morphological evolution can be uncoupled.

Factors that induce facultative parasitic behavior may include a failure to resorb developing oocytes (references in 224). A shortage of nest sites has been widely implicated in facultative parasitism in nest-making animals (references in 224), but its relative importance is unknown for bees. A shortage of nest sites, or loss of a nest because of predation or other factors, may be less important in lineages that have open, communal groups (1, 53, 112, 179, 227) because a female could join another group. Joining behavior (but not necessarily in relation to nest loss) has been confirmed by genetic studies (53, 112). The open nature of communal living possibly helps explain why lineages with widespread communal behavior (e.g. Andrenidae, Agapostemonini) have not generated many parasitic lineages.

Obligate parasitism and expression of morphological novelty Obligately parasitic female bees frequently (but to differing degrees) show a suite of external characters putatively related to their parasitic behavior (e.g. loss or reduction of pollen-collecting structures, loss of a toothed mandible, reinforced exoskeleton, changes in proportion of antennal structures, bright or metallic coloration) (see 141, 224, 228). Nothing is known about the evolutionary origins or development of such structures.

Some external features (e.g. loss or reduction of pollen-collecting structures, loss of toothed mandible, relative lengths of the antennal scape and flagellum) seem to represent the masculinization of the female phenotype (141, 228). Sex transfers of phenotypic development patterns have been discussed for other insects (e.g. 47, 107). Strepsiptera parasitism (191) and other pathologies (240) can induce various degrees of masculinization. In *Andrena vega* stylopization decreases the volume of the corpora allata (26) and probably reduces titers of juvenile hormone (JH). Bonetti & Kerr (23) show that male larvae treated with topical JH are feminized as adults. Thus, studies of stylops and other pathogens reveal the potential of developmental systems to express preexisting traits under novel conditions.

Obligate parasites have also undergone evolutionary changes in ovarian physiology and morphology (references in 6). Parasitic bees have either a greater number of oocytes per ovariole or a greater number of ovarioles per ovary, relative to the putative ancestors. Associated with this increase in fecundity is a relative decrease in egg size. Rozen (183) hypothesized that the smaller size of parasite eggs is related to the need to hide eggs within a host cell. Smaller egg size is also expected from the decreased parental investment per egg, according to arguments associated with *r*- and *K*-selection (131).

SUMMARY

The spatial distribution of bees influences interactions with parasites and intraspecific competitors for food. The study of many resource-specializing (oligolectic) bees allows us to make illuminating comparisons with other phytophagous insects, because bees provide an indirect service (pollination) to the plant, unlike herbivores. Hypotheses proposed to explain resource specialization among other phytophagous insects are not generally applicable to bees. Instead, diverse oligolectic (and generalist) bees utilize resources from flowers that are predictably abundant in time and space. Apart from phenological matching, these oligolectic bees usually do not have striking behavioral, physiological, or anatomical modifications associated with their specialized behaviors. Some cases of bee specialization, however, are probably explained by analogy to the biochemical arms race models proposed for herbivores. Bees that are oligolectic on rare and patchily distributed plants often possess specific behavioral or anatomical keys that allow them access to pollen, nectar, or oil that a plant has locked away. Resources stored by bees present a rich target for natural enemies. Natural history observations suggest these enemies have shaped bees' foraging behavior, nest architecture, and nest-site selection. Opportunistic, facultative parasitism is common in bees, and obligate parasitism has repeatedly evolved. The convergent phenotypes of parasitic bees yield

insights into the relationship between the evolution of condition-sensitive behavior and morphology and the expression of novel combinations of traits.

Comparative studies of bees provide exceptional opportunities to those interested in merging natural history studies with research addressing underlying mechanisms. We know a good deal about what bees do, but we know little about how they do it, and therefore we can only speculate about why. Significant advances in understanding "why" questions are likely to come from those areas that address the "how" questions.

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Literature Cited

1. Abrams J, Eickwort GC. 1981. Nest switching and guarding by the communal sweat bee *Agapostemon virescens* (Hymenoptera: Halictidae). *Insectes Soc.* 28:105-16
2. Alcock J, Jones CE, Buchmann SL. 1976. The nesting behavior of three species of *Centris* bees (Hymenoptera: Anthophoridae). *J. Kans. Entomol. Soc.* 49:469-74
3. Alexander BA. 1990. A cladistic analysis of the nomadine bees (Hymenoptera: Apoidea). *Syst. Entomol.* 15:121-52
4. Alexander BA. 1991. Nomada phylogeny reconsidered (Hymenoptera: Anthophoridae). *J. Nat. Hist.* 25:315-30
5. Alexander BA. 1992. An exploratory analysis of cladistic relationships within the superfamily Apoidea, with special reference to sphecids wasps (Hymenoptera). *J. Hymenoptera Res.* 1:26-61
6. Alexander BA, Rozen JG Jr. 1987. Ovaries, ovarioles, and oocytes in parasitic bees (Hymenoptera: Apoidea). *Pan-Pac. Entomol.* 63:155-64
- 6a. Allen PM, Sanglier M. 1978. Dynamic model of urban growth. *J. Soc. Biol. Struct.* 1:265-80
7. Atkins EL. 1992. Injury to honey bees by poisoning. In *The Hive and the Honey Bee*, ed. JM Graham, pp. 13-21. Hamilton, IL: Dadant & Sons. 6th ed.
8. Ayala R, Griswold TL, Bullock SH. 1993. The native bees of México. In *Biological Diversity of México, Origins and Distributions*, ed. TP Ramamoorthy, R Bye, A Lot, J Fa, pp. 179-225. Sunderland, MA: Sinauer. 812 pp.
9. Baker HG, Baker I. 1979. Starch in angiosperm pollen grains and its evolutionary significance. *Am. J. Bot.* 66:591-600
10. Batra SWT, Bohart GE. 1970. Alkali

- bees: response of adults to pathogenic fungi in brood cells. *Science* 165:607-8
11. Batra SWT, Schuster JC. 1977. Nests of *Centris*, *Melissodes*, and *Colletes* in Guatemala (Hymenoptera: Apoidea). *Biotropica* 9:135-38
 12. Bawa KS. 1990. Plant-pollinator interactions in tropical rain forests. *Annu. Rev. Ecol. Syst.* 21:399-422
 13. Bennett B, Breed MD. 1985. The nesting biology, mating behavior and foraging ecology of *Perdita opuntiae* (Hymenoptera: Andrenidae). *J. Kans. Entomol. Soc.* 58:185-94
 14. Bernays EA, Chapman RF. 1994. *Host-Plant Selection by Phytophagous Insects*. New York: Chapman & Hall. 312 pp.
 15. Bernays EA, Wcislo WT. 1994. Sensory capabilities, information processing, and resource specialization. *Q. Rev. Biol.* 69:187-204
 16. Betancourt JL, Van Devender TR, Martin PS, eds. 1990. *Packrat Middens: the Last 40,000 Years of Biotic Change*. Tucson: Univ. Ariz. Press. 467 pp.
 17. Blows MW, Schwarz MP. 1991. Spatial distribution of a primitively social bee: Does genetic population structure facilitate altruism? *Evolution* 45:680-93
 18. Bohart GE. 1970. The evolution of parasitism among bees. *Utah State Univ. Fac. Honor Lec.* 41:1-30
 19. Bohart GE, Griswold TL. 1987. A revision of the Dufourea genus *Micralictoides* Timberlake (Hymenoptera: Halictidae). *Pan-Pac. Entomol.* 63:178-93
 20. Bohart GE, Youssef NN. 1972. Notes on the biology of *Megachile* (*Megachiloides*) *umatillensis* Mitchell (Hymenoptera: Megachilidae) and its parasites. *Trans. R. Entomol. Soc. London* 124:1-19
 21. Bohart GE, Youssef NN. 1976. The biology and behavior of *Evyalaeus galpinsiae* Cockerell (Hymenoptera: Halictidae). *Wasmann J. Biol.* 34:185-234
 22. Bohart RM, Menke AS. 1976. *Sphecids Wasps of the World*. Berkeley: Univ. Calif. Press. 695 pp.
 23. Bonetti AM, Kerr WE. 1985. Sex determination in bees. XX. Estudo da ação genica em *Melipona marginata* e *Melipona compressipes* a partir de análise morfológica. *Rev. Brasil. Genet.* 4:629-38
 24. Boucot AJ. 1990. *Evolutionary Palaeobiology of Behavior and Coevolution*. Amsterdam: Elsevier. 725 pp.
 25. Bouseman JK. 1976. *Dufourea monardae* (Viereck) in Illinois and Michigan (Hymenoptera: Apoidea). *J. Kans. Entomol. Soc.* 49(4):531-32
 26. Brandenburg J. 1956. Das endokrine system des Kopfes von *Andrena vega* Pz. (Ins. Hymenopt.) und Wirkung der Stylopisation (Stylops, Ins. Strepsipt.). *Z. Morphol. Oekol. Tierre* 45:343-64
 27. Bronstein JL. 1995. The plant/pollinator landscape. In *Mosaic Landscapes and Ecological Processes*, ed. L Fahrig, L Hansson, G Merriam. New York: Chapman & Hall. In press
 28. Brooks DR, McLennan DA. 1993. *Parascript: Parasites and the Language of Evolution*. Washington, DC: Smithsonian. Inst. 429 pp.
 29. Brothers DJ. 1972. Biology and immature stages of *Pseudomethoca frigida*, with notes on other species (Hymenoptera: Mutillidae). *Univ. Kans. Sci. Bull.* 50:1-38
 30. Brothers DJ, Carpenter JM. 1993. Phylogeny of Aculeata: Chrysoidea and Vespoidea. *J. Hymenoptera Res.* 2:227-301
 31. Brown CR. 1986. Cliff swallow colonies as information centers. *Science* 234:83-5
 32. Buchmann SL. 1983. Buzz pollination in angiosperms. See Ref. 104b, pp. 73-113
 33. Buchmann SL. 1987. The ecology of oil flowers and their bees. *Annu. Rev. Ecol. Syst.* 18:343-69
 34. Buchmann SL, Cane JH. 1989. Bees assess pollen returns while sonicating *Solanum* flowers. *Oecologia* 81:289-94
 35. Callan E McC. 1977. Observations on *Centris rufosuffusa* Cockerell (Hymenoptera: Anthophoridae) and its parasites. *J. Nat. Hist.* 11:127-35
 36. Cane JH. 1983. Olfactory evaluation of *Andrena* host nest suitability by kleptoparasitic *Nomada* bees. *Anim. Behav.* 31:138-44
 37. Cane JH. 1986. Predator deterrence by mandibular gland secretions of bees (Hymenoptera: Apoidea). *J. Chem. Ecol.* 12:1295-309
 38. Cane JH. 1992. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *J. Kans. Entomol. Soc.* 64:406-13
 39. Cane JH, Buchmann SL. 1989. Novel pollen-harvesting behavior by the bee *Protandrena mexicanorum* (Hymenoptera: Andrenidae). *J. Insect Behav.* 2:431-36
 40. Cane JH, Eickwort GC, Wesley FR, Spielholz J. 1983. Foraging, grooming and mate-seeking behaviors of *Macropis nuda* (Hymenoptera, Melittidae) and use of *Lysimachia ciliata* (Primulaceae) oils in larval provisions and cell linings. *Am. Midl. Nat.* 110:257-64
 41. Cane JH, Eickwort GC, Wesley FR, Spielholz J. 1985. Pollination ecology of *Vaccinium stamineum* (Ericaceae: Vaccinioideae). *Am. J. Bot.* 72:135-42
 42. Cane JH, Gerdin S, Wife G. 1983. Mandibular gland secretions of solitary bees (Hymenoptera: Apoidea): potential for nest cell disinfection. *J. Kans. Entomol. Soc.* 56:199-204
 43. Cane JH, Payne JA. 1988. Foraging ecology of the bee *Habropoda laboriosa* (Hymenoptera: Anthophoridae), an oligolectic of blueberries (Ericaceae: *Vaccinium*) in the southeastern United States. *Ann. Entomol. Soc. Am.* 81:419-27
 44. Cane JH, Payne JA. 1993. Regional, annual and seasonal variation in pollinator guilds: intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). *Ann. Entomol. Soc. Am.* 86:577-88
 45. Cardale JC. 1993. *Zoological Catalogue of Australia*, Vol. 10, *Hymenoptera: Apoidea*, ed. WWK Houston, GV Maynard. Canberra: AGPS. 406 pp.
 46. Chittka L, Beier W, Hertel H, Steinmann, Menzel R. 1992. Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in Hymenoptera. *J. Comp. Physiol. A* 170:545-63
 47. Clarke C, Clarke FMM, Collin SC, Gill ACL, Turner JRG. 1985. Male-like females, mimicry, and transvestism in butterflies (Lepidoptera: Papilionidae). *Syst. Entomol.* 10:257-83
 48. Clausen CP. 1940. *Entomophagous Insects*. New York: McGraw-Hill. 688 pp.
 49. Cockerell TDA. 1933. The excessive abundance of certain bees. *Am. Nat.* 67:1-3
 50. Corbet SA. 1990. Pollination and the weather. *Isr. J. Bot.* 39:13-30
 51. Cripps C, Rust RW. 1989. Pollen preferences of seven *Osmia* species (Hymenoptera: Megachilidae). *Environ. Entomol.* 18:133-38
 52. Daly HV. 1973. Bees of the genus *Ceratina* in America north of Mexico (Hymenoptera: Apoidea). *Univ. Calif. Publ. Entomol.* 74:1-114
 53. Danforth BN, Neff JL, Barretto-Ko P. 1995. Nestmate relatedness in a communal bee, *Perdita texana*, (Hymenoptera: Andrenidae), based on DNA fingerprinting. *Evolution*. In press
 54. Danforth BN, Visscher PK. 1993. Dynamics of a host-cleptoparasite relationship: *Holcopasites ruthae* as a parasite of *Calliopsis pugionis* (Hymenoptera: Anthophoridae, Andrenidae). *Ann. Entomol. Soc. Am.* 86:833-40
 55. Dobson HEM. 1987. Role of flower and pollen aromas in host-plant recognition by solitary bees. *Oecologia* 72:618-23
 56. Dobson HEM. 1988. Survey of pollen and pollenkitt lipids: chemical cues to flower visitors? *Am. J. Bot.* 75:170-82
 57. Dobson HEM. 1994. Floral volatiles in insect biology. In *Insect-Plant Interactions*, ed. EA Bernays, 5:47-81. Boca Raton, FL: CRC
 58. Dukas R, Real LA. 1993. Cognition in bees: from stimulus reception to behavioral change. In *Insect Learning*, ed. DR Papaj, AC Lewis, pp. 343-73. New York: Chapman & Hall
 59. Duffield RM, Wheeler JW, Eickwort GC. 1984. Sociochemicals of bees. In *Chemical Ecology of Insects*, ed. WJ Bell, RT Cardé, pp. 287-428. Sunderland, MA: Sinauer
 60. Eckhart VM. 1992. Spatio-temporal variation in abundance and variation in foraging behavior of the pollinators of gynodioecious *Phacelia linearis* (Hydrophyllaceae). *Oikos* 64:573-86
 61. Eickwort GC. 1973. Biology of the European mason bee, *Hoplitis anthocopoides* (Hymenoptera: Megachilidae), in New York state. *Search* 3:1-31
 62. Eickwort GC. 1981. Presocial insects. In *Social Insects*, ed. HR Hermann, 2:199-280. New York: Academic
 63. Eickwort GC. 1993. Evolution and life-history patterns of mites associated with bees. In *Mites: Ecological and Evolutionary Analyses of Life History Patterns*, ed. M. Houck, pp. 218-51. New York: Chapman & Hall
 64. Eickwort GC, Eickwort KR, Linsley EG. 1977. Observations on nest aggregations of the bees *Diadasia olivacea* and *D. diminuta* (Hymenoptera: Anthophoridae). *J. Kans. Entomol. Soc.* 50:1-17
 65. Eickwort GC, Ginsberg HS. 1980. Foraging and mating behavior in Apoidea. *Annu. Rev. Entomol.* 25:421-46
 66. Eickwort GC, Kukuk PF, Wesley FR. 1986. The nesting biology of *Dufourea novaeangliae* (Hymenoptera: Halictidae) and the systematic position of the Dufoureae based on behavior and development. *J. Kans. Entomol. Soc.* 59:103-20
 67. Eickwort GC, Matthews RW, Carpenter J. 1981. Observations on the nesting behavior of *Megachile rubi* and *M. texana* with a discussion of the significance of soil nesting in the evolution of megachilid bees (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* 54:557-70

68. Erickson EH, Enns WR, Werner FG. 1976. Bionomics of the bee-associated Meloidae (Coleoptera): bee and plant hosts of some Nearctic beetles—a synopsis. *Ann. Entomol. Soc. Am.* 69:959–70
69. Estes JR, Thorp W. 1975. Pollination ecology of *Pyrrhopappus carolinianus* (Compositae). *Am. J. Bot.* 62(2):148–59
70. Evans HE, West Eberhard MJ. 1970. *The Wasps*. Ann Arbor: Univ. Mich. Press. 265 pp.
71. Fabre JH. (1915) 1920. *Bramble-bees and Others*. New York: Dodd, Mead. 456 pp. (Transl.)
72. Feldlaufer MF, Buchmann SL, Lusby WR, Weirich GF, Svoboda JA. 1993. Neutral sterols and ecosteroids of the solitary cactus bee *Diadasia rinconis* Cockerell (Hymenoptera: Anthophoridae). *Arch. Insect Biochem. Physiol.* 23: 91–98
73. Feeny P. 1976. Plant apparency and chemical defense. *Adv. Phytopathol.* 10: 1–40
74. Ferton C. 1923. *La Vie des Abeilles et des Guêpes*, ed. E Rabaud, F Picard. Paris: Étienne Chiron. 376 pp.
75. Field J. 1992. Intraspecific parasitism as an alternative reproductive tactic in nest-building wasps and bees. *Biol. Rev.* 67:99–126
76. Frankie GW, Newstrom L, Vinson SB, Barthell JF. 1993. Nesting-habitat preference of selected *Centris* bee species in Costa Rican dry forest. *Biotropica* 25:322–33
77. Gauld ID, Bolton B, eds. 1988. *The Hymenoptera*. Oxford: Oxford Univ. Press. 332 pp.
78. Gibling-Davis RM, Norden BB, Batra SWT, Eickwort GC. 1990. Commensal nematodes in the glands, genitalia, and brood cells of bees (Apoidea). *J. Nematol.* 22:150–61
79. Gilliam M, Buchmann SL, Lorenz, Schmalzel RJ. 1990. Bacteria belonging to the genus *Bacillus* associated with three species of solitary bees. *Apidologie* 21:99–105
80. Graenicher S. 1909. Wisconsin flowers and their pollination. *Bull. Wisc. Nat. Hist. Soc.* 7:19–77
81. Grant V. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. *Proc. Natl. Acad. Sci. USA* 91:3–10
82. Greenberg L. 1982. Year-round culturing and productivity of a sweat bee, *Lasiglossum zephyrum* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 55: 13–22
83. Guirguis GN, Brindley WA. 1974. Insecticide susceptibility and response to selected pollens of larval alfalfa leaf-cutting bees, *Megachile pacifica* (Panzer) (Hymenoptera: Megachilidae). *Environ. Entomol.* 3:691–94
84. Harborne JB. 1993. *Introduction to Ecological Biochemistry*. New York: Academic. 318 pp. 4th ed.
85. Harder LD. 1983. Functional differences of the proboscides of short- and long-tongued bees (Hymenoptera, Apoidea). *Can. J. Zool.* 61:1580–86
86. Harder LD, Barrett SCH. 1993. Pollen removal from tristylous *Pontederia cordata*: effects of anther position and pollinator specialization. *Ecology* 74: 1059–72
87. Hefetz A. 1987. The role of Dufour's gland secretions in bees. *Physiol. Entomol.* 12:243–53
88. Hefetz A, Tengö J. 1992. Dispersed versus gregarious nesting strategies in the mason bee *Chalicodoma siculum*. *J. Zool.* 226:529–37
89. Heithaus ER. 1979. Flower-feeding specialization in wild bee and wasp communities in seasonal neotropical habitats. *Oecologia* 42:179–94
90. Heithaus ER. 1979. Community structure of neotropical flower visiting bees and wasps: diversity and phenology. *Ecology* 60:190–202
91. Helms KR. 1994. Sexual size dimorphism and sex ratios in bees and wasps. *Am. Nat.* 143:418–34
92. Herbst P. 1922. Zur Biologie der Gattung *Chilicola* Spin. (Apidae, Hymen.). *Entomol. Mitt. Zool. Mus. Hamburg* 11: 63–68
93. Hölldobler B, Wilson EO. 1990. *The Ants*. Cambridge, MA: Harvard Univ. Press. 732 pp.
94. Houston TF. 1989. *Leioproctus* bees associated with Western Australian smoke bushes (*Conospermum* spp.) and their adaptations for foraging and concealment (Hymenoptera: Colletidae: Paracolletini.). *Rec. West. Aust. Mus.* 14:275–92
95. Houston TF. 1991. Ecology and behavior of the bee *Amegilla dawsoni* Rayment with notes on a related species (Hymenoptera: Anthophoridae). *Rec. West. Aust. Mus.* 15:535–54
96. Houston TF. 1992. Three new, monolecitic species of *Euryglossa* (*Euhesma*) from Western Australia (Hymenoptera: Colletidae). *Rec. West. Aust. Mus.* 15: 719–28
97. Hull FM. 1973. *Bee Flies of the World*. Washington, DC: Smithsonian. 687 pp.
98. Hurd PD Jr. 1957. Notes on the autumnal emergence of the vernal desert bee, *Hesperapis fulvipes* Crawford. *J. Kans. Entomol. Soc.* 30:10
99. Hurd PD Jr. 1979. Superfamily Apoidea. In *Catalog of Hymenoptera in North America North of Mexico*, ed. KV Krombein, PDJ Hurd, DR Smith, BD Burks, 2:1741–2209. Washington, DC: Smithsonian. Inst.
100. Hurd PD Jr, LaBerge WE, Linsley EG. 1980. Principal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera: Apoidea). *Smithson. Contrib. Zool.* 310: 1–158
101. Hurd PD Jr, Linsley EG. 1975. The principal *Larrea* bees of the southwestern United States (Hymenoptera: Apoidea). *Smithson. Contrib. Zool.* 193: 1–74
102. Hurd PD Jr, Linsley EG, Whitaker TW. 1971. Squash and gourd bees (Pleonapis, Xenoglossa) and the origin of the cultivated *Cucurbita*. *Evolution* 25: 218–34
103. Hurd PD Jr, Moure JS. 1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera: Apoidea). *Univ. Calif. Publ. Entomol.* 29:1–365
104. Iwata K. 1976. *Evolution of Instinct: Comparative Ethology of Hymenoptera*. New Delhi: Amerind. 535 pp.
- 104a. Jaenike J. 1990. Host specialization in phytophagous insects. *Annu. Rev. Ecol. Syst.* 21:243–73
- 104b. Jones CE, Little RJ, eds. 1983. *Handbook of Experimental Pollination Biology*. New York: Van Nostrand Reinhold. 558 pp.
105. Kaitala V, Smith BH, Getz WM. 1990. Nesting strategies of primitively eusocial bees: a model of nest usurpation during the solitary state of the nesting cycle. *J. Theor. Biol.* 144:445–71
106. Kathirithamby J. 1989. Review of the order Strepsiptera. *Syst. Entomol.* 14: 41–92
- 106a. Kerfoot WB. 1967. The lunar periodicity of *Specodagastra texana*, a nocturnal bee (Hymenoptera: Halictidae). *Anim. Behav.* 15:479–86
- 106b. Kerfoot WB. 1967. Nest architecture and associated behavior of the nocturnal bee *Specodagastra texana* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 40:84–93
107. Kerr WE, da Cunha RA. 1990. Sex determination in bees. XXVI. Masculinism of workers in the Apidae. *Rev. Brasil. Genet.* 13:479–89
108. Kimsey LS, Bohart RM. 1990. *The Chrysidid Wasps of the World*. Oxford: Oxford Univ. Press. 652 pp.
109. King MJ. 1993. Buzz foraging mechanism of bumble bees. *J. Apic. Res.* 32: 41–49
110. Kojima J-i. 1993. A latitudinal gradient in intensity of applying ant-repellant substance to the nest petiole in paper wasps (Hymenoptera: Vespidae). *Insectes Soc.* 40:403–21
111. Krombein KV. 1967. *Trap-Nesting Wasps and Bees*. Washington, DC: Smithsonian. Inst. 570 pp.
112. Kukuk PF, Sage GK. 1994. Reproductivity and relatedness in a communal halictine bee *Lasiglossum (Chilalictus) helichalceum*. *Insectes Soc.* 41:443–56
113. Langenheim JH. 1990. Plant resins. *Am. Sci.* 78:16–24
114. Laroca S, Michener CD, Hofmeister RM. 1989. Long mouthparts among "short-tongued" bees and the fine structure of the labium in *Niltonia* (Hymenoptera, Colletidae). *J. Kans. Entomol. Soc.* 62:400–10
- 114a. LaSalle J, Gauld ID, eds. 1993. *Hymenoptera and Biodiversity*. Wellesford: CAB Int. 348 pp.
115. Lavery TM. 1994. Bumble bee learning and flower morphology. *Anim. Behav.* 47:31–45
116. Lin N, Michener CD. 1972. Evolution of sociality in insects. *Q. Rev. Biol.* 47:131–59
117. Lind H. 1984. Nest-provisioning cycle and daily routine of behaviour in *Dasygaster plumipes* (Hym., Apidae). *Entomol. Medd.* 36:343–72
118. Linsley EG. 1958. The ecology of solitary bees. *Hilgardia* 27:543–99
119. Linsley EG. 1978. Temporal patterns of flower visitation by solitary bees, with particular reference to the southwestern United States. *J. Kans. Entomol. Soc.* 51:531–46
120. Linsley EG, MacSwain JW. 1942. Bionomics of the meloid genus *Hornia* (Coleoptera). *Univ. Calif. Publ. Entomol.* 7:189–206
121. Linsley EG, MacSwain JW. 1952. Notes on the biology and host relationships of some species of *Nemognatha* (Coleoptera: Meloidae). *Wasmann J. Biol.* 10: 91–102
122. Linsley EG, MacSwain JW. 1952. Notes on some effects of parasitism upon a small population of *Diadasia bituberculata* (Cresson). *Pan-Pac. Entomol.* 28: 131–35
123. Linsley EG, MacSwain JW. 1957. The nesting habits, flower relationships, and parasites of some North American species of *Diadasia* (Hymenoptera: Anthophoridae). *Wasmann J. Biol.* 15: 199–235

124. Linsley EG, MacSwain JW. 1958. The significance of floral constancy among bees of the genus *Diadasia* (Hymenoptera: Anthophoridae). *Evolution* 12: 219-23
125. Linsley EG, MacSwain JW. 1959. Ethology of some *Ranunculus* insects with emphasis on competition for pollen. *Univ. Calif. Publ. Entomol.* 16:1-46
126. Linsley EG, MacSwain JW, Michener CD. 1980. Nesting biology and associates of *Melitoma* (Hymenoptera, Anthophoridae). *Univ. Calif. Publ. Entomol.* 90:1-45
127. Linsley EG, MacSwain JW, Raven PH. 1963. Comparative behavior of bees and Onagraceae. I. *Oenothera* bees of the Colorado desert. *Univ. Calif. Publ. Entomol.* 33:1-24
128. Linsley EG, MacSwain JW, Raven PH, Thorp RW. 1973. Comparative behavior of bees and Onagraceae. V. *Camissonia* and *Oenothera* bees of cismontane California and Baja California. *Univ. Calif. Publ. Entomol.* 71:1-68
129. Linsley EG, MacSwain JW, Smith RF. 1952. The life history and development of *Rhipiphorus smithi* with notes on their phylogenetic significance. (Coleoptera, Rhipiphoridae). *Univ. Calif. Publ. Entomol.* 9:291-314
130. Lunau K. 1992. A new interpretation of flower guide colouration: absorption of ultraviolet light enhances colour saturation. *Plant Syst. Evol.* 183:51-65
131. MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton: Princeton Univ. Press. 203 pp.
132. Maeta Y, MacFarlane RP. 1993. Japanese Conopidae (Diptera): their biology, overall distribution, and role as parasites of bumble bees (Hymenoptera, Apidae). *Jpn. J. Entomol.* 61:493-509
133. Maeta Y, Saito K, Hyodo K, Sakagami SF. 1993. Diapause and non-delayed eusociality in a univoltine and basically solitary bee, *Ceratina japonica* (Hymenoptera, Anthophoridae). I. Diapause termination by cooling and application of juvenile hormone analog. *Jpn. J. Entomol.* 61:203-11
134. Malyshev SI. 1935. The nesting habits of solitary bees. *Eos* 11:201-309
135. Malyshev SI. 1968. *Genesis of the Hymenoptera and the Phases of Their Evolution*. London: Methuen. 319 pp.
136. Messer AC. 1985. Fresh dipterocarp resins gathered by megachilid bees inhibit growth of pollen-associated fungi. *Biotropica* 17:175-76
137. Michener CD. 1953. Comparative morphology and systematic studies of bee larvae with a key to the families of hymenopterous larvae. *Univ. Kans. Sci. Bull.* 35:987-1102
138. Michener CD. 1964. Evolution of nests of bees. *Am. Zool.* 4:227-39
139. Michener CD. 1964. The bionomics of *Exoneurella*, a solitary relative of *Exoneura* (Hymenoptera: Apoidea: Ceratini). *Pac. Insects* 6:411-26
140. Michener CD. 1974. *The Social Behavior of the Bees*. Cambridge, MA: Harvard Univ. Press. 404 pp.
141. Michener CD. 1978. The parasitic groups of Halictidae. *Univ. Kans. Sci. Bull.* 51:291-339
142. Michener CD. 1979. Biogeography of the bees. *Ann. Mo. Bot. Gard.* 66:277-347
143. Michener CD. 1985. From solitary to eusocial: Need there be a series of intervening species? In *Experimental Behavioral Ecology and Sociobiology*, ed. B Hölldobler, M Lindauer, pp. 293-305. Stuttgart: Fischer
144. Michener CD. 1988. The genus *Lithurge* in the Antilles (Hymenoptera, Megachilidae). *Folia Entomol. Mexicana* 76: 159-64
145. Michener CD, Greenberg L. 1980. Ctenoplectridae and the origin of long-tongued bees. *Zool. J. Linn. Soc.* 69: 188-203
146. Michener CD, Lange RB, Bigarella J, Salamuni R. 1958. Factors influencing the distribution of bees' nest in earth banks. *Ecology* 39:207-17
147. Michener CD, McGinley RJ, Danforth BN. 1994. *The Bee Genera of North and Central America*. Washington, DC: Smithsonian. Inst. 209 pp.
148. Michener CD, Rettenmeyer CW. 1956. The ethology of *Andrena erythronii* with comparative data on other species (Hymenoptera, Andrenidae). *Univ. Kans. Sci. Bull.* 37:645-84
149. Minckley RL, Wcislo WT, Yanega D, Buchmann SL. 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. *Ecology* 73:1406-19
150. Moldenke AR. 1979. Host-plant coevolution and the diversity of bees in relation to the flora of North America. *Phytology* 43:357-419
151. Müller H. 1872. Anwendung der Darwinischen Lehre auf Bienen. *Verh. Naturhist. Ver. Preuss. Rheinl. Westf.* 29:1-96
152. Neff JL, Rozen JG Jr. 1995. Foraging and nesting biology of the bee *Anthemurgus passiflorae* (Hymenoptera: Apoidea) and descriptions of its immature stages, with observations on its floral host, *Passiflora lutea* (Passifloraceae). *Am. Mus. Novit.* In press
153. Neff JL, Simpson BB. 1988. Vibratile pollen-harvesting by *Megachile mendica* Cresson (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* 61: 242-44
154. Neff JL, Simpson BB. 1990. The roles of phenology and reward structure in the pollination biology of wild sunflower (*Helianthus annuus* L., Asteraceae). *Isr. J. Bot.* 39:197-216
155. Neff JL, Simpson BB. 1991. Nest biology and mating behavior of *Megachile fortis* in central Texas (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* 64:324-36
156. Neff JL, Simpson BB. 1992. Partial bivoltinism in a ground-nesting bee: the biology of *Diadasia rinconis* in Texas (Hymenoptera, Anthophoridae). *J. Kans. Entomol. Soc.* 65:377-92
157. Neff JL, Simpson BB. 1993. Bees, pollination systems and plant diversity. See Ref. 114a, pp. 143-68
158. Neff JL, Simpson BB, Dorr LJ. 1982. The nesting biology of *Diadasia afflicta* Cress. (Hymenoptera: Anthophoridae). *J. Kans. Entomol. Soc.* 55:499-518
159. Nonacs P, Tobin JE. 1992. Selfish larvae: development and the evolution of parasitic behavior in the Hymenoptera. *Evolution* 46:1605-20
160. O'Toole C, Raw A. 1991. *Bees of the World*. New York: Facts on File. 192 pp.
161. Parker FD. 1978. Biology of the bee genus *Proteritades* Titus (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* 51:145-73
162. Parker FD. 1986. Nesting, associates, and mortality of *Osmia sanrafaelae* Parker. *J. Kans. Entomol. Soc.* 59:367-77
163. Peitsch D, Fietz A, Hertel H, de Souza J, Ventura DF, Menzel R. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* 170:23-40
164. Plateaux-Quénu C. 1972. *La Biologie des Abeilles Primitives*. Paris: Masson et Cie. 200 pp.
165. Popov VV. 1945. Parazitizm pchelinykh, ego osobennosti i evolutsiya. *Zh. Obshch. Biol.* 6:183-203; *US Dept. Agric. Transl.* T776-59121
166. Popov VV. 1958. Special features of the correlated evolution of *Macropis*, *Epeoloides* (Hymenoptera, Apoidea) and *Lysimachia* (Primulaceae). *Entomol. Obozr.* 37:433-51
167. Radchenko VG, Pesenko YA. 1994. *Biologiya pchel* (Hymenoptera, Apoidea). Saint Petersburg: Rossiiskais Acad. Nauk. Zool. Inst. 350 pp.
168. Rasnitsyn AP, Michener CD. 1991. Miocene fossil bumblebee from the Soviet far east with comments on the chronology and distribution of fossil bees (Hymenoptera: Apidae). *Ann. Entomol. Soc. Am.* 84:583-89
169. Rayner CJ, Langridge DF. 1985. Amino acids in bee-collected pollens from Australian indigenous and exotic plants. *Aust. J. Exp. Agric.* 25:722-26
170. Robertson C. 1925. Heterotrophic bees. *Ecology* 6:412-36
171. Roig-Alsina A, Michener CD. 1993. Studies of the phylogeny and classification of long-tongued bees. *Univ. Kans. Sci. Bull.* 55:123-62
172. Rosenheim JA. 1990. Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Ann. Entomol. Soc. Am.* 83: 277-86
173. Rosenheim JA, Meade T, Powch IG, Schoenig SE. 1989. Aggregation by foraging insect parasitoids in response to local variations in host density: determining the dimensions of a host patch. *J. Anim. Ecol.* 58:101-17
174. Roubik DW. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge: Cambridge Univ. Press. 514 pp.
175. Roubik DW. 1992. Loose niches in tropical communities: Why are there so few bees and so many trees? In *Effects of Resource Distribution on Animal-Plant Interactions*, ed. MD Hunter, T Ohgushi, PW Price, pp. 327-54. New York: Academic
176. Roubik DW, Michener CD. 1985. Nesting biology of *Crawfordapis* in Panam (Hymenoptera, Colletidae). *J. Kans. Entomol. Soc.* 57:662-71
177. Roubik DW, Yanega D, Aluja M, Buchmann SL, Inouye DW. 1995. On optimal nectar foraging by some tropical bees (Hymenoptera: Apoidea). *Apidologie*. In press
178. Rozen JG Jr. 1963. Notes on the biology of *Nomadopsis*, with descriptions of four new species (Apoidea, Andrenidae). *Am. Mus. Novit.* 2142:1-17
179. Rozen JG Jr. 1989. Life history studies of the "primitive" panurgine bees (Hymenoptera: Andrenidae: Panurginae). *Am. Mus. Novit.* 2962:1-27
180. Rozen JG Jr. 1989. Morphology and systematic significance of first instars of the cleptoparasitic bee tribe Epeolini (Anthophoridae: Nomadinae). *Am. Mus. Novit.* 2957:1-19
181. Rozen JG Jr. 1991. Evolution of cleptoparasitism in anthophorid bees as re-

- vealed by their mode of parasitism and first instars (Hymenoptera: Apoidea). *Am. Mus. Novit.* 3029:1-36
182. Rozen JG Jr. 1992. Systematics and host relationships of the cuckoo bee genus *Oreopasites* (Hymenoptera: Anthophoridae: Nomadinae). *Am. Mus. Novit.* 3046:1-56
 183. Rozen JG Jr. 1992. Biology of the bee *Ancylandrena larreae* (Andrenidae: Andreninae) and its cleptoparasite *Hexepeolus rhodogyne* (Anthophoridae: Nomadinae) with a review of egg deposition in the Nomadinae (Hymenoptera: Apoidea). *Am. Mus. Novit.* 3038:1-15
 184. Rozen JG Jr. 1994. Biology and immature stages of some cuckoo bees belonging to Brachynomadini, with descriptions of two new species (Hymenoptera: Apidae: Nomadinae). *Am. Mus. Novit.* 3089:1-23
 185. Rozen JG Jr. 1994. Revision of the cleptoparasitic bee tribe Protepeolini, including biologies and immature stages (Hymenoptera: Apoidea: Apidae). *Am. Mus. Novit.* 3099:1-38
 186. Rozen JG Jr, Buchmann SL. 1990. Nesting biology and immature stages of the bees *Centris caesalpiniae*, *C. pallida*, and the cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae). *Am. Mus. Novit.* 2985:1-30
 187. Rozen JG Jr, Jacobson NR. 1980. Biology and immature stages of *Macropis nuda*, including comparisons to related bees (Apoidea, Melittidae). *Am. Mus. Novit.* 2702:1-11
 188. Rozen JG Jr, McGinley RJ. 1976. Biology of the bee genus *Conanthalictus* (Halictidae, Dufoureae). *Am. Mus. Novit.* 2602:1-6
 189. Rust RW, Thorp RW. 1973. The biology of *Stelis chlorocyanea*, a parasite of *Osmia nigrifrons* (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* 46: 548-62
 190. Sakagami SF, Laroca S. 1971. Observations on the bionomics of some neotropical xylocopine bees, with comparative and biofaunistic notes (Hymenoptera, Anthophoridae). *J. Fac. Sci. Hokkaido Univ. Ser. VI Zool.* 18:57-127
 191. Salt G. 1928. The effects of stylopization on Aculeate Hymenoptera. *J. Exp. Zool.* 48:223-33
 192. Schultz JC, Otte D, Enders F. 1977. *Larrea* as a habitat component for desert arthropods. In *Creosote Bush: Biology and Chemistry of Larrea in New World Deserts*, ed. TJ Mabry, JH Hunziker, DRJ Difeo, pp. 176-208. Stroudsburg: Dowden, Hutchinson & Ross
 193. Shaw SR. 1988. Euphorine phylogeny: the evolution of diversity in host-utilization by parasitoid wasps (Hymenoptera: Braconidae). *Ecol. Entomol.* 13: 323-35
 194. Sick M, Ayasse M, Tengö J, Engels W, Lübke G, Francke W. 1994. Host-parasite relationships in six species of *Sphecodes* bees and their halictid hosts: nest intrusion, intranidal behavior, and Dufour's gland volatiles (Hymenoptera: Halictidae). *J. Insect Behav.* 7:101-17
 195. Silveira FA. 1993. The mouthparts of *Ancyla* and the reduction of the labiomaxillary complex among long-tongued bees (Hymenoptera: Apoidea). *Entomol. Scand.* 24:293-300
 196. Simpson BB, Neff JL. 1983. Evolution and diversity of floral rewards. See Ref. 104b, pp. 142-59
 197. Simpson BB, Neff JL. 1987. Pollination ecology in the arid Southwest. *Aliso* 11:417-40
 - 197a. Simpson BB, Neff JL, Moldenke AR. 1977. Reproductive systems of *Larrea*. In *Creosote Bush: Biology and Chemistry of Larrea in New World Deserts*, ed. TJ Mabry, JH Hunziker, DRJ Difeo, pp. 92-114. Stroudsburg, PA: Dowden, Hutchinson & Ross
 198. Snelling RR. 1983. The North American species of the bee genus *Lithurge*, Hymenoptera: Megachilidae. *Contrib. Sci. Los Angeles Co. Mus. Nat. Hist.* 343:1-11
 199. Stage GI. 1966. *Biology and systematics of the American species of the genus Hesperapis Cockerell*. PhD dissertation. Univ. Calif., Berkeley. 461 pp.
 200. Stanley RG, Linsens HF. 1974. *Pollen: Biology, Biochemistry, Management*. Heidelberg: Springer-Verlag. 307 pp.
 201. Steiner KE, Whitehead VB. 1991. Oil flowers and oil bees: further evidence for pollinator adaptation. *Evolution* 45: 1493-501
 202. Stephen WP, Bohart GE, Torchio PF. 1969. The biology and external morphology of bees. *Oreg. State Univ. Agric. Exp. Stn. Publ.* 140 pp.
 203. Stone GN. 1994. Patterns of evolution of warm-up rates and body temperatures in flight in solitary bees of the genus *Anthophora*. *Funct. Ecol.* 8:324-35
 204. Strickler K. 1979. Specialization and foraging efficiency of solitary bees. *Ecology* 60:998-1009
 205. Struck M. 1994. Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. *J. Arid Environ.* 28:51-74
 206. Szymas B. 1991. The parasitic entomofauna as a factor limiting populations of solitary bees. *Przegl. Zool.* 35:307-13
 207. Takhtajan AL. 1986. *Floristic Regions of the World*. Berkeley: Univ. Calif. Press. 522 pp.
 208. Tengö J, Sick M, Ayasse M, Engels W, Svensson BG, et al. 1992. Species specificity of Dufour's gland morphology and volatile secretions in kleptoparasitic *Sphecodes* bees (Hymenoptera: Halictidae). *Biochem. Syst. Ecol.* 20:351-62
 209. Tepedino VJ, Knapp AK, Eickwort GC, Ferguson DC. 1989. Death camas (*Zigadenus nuttallii*) in Kansas: pollen collectors and a florivore. *J. Kans. Entomol. Soc.* 62:411-12
 210. Tepedino VJ, McDonald LL, Rothwell R. 1979. Defense against parasitization in mud-nesting Hymenoptera: Can empty cells increase net reproductive output? *Behav. Ecol. Sociobiol.* 6:99-104
 211. Thomas BA, Spicer RA. 1987. *The Evolution and Paleobiology of Land Plants*. London: Dioscorides. 309 pp.
 212. Thompson JN. 1994. *The Coevolutionary Process*. Chicago: Univ. Chicago Press. 376 pp.
 213. Thorp RW. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). *Univ. Calif. Publ. Entomol.* 52:1-146
 214. Thorp RW. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Ann. Mo. Bot. Gard.* 66:788-812
 215. Torchio PF. 1989. Biology, immature development, and adaptive behavior of *Stelis montana*, a cleptoparasite of *Osmia* (Hymenoptera: Megachilidae). *Ann. Entomol. Soc. Am.* 82:616-32
 216. Torchio PF, Bosch J. 1992. Biology of *Tricranis stansburyi*, a meloid beetle cleptoparasite of the bee *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). *Ann. Entomol. Soc. Am.* 85:713-21
 217. Torchio PF, Rozen JG Jr, Bohart GE, Favreau MS. 1967. Biology of *Dufourea* and of its cleptoparasite, *Neopasites* (Hymenoptera: Apoidea). *J. NY Entomol. Soc.* 75:132-46
 218. Vander Wall SB. 1990. *Food Hoarding in Animals*. Chicago: Univ. Chicago Press. 445 pp.
 219. Velthuis HH. 1992. Pollen digestion and the evolution of sociality in bees. *Bee World* 73:77-89
 - 219a. Vinson SB, Frankie GW, Barthell J. 1993. Threats to the diversity of solitary bees in a Neotropical dry forest in Central America. See Ref. 114a, pp. 53-81
 220. Vogel S. 1974. *Ölblumen und Olsam-*
 - melnde Bienen*. Wiesbaden: Franz Steiner. 267 pp.
 221. Waser NM. 1986. Flower constancy: definition, cause, and measurement. *Am. Nat.* 127:593-603
 222. Watmough RH. 1983. Mortality, sex ratio and fecundity in natural populations of large carpenter bees (*Xylocopa* spp.). *J. Anim. Ecol.* 52:111-25
 223. Wcislo WT. 1984. Gregarious nesting of a digger wasp as a "selfish herd" response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sacrophagidae) [sic]. *Behav. Ecol. Sociobiol.* 15: 157-60
 224. Wcislo WT. 1987. The role of seasonality, host-synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta), with special reference to bees (Apoidea). *Biol. Rev.* 62:515-43
 225. Wcislo WT. 1989. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* 20:137-69
 226. Wcislo WT. 1990. Parasitic and courtship behavior of *Phalacrotophora halictorum* (Diptera: Phoridae) at a nesting site of *Lasioglossum figueresi* (Hymenoptera: Halictidae). *Rev. Biol. Trop.* 38: 205-09
 227. Wcislo WT. 1993. Communal nesting in a North American pearly-banded bee, *Nomia tetrazonata*, with notes on nesting behavior in *Dieunomia heteropoda* (Hymenoptera: Halictidae: Nomiinae). *Ann. Entomol. Soc. Am.* 86: 813-21
 228. Wcislo WT. 1995. Sensilla numbers and antennal morphology of parasitic and non-parasitic bees (Hymenoptera: Apoidea). *Int. J. Insect Morphol. Embryol.* 24:63-81
 229. Wcislo WT, Minckley RL, Leschen RAB, Reyes S. 1994. Rates of parasitism by natural enemies of a solitary bee, *Dieunomia triangulifera* (Hymenoptera, Coleoptera, and Diptera) in relation to phenologies. *Sociobiology* 23: 265-73
 230. Wcislo WT, Wille A, Orozco E. 1993. Nesting biology of tropical solitary and social sweat bees, *Lasioglossum (Dialictus) figueresi* Wcislo and L. (D.) *aeneiventris* (Friese) (Hymenoptera: Halictidae). *Insectes Soc.* 40:21-40
 231. Weberling F. 1989. *Morphology of Flowers and Inflorescences*. Cambridge: Cambridge Univ. Press. 405 pp. (Transl.)
 232. West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. *Proc. Am. Philos. Soc.* 123: 222-34

233. West-Eberhard MJ. 1986. Alternative adaptations, speciation, and phylogeny (a review). *Proc. Natl. Acad. Sci. USA* 83:1388-92
234. West-Eberhard MJ. 1992. Behavior and evolution. In *Molds. Molecules and Metazoans*, ed. PR Grant, HS Horn, pp. 57-79. Princeton: Princeton Univ. Press
235. Westrich P. 1989. *Die Wildbienen Baden-Württembergs*, Band I. Stuttgart: Eugen Ulmer GmbH. 431 pp.
236. Whitehead VB. 1984. Distribution, biology and flower relationships of fide-liid bees of southern Africa (Hymenoptera, Apoidea, Fideliidae). *S. Afr. J. Zool.* 19:87-90
237. Winston ML. 1987. *The Biology of the Honey Bee*. Cambridge, MA: Harvard Univ. Press. 281 pp.
238. Wolda H, Roubik DW. 1986. Nocturnal bee abundance and seasonal activity in a Panamanian forest. *Ecology* 67:426-33
239. Wu Y-r, Michener CD. 1986. Observations on Chinese *Macropis* (Hymenoptera: Apoidea: Melittidae). *J. Kans. Entomol. Soc.* 59:42-48
240. Wülker W. 1964. Parasite-induced changes of internal and external sex characters in insects. *Exp. Parasitol.* 15: 561-97
241. Zimmerman EC. 1970. Adaptive radiation in Hawaii with special reference to insects. *Biotropica* 2:32-38