Temporal, Spatial, Sex-Ratio and Body-Size Heterogeneity of Prey Species Taken by the Beewolf Philanthus sanbornii (Hymenoptera: Sphecidae)

J. W. Stubblefield, J. Seger, J. W. Wenzel and M. M. Heisler

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Temporal, spatial, sex-ratio and body-size heterogeneity of prey species taken by the beewolf *Philanthus sanbornii* (Hymenoptera: Sphecidae)

J. W. STUBBLEFIELD[1], J. SEGER[2]†, J. W. WENZEL[3]‡ AND
M. M. HEISLER[4]§

[1] *Cambridge Energy Research Associates, Charles Square, 20 University Road, Cambridge, Massachusetts 02138, U.S.A.*
[2] *Department of Biology, University of Utah, Salt Lake City, Utah 84112, U.S.A.*
[3] *Department of Organismal and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.*
[4] *Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, U.S.A.*

SUMMARY

More than 3000 prey representing 108 species of bees and wasps were identified from exoskeletal remains taken from nests of the beewolf *Philanthus sanbornii* at a site in eastern Massachusetts over a period of five years. Quantitative reference samples totalling more than 4000 items were collected from flowers at the same site over a period of four years. These data give a uniquely detailed view of the way in which a generalist predator exploits a diverse prey community. Most species show striking year-to-year variation in relative abundance, in both the prey and reference collections, but the overall abundances of species tend to be similar in the two collections, as do their sex ratios. This shows: (i) that *P. sanbornii* takes virtually every bee and wasp species found at flowers during its flight season (except for the relatively small number of species too large to handle); (ii) that prey are taken at rates roughly proportional to their local abundances (with a few exceptions); and (iii) that the local bee and wasp communities have lively dynamics (at least on spatial scales equivalent to the flight ranges of *P. sanbornii* females). Prey species are non-randomly distributed among nests of individual females within years, and among cells within nests, in a pattern suggesting that females often return repeatedly to hunting sites at which they have had success; the pattern does not suggest that individual females develop preferences for particular prey taxa. The size–abundance distributions of female bees appear to be trimodal at both the individual and species levels, most strongly so when cleptoparasitic species are removed from the sample. Such patterns are seen weakly or not at all in the size–abundance distributions of male bees, male wasps, and female wasps. Bees and wasps of both sexes visit flowers for nectar, but only non-parasitic female bees harvest pollen; this suggests that the multimodality may be caused by aspects of pollen collection that tend to scale with size. The seven *Philanthus* species of eastern North America vary greatly in size, but they share a common set of relatively small prey species. As in other parts of North America, larger species of *Philanthus* tend to have relatively broad diets because they also take larger prey that are not available to their smaller congeners. However, long-tongued bees appear to be under-represented in the diets of most North American *Philanthus* outside the *zebratus* species group.

1. INTRODUCTION

Community ecology seeks to describe and to explain the structures of natural communities. To this end, individual studies attempt to characterize: (i) the compositions of particular species assemblages; (ii) the ways in which their component species interact; and (iii) the dynamical consequences of those interactions. Food webs provide an important focus for work on these problems (e.g. Cohen 1978; Pimm 1982, 1991; Cohen *et al.* 1990), in part because prey–predator relationships are relatively easy to document and in part because they are major conduits for flows of matter and energy. Here we present a highly detailed account of the diet of a generalist predator, the beewolf *Philanthus sanbornii*, which hunts a wide range of flower-visiting aculeate Hymenoptera. This system comprises only part of a complete food web, but it includes most of a diverse bee community, and our study describes it with unusual resolution of temporal and individual variation. This level of resolution is made possible by some special features of beewolf

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† To who correspondence should be sent.
‡ Present address: American Museum of Natural History, Central Park West and 79th Street, New York, New York 10020, U.S.A.
§ Present address: Pioneer Futures Incorporated, 90 West Street, New York, New York 10006, U.S.A.

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natural history that have not previously been exploited in this way.

Solitary wasps of the genus *Philanthus* prey on other aculeate Hymenoptera (mainly bees), but within this broad dietary restriction they show a wide range of additional specificities. For example, the Afro-European *P. triangulum* specializes exclusively on honeybees (e.g. Tinbergen 1935, 1972; Simon Thomas & Simon Thomas 1972), while at the opposite extreme, the North American *P. zebratus* took 78 species, 43 genera and ten families in a sample of 402 prey individuals (Evans & O'Neill 1988). Other species of *Philanthus* show various intermediate levels of specificity (O'Neill & Evans 1982; Evans & O'Neill 1988). Because female bees forage at flowers, they cannot escape the notice of hunting *Philanthus* females. In many places and at many times of the year, a typical bee is vulnerable to more than one species of *Philanthus*.

We identified prey from exoskeletal remains taken from completed nests of *P. sanbornii* in five years (1978, 1980–83) at a site in eastern Massachusetts. We also collected wasps and bees directly from flowers at the same site (1984–1987). These methods allow us to (i) analyse distributions of prey taxa at three hierarchical levels of aggregation (rearing cells within nests, nests within years, and years within the duration of the study), and (ii) compare the prey captured by *P. sanbornii* to a crude but independent estimate of the prey potentially available. There is considerable taxonomic heterogeneity at every level of aggregation, indicating that: (i) individual females are relatively 'specialized' at any given moment; (ii) the targets of their specialization change rapidly and idiosyncratically; and (iii) most prey species show dramatic changes of relative abundance from year to year. However, in any given year the *P. sanbornii* population as a whole shows little selectivity, taking most species of wasps and bees (over a wide range of sizes) in proportion to their abundances at flowers, although a few species are conspicuously underutilized. These patterns suggest that hunting females develop temporary fidelities to particular sites, but not to particular prey taxa, and that an apparent prey 'specialization' is caused by spatial and temporal heterogeneity in the distributions of flowering plants and their insect visitors.

The sex ratios of the 78 species of bees in the prey list are strongly female biased, on average, but males exceed females in five species, and in two of these males are known to patrol flowers of the plant on which their females are specialized foragers. Sex ratios of the 29 wasp species are on average slightly male biased. These patterns suggest that the risk of predation by *P. sanbornii* is roughly proportional to the amount of time spent at flowers. Bees would appear to be 'favoured' as prey only in the sense that their density at flowers tends to be much higher than that of wasps. *P. sanbornii* and its smaller sympatric congeners appear to share many or most of their prey species, within the ranges of prey sizes taken by the smaller species of *Philanthus*. However, long-tongued bees appear to be under-utilized by many North American *Philanthus* outside the *zebratus* species group to which *sanbornii* belongs.

A previously unknown pattern of multimodality is seen in the size distribution of female bees. Within the range of sizes taken by *P. sanbornii* there are three 'popular' sizes separated by two relatively unpopular gaps. The pattern is seen both at the level of individuals and at the level of species. It is strongest for females of nonparasitic bees, and weak or absent for males, cleptoparasites, and wasps. It does not appear to be caused by size-selective hunting behaviour, since the reference collection is similar in virtually every respect to the prey collection. An analysis of representative faunal samples from several widely separated locations in North America and Australia (J. Seger, J. W. Stubblefield, J. S. Burner & V. J. Tepedino, unpublished data) suggests that multimodal patterns are of general occurrence and that they may be caused by aspects of pollen foraging that tend to scale with size.

2. BACKGROUND, MATERIALS AND METHODS

(*a*) *The genus* Philanthus

There are roughly 100 species of *Philanthus* ('beewolves') in Europe, Africa and Asia, and 35 in North America (Bohart & Grissell 1975; Bohart & Menke 1976). *P. triangulum* is the only old-world species whose biology is well known, but many of the North American species have been studied in some detail; key references include Armitage (1965), Evans (1973), Alcock (1975*a*,*b*), Gwynne (1980), O'Neill & Evans (1981, 1982), Kurczewski & Miller (1983), and especially the recent book by Evans & O'Neill (1988). The closely related genus *Trachypus* contains about 20 species. It ranges from southern South America to Mexico and adjacent parts of the United States. *Philanthus* and *Trachypus* are the only philanthine genera known to prey exclusively on bees and wasps, and a recent cladistic analysis by Alexander (1992) supports the traditional view that they form a monophyletic group within the subfamily.

Like most wasps, adult *Philanthus* of both sexes feed on floral nectar; females hunt solely to provide food for their offspring. Females of *P. triangulum* sometimes feed on nectar forced from the crops of captured bees, or on haemolymph obtained by biting prey at the bases of the forelegs (Hirschfelder 1952; Simon Thomas & Simon Thomas 1972). We have not seen these behaviours in *P. sanbornii*, but even if they were to occur, predation would still be almost entirely an act of parental investment.

Many aculeate wasps prey either on larvae (e.g. caterpillars) or on soft-bodied adult arthropods (e.g. flies, spiders) whose fragile exoskeletons cannot easily be identified after the prey have been consumed by the larval wasp. Philanthines prey on adults of the well armored orders Hymenoptera and Coleoptera. The wasp larva eats only the soft tissues of the prey, leaving behind the durable and informative exoskeletal parts. Prey items can therefore be enumerated, measured, and identified, long after they were eaten. The prey associated with an individual *Philanthus* larva in its rearing cell were taken by its mother on a series of hunting trips, often in a single day. A female may produce as many as 25 offspring in her permanent burrow system or 'nest'. Thus at the end of the season, each nest is a detailed historical record of one female's lifetime of hunting and parental investment.

Owing to this unusual combination of features, *Philanthus* is well suited for ecologically oriented studies of predation, yet few studies have focused specifically on predation, and none has fully exploited the possibilities offered by this system. The only community-level study is that of O'Neill & Evans (1982), on four sympatric species at a site in Colorado. The prey taken by these four species show substantially different distributions of size and taxonomic affinity. O'Neill & Evans also review the available prey records for all North American *Philanthus*. (Evans & O'Neill (1988) give additional details and subsequent data.) Samples of 15 to 460 prey have been taken from 43 populations of 19 species. As was mentioned above, the species differ widely in degree of apparent specialization.

(*b*) *Natural history of* P. sanbornii

Philanthus sanbornii Cresson occurs throughout much of North America east of the Rocky Mountains, where it is the largest member of the genus. Adult females vary in wet mass from less than 60 mg to more than 130 mg, with a mean of slightly less than 100 mg. For comparison, a typical worker honeybee (*Apis mellifera*) weighs 70–90 mg.

Little has been published on *P. sanbornii*, probably because the species is less common than several other eastern species. Evans (1955) observed females taking honeybees (and a few native bees) at a site in Kansas. Evans & Lin (1959) briefly describe nest architecture and give three prey records (all honeybees) for a population of *P. sanbornii* (as *P. eurynome* Fox) at the Archbold Biological Station in Florida. Kurczewski & Miller (1983) also studied a small population at the Archbold Biological Station. They discuss nest architecture, female nesting behaviour, and prey selection (19 honeybees, 25 *Colletes brimleyi*, 1 *Augochloropsis metallica*, 1 *Megachile mendica*, and 2 *Epeolus zonatus*). O'Neill & Evans (1982) and Evans & O'Neill (1988) include 151 prey records from populations at Bedford and Carlisle, Massachusetts (about 20 km from our site), in their reviews of prey selection in the genus. All but eight of the 37 prey species in their sample also occur in ours.

P. sanbornii appears to be univoltine even in the southern part of its range (H. E. Evans, personal communication) and is definitely so in Massachusetts. At our site, males typically begin emerging from their natal burrows around 18 June, and the first females are usually seen around 21 June. Each adult female establishes her own nest (usually a new one), within a few days of emergence. But some nests of the previous year are reused, presumably by a daughter of its previous owner. Males return to their natal burrows at night, unless evicted by a female who has taken the burrow over for reproduction; evicted males dig shallow sleeping burrows in the main nesting area. In Massachusetts, the most active part of the flight season is roughly 25 June through 25 July, and by 1 August few if any adults are still alive.

A female's main burrow is typically 7–8 mm in diameter and 50–70 cm in length. It descends first at a shallow angle, and then heads down steeply to a depth of 20–35 cm, where it becomes approximately level. (In Florida, burrows are much deeper than this (Evans & Lin 1959; Kurczewski & Miller 1983)). Each rearing cell is an enlargement (8–16 mm in diameter, 20–30 mm long) at the end of a lateral burrow (5–15 cm long) that projects more or less horizontally from the main burrow (figure 1). In the classification of Evans & O'Neill (1988), the nest architecture is proclinate (main burrow projects forward) and regressive (subsequent cells connect to the main burrow at points closer to the nest entrance than previous cells). In all species of *Philanthus* for which there is evidence, the female first makes a series of hunting trips, then digs a cell, stocks it with the accumulated prey, lays an egg on the ventral surface of one of the prey, and closes the cell by backfilling the lateral burrow. (Evans & O'Neill (1988) review the evidence.) *P. sanbornii* appears to follow this typical sequence.

One prey item is captured on each hunting trip. A typical trip takes 10–15 min (range: 2–90). On returning to the nest with prey the female spends 5–15 min inside. During this interval we have recorded distinctive sounds from geophones buried near the nest. These sounds are unlike those heard at other times (Seger *et al.* 1990) and may be caused by cleaning behaviours. Like Kurczewski & Miller (1983) we often see bees loaded with pollen when being carried into the nest, but we never find pollen on bees in completed cells, and during excavation we occasionally find pollen in regions of loose sand near the main burrow. After reappearing at the nest entrance, the female waits roughly a minute and then departs on the next trip.

Completed cells contain 2–17 prey items, depending on the average size of the prey; the mean is roughly seven items for male offspring and nine items for females. One complete cell per day appears to be the average rate of work in good weather. The egg hatches within a few days, and the larva begins eating the prey. Within about a week it has reduced the prey to a pile of disarticulated and cleaned exoskeletal parts. The larva then spins the cocoon in which it will spend the next 10 to 11 months. Pupation occurs the following May, inside the cocoon. The young adult wasp ecloses in mid-June and digs its way out through the backfilled burrow system, if possible; otherwise it digs straight up through the undisturbed sand.

(*c*) *Study site and population*

Our study site is an abandoned sand pit in Littleton, Massachusetts (42°31′22″N, 71°30′54″W). When we discovered the Littleton population on 10 July 1978, it consisted of approximately 50 active nests that were strikingly clustered, occupying an area no larger

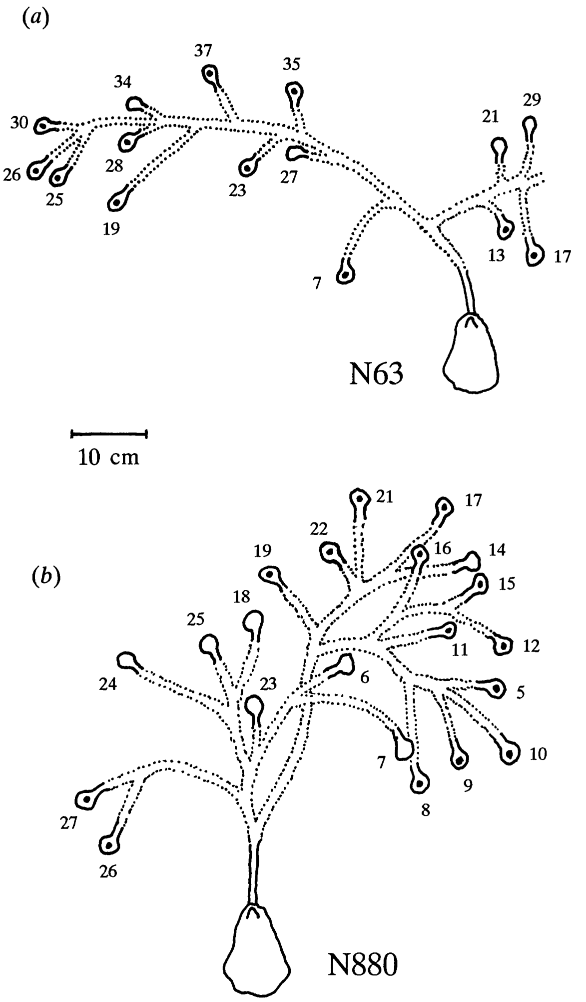

Figure 1. Plan views of two nests. Nest 63 of 1980 (*a*) was excavated several weeks after the end of the flight season. Eleven cells held mature larvae in cocoons (solid dots), with the exoskeletal remains of prey. Four cells held prey but no wasp larva; some of these cells had apparently been attacked by sarcophagid flies, but a few showed no evidence of parasitism and may therefore represent developmental failures. Most of the burrow system had been backfilled and could not easily be traced; its path is inferred from the placement and orientation of the cells and the nest entrance. Nest 880 of 1982 (*b*) was excavated near the end of the season, shortly after the disappearance of its owner. *Philanthus* larvae were still feeding in cells 6 and 7. The other cells without cocoons appeared to be failures of the kinds described above. These two nests are larger than average, but they are typical in other respects. They show two basic architectural plans that are frequently seen. The linear plan exemplified by Nest 63 is the easiest to interpret. The first cells constructed are clearly those farthest from the nest entrance; these usually contain female offspring. Cells nearer the entrance usually contain males, implying that the mother wasp tends to make daughters before sons. The compact, highly branched plan exemplified by Nest 880 is more difficult to interpret; there is usually no clear segregation of male and female offspring, but small clusters may still be evident. Many nests show mixtures of these two styles. Cells range in depth from 15 cm to 35 cm below the surface, with a mean of around 25 cm.

than 10 × 20 m (0.02 ha) in the middle of a much larger area of flat, level, firmly packed, sparsely vegetated sand. The perimeter of the occupied area expanded in every subsequent year through 1987, when the site was destroyed by industrial development. By 1984 the minimum rectangle enclosing all of the nests was approximately 75 × 150 m (1.1 ha), but there have never been more than about 200 successful nests (usually 100–150). From this rate of geographical expansion we estimate that in 1978 the population was only three to five years old.

(*d*) *Collection and reconstruction of prey*

Most of the prey described here were taken from nests that we excavated after the end of the flight season; a few were taken from active nests excavated in mid-season, and a few were freshly caught 'rejects' that we found at the entrances of active nests. The yearly samples range in size from 50 complete cells and 412 total items (1982), to 118 cells and 942 items (1978). For all years combined, 95% of the 3138 items are from complete cells (table 1). As each cell was encountered during excavation, its location in three dimensions was recorded to the nearest centimeter. Prey remains were collected directly into a numbered vial, and the mature larva (if present) was placed in a separate vial.

Because the prey had usually been consumed, we 'reconstructed' them from the recovered exoskeletons. Major skeletal parts from a single cell are first cleaned and sorted into sets that represent individual prey. The parts needed for determination are then mounted on points, and the others are returned to the original collection vial. The standard mount includes head capsule, scutum, mesosomal 'box', and first tergum. These four parts are usually more than adequate for secure determination, and their redundancy virtually guarantees that every individual present in the cell will be detected, even if some major parts were lost during excavation.

If an item presents difficulties, or if it belongs to a rare species, then all reliably associated parts are mounted. Legs, antennae, and mouthparts are seldom recovered in usable form. Colours often fade rapidly, and pubescence is often matted or otherwise obscured. Thus many commonly used key characters are missing from our reconstructions. Nonetheless, it has proved possible to make reliable determinations of almost all prey items on the basis of skeletal characters, some of which are more clearly revealed in our 'exploded' specimens than they are in intact ones. Our ability to reconstruct and identify prey has steadily improved during the course of this study. We have no doubts about any generic determinations, and we are confident that virtually all items (probably more than 99.5%) are correctly grouped into species, even though in a few cases there still remains some uncertainty as to the name that should be applied. A few inherently difficult *Dialictus* have been given numbered designations (*Dialictus* spp. 1–4). A complete species list is given in Appendix 1.

The head widths of reconstructed prey with intact head capsules were measured to the nearest 0.05 mm, using an optical micrometer in one eyepiece of a stereomicroscope. Repeated measurements of ran-

Table 1. *Summary of prey records by year (1978–83)*

(n_T is the total number of prey individuals, and n_C is the number of prey from complete cells. Most of the individuals not from complete cells (158 items, 5.0%) are rejected prey found near active nest entrances (92 items, 2.9%). Twelve cells (54 items, 1.7%) are considered to be genuinely incomplete, either because they had been disturbed by ants or because we lost some of their contents during excavation. Six cells (12 items, 0.4%) are prey caches found in or near cells under construction. I/C is the average number of prey per complete cell. HW is the average head width of all prey (mm). $D = 1/\Sigma p_i^2$ is Simpson's measure of dietary niche breadth, where the p_i are proportions of the sample made up by individual genera (D_G) or species (D_S).)

year	n_T	cells	n_C	I/C	HW	fams	genera	spp.	D_G	D_S
1978	942	118	895	7.6	2.55	8	26	64	3.9	9.2
1980	527	74	508	6.9	2.70	11	29	57	6.6	15.1
1981	580	64	519	8.1	2.61	10	30	60	5.9	13.4
1982	412	50	386	7.7	2.59	9	26	56	5.1	15.0
1983	677	65	672	10.3	2.31	10	27	49	1.8	3.6
	3138	371	2980	8.0	2.54	12	43	108	4.3	11.9

domly selected items were almost always within one measurement unit of the original value, so the accuracy of individual head widths can be taken as roughly ±0.05 mm. Average head widths for all species are given in Appendix 1.

In 1984–87 we made extensive collections of the local wasp and bee faunas. Every few days throughout the flight season, at times when *P. sanbornii* was on the wing, we visited stands of flowering plants within one kilometer of the nesting area. Using hand nets, we attempted to collect all wasps and bees (except *Apis*) that we saw coming to flowers. These reference collections are not yet fully analysed, but we summarize aspects of their taxonomic distribution that bear on the interpretation of the prey data for 1978–83 (see Appendix 2). The reference collections will be described in detail elsewhere, together with prey samples for the same four years (1984–87).

3. PREY SPECIES DISTRIBUTIONS

Under this heading we summarize the taxonomic and abundance distributions of the prey and reference samples. In the Discussion we briefly compare the prey data for *P. sanbornii* to those for other species of *Philanthus* in New England and in North America as a whole.

Most prey taxa are relatively rare. Of the 108 prey species encountered through 1983, only about half are seen in a typical year; similarly, only about two-thirds of the 43 genera and four-fifths of the 12 families are seen in a typical year (table 1). The species–abundance distributions for wasps and bees are approximately canonical lognormal, and the modes appear to be well to the right of the veil lines (figure 2). Overall, 51 species (47%) are represented by three or fewer items (three items = 0.1% of the sample). Eight species (7%) are represented by more than 125 items (4.0% of the sample), and these eight dominant species account for 69% of all prey; each was seen in each of the five years, while only 13 of the 100 species with fewer than 125 items were seen in all years.

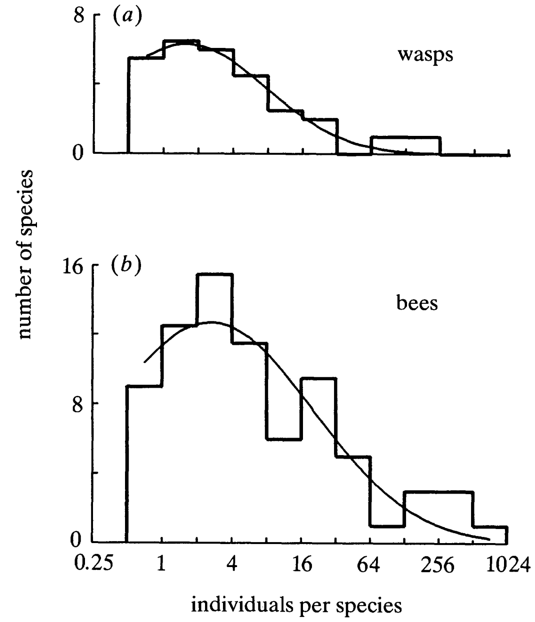

Figure 2. Species–abundance distributions of prey. Species are assigned to binary octaves in the usual way (e.g. Pielou 1977). The curves are normal distribution functions, fit by the least-squares criterion to the observed distributions. Estimated parameters for the 29 species of wasps (*a*) are $S_0 = 6.36$, $a = 0.31$, and $\gamma = 0.83$, in the notation used by May (1975). The observed distribution is roughly lognormal ($\gamma = 1$), and the total estimated number of wasp species in the pool at risk of being caught by *P. sanbornii* is $S_T \approx 37$, which is probably an underestimate. Parameters for the 78 species of bees are $S_0 = 12.7$, $a = 0.31$, and $\gamma = 0.91$, implying that $S_T \approx 94$. Extrapolating from the discovery curve (figure 3) and the reference collection, we would estimate the actual number of bee species to be over 100. One reason why these distributions may underestimate the actual number of species is that all species (including rare ones) tend to occur in runs within the nests of individual females. This implies that we tend to see either none of a species, or several. Thus relatively too few species are represented by one or two items, and the mode of the distribution therefore appears to be farther to the right of the veil line (zero observations) than it really is, giving rise to an overestimate of the proportion of species already seen.

Table 2. *Taxonomic summary, all years combined (1978–83)*

family	*n*	% of total	genus	spp.	*n*	% of family	% of total
Stratiomyidae	3	0.10	*Odontomyia*	1	3	100.0	0.10
Chrysididae	1	0.03	*Hedychrum*	1	1	100.0	0.03
Tiphiidae	7	0.22	*Myzinum*	2	7	100.0	0.22
Vespidae	44	1.40	*Parancistrocerus*	2	12	27.3	0.38
			Euodynerus	1	22	50.0	0.70
			Ancistrocerus	3	7	15.9	0.22
			Symmorphus	1	1	2.3	0.03
			Zethus	1	1	2.3	0.03
			Vespula	1	1	2.3	0.03
Sphecidae	288	9.18	*Astata*	2	4	1.4	0.13
			Oxybelus	1	1	0.3	0.03
			Ectemnius	4	42	14.6	1.34
			Lestica	2	77	26.7	2.45
			Gorytes	2	7	2.4	0.22
			Pseudoplisus	1	1	0.3	0.03
			Aphilanthops	1	137	47.6	4.37
			Cercerus	4	19	6.6	0.61
Colletidae	6	0.19	*Colletes*	2	5	83.3	0.16
			Hylaeus	1	1	16.7	0.03
Andrenidae	683	21.77	*Andrena*	14	683	100.0	21.77
Halictidae	1909	60.83	*Dufourea*	1	5	0.3	0.16
			Augochloropsis	1	23	1.2	0.73
			Augochlora	1	37	1.9	1.18
			Augochlorella	1	44	2.3	1.40
			Agapostemon	2	37	1.9	1.18
			Halictus	3	1286	67.4	40.98
			Lasioglossum	2	163	8.5	5.19
			Evylaeus	6	18	0.9	0.57
			Dialictus	14	293	15.3	9.34
			Sphecodes	2	3	0.2	0.10
Melittidae	6	0.19	*Melitta*	2	6	100.0	0.19
Megachilidae	81	2.58	*Heriades*	1	1	1.2	0.03
			Hoplitis	3	13	16.0	0.41
			Osmia	4	11	13.6	0.35
			Megachile	6	51	63.0	1.63
			Chalicodoma	1	3	3.7	0.10
			Coelioxys	2	2	2.5	0.06
Anthophoridae	50	1.59	*Epeolus*	1	2	4.0	0.06
			Nomada	3	15	30.0	0.48
			Melissodes	1	25	50.0	0.80
			Ceratina	1	8	16.0	0.25
Apidae	60	1.19	*Bombus*	1	1	1.7	0.03
			Apis	1	59	98.3	1.88

Diversity (as gauged by Simpson's D) varies enormously among years, at both the genus and species levels (table 1). It is poorly correlated with sample size, and even with the yearly totals of species, genera, and families. Year-to-year variation is examined in more detail below.

A quantitative taxonomic summary of families and genera is given in table 2. (See Appendix 1 for the abundances of species, and table 3 for year-by-year abundances of the top 25.) Sixty-one per cent of all prey are bees of the family Halictidae, 22% are bees of the family Andrenidae, and 9% are wasps of the family Sphecidae. Of the latter, more than half belong to *P. sanbornii*'s own subfamily Philanthinae; most of these are males of *Aphilanthops frigidus*, the eighth most abundant species. The tenth most abundant species is also a sphecid wasp (*Lestica producticollis*, in the subfamily Crabroninae). The remaining 8% of the prey are divided among three families of wasps, five families of bees, and one family of flies.

The flies are three males of *Odontomyia plebeja* Loew, one of many excellent wasp-mimics in the soldier-fly family Stratiomyidae. The first was found during reconstruction of a cell from 1980. Like the other items

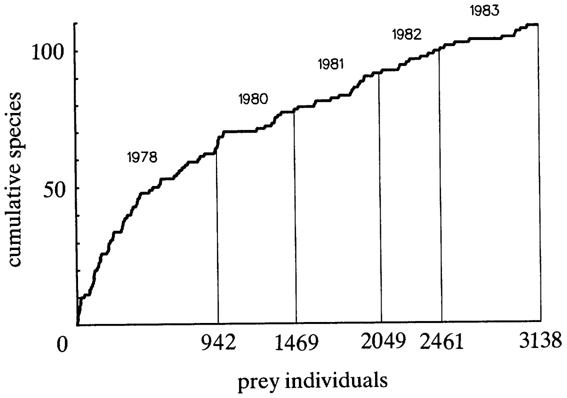

Figure 3. First occurrences of prey species. The curve shows the total number of prey species encountered as a function of the number of prey items identified. A very similar curve is produced by running the history of the study backwards, from 1983 through 1978.

in the cell, the fly had been consumed. The second and third individuals of *O. plebeja* were found lying immediately outside of two different nest entrances in 1981. Like the first individual, they had apparently been mistaken for wasps and captured as they fed at flowers. But their subsequent ejection from the nests of the *P. sanbornii* females who caught them suggests that the females may later have recognized something strange about these prey. Gambino (1985) found a male of the syrphid *Sphaerophoria cylindrica* (Say) in a nest of *Philanthus neomexicanus*. These four flies are the only documented non-hymenopteran prey of *Philanthus*, and the only Diptera known to have been taken by any members of the Philanthinae.

The 92 rejected prey in the sample are nearly 3% of the total, but they were collected from nest entrances during surveys of the entire population, so their abundance in the sample probably overestimates the actual rate of rejection. Leaving aside the two *O. plebeja* individuals, the species distribution of rejected prey is qualitatively similar to that of accepted prey. In particular, no species occurs solely as rejected prey. Quantitatively, the 90 rejected Hymenoptera differ in some respects from the overall taxonomic distribution. For example, wasps are nearly twice as frequent as expected (20%, as compared to less than 11% among accepted prey). Rare species make up a larger proportion of the rejected sample than they do of the accepted sample. Seventeen of the 90 rejected Hymenoptera (19%) belong to species with fewer than 20 individuals in the overall sample (species not in the top 25). This is nearly twice the frequency at which these rare species occur in the accepted sample (10%). Running opposite to both of these trends is an overabundance of honeybees (12%, as compared to 1.6% among accepted prey). Temporally, the frequency of honeybees increases dramatically from 0%, 9% and 6% of rejects in the last two weeks of June and the first week of July, to 20% and 50% in the second and third weeks of July. These departures from expectation are all significant ($p<0.05$; G-tests or binomial probabilities). But aside from the relative rarity of the over-represented rejects (except for honeybees), there is nothing obviously unusual about them.

Why are prey ever rejected? Sarcophagid flies are a major cause of larval mortality in many *Philanthus* populations including ours (Evans & O'Neill 1988). Females might plausibly reject prey that had been parasitized, but we have never found eggs or maggots on rejected individuals (perhaps not surprisingly, as they would be easy to miss). There appears to be temporal heterogeneity in the overall rate of rejection, both among years (more than half of all items being from 1981) and within years (most items being found in the first two weeks of July, when the population of active females is already in decline).

The major prey family in most *Philanthus* populations is Halictidae (O'Neill & Evans 1982; Evans & O'Neill 1988), so the Littleton population of *P. sanbornii* is typical in this respect. There are more species in our sample than in any of the others, but this is not surprising given that it is one to two orders of magnitude larger than the others and is spread over five years. The Littleton population shows only average prey diversity as measured by *D*, which reflects evenness of usage in addition to the number of taxa. O'Neill & Evans (1982) give diversities (at the genus level) for the 30 populations covered in their review. The median is 3.4, and the range is from 1.0 (for *P. bicinctus* at a site in Colorado, where all prey are *Bombus*) to 12.4 (for *P. zebratus* at a site in Wyoming, where *Andrena* is the major genus at 16%, and Sphecidae the major family at 23%). For *P. sanbornii* at Littleton, the corresponding generic diversity is 4.3, only slightly above the median. The reason for this surprisingly low diversity is that two genera (*Andrena* and *Halictus*) overwhelmingly dominate the sample (table 2).

Even at the specific level, quantitative measures of diversity are lower than might be expected, given the large number of species in the prey list. The value of *D* is 11.9 for all years combined, and the yearly values range from 3.6 to 15.1 (table 1). Again, the reason is that a small minority of species dominate the sample (figure 2 and table 3).

The rate at which we encountered new species (as a function of the total number of items seen) declined rapidly for the first few hundred items, as expected under any highly skewed species–abundance distribution (figure 3). But the rate of discovery has declined only slightly since then, implying that we should find many new (but rare) species in the prey samples for 1984–87, which we have not yet worked up. Already there are several species in the prey list that have not previously been recorded as occurring in Massachusetts.

From our own review of the taxonomic literature (Krombein *et al.* 1979; Mitchell 1960, 1962; and more recent generic revisions) we estimate that there are roughly 420 species of bees in New England, New York, and eastern Canada. Of these, around 320 have been taken in southern New England (Connecticut, Rhode Island, and Massachusetts). If we consider only those species known to occur in southern New

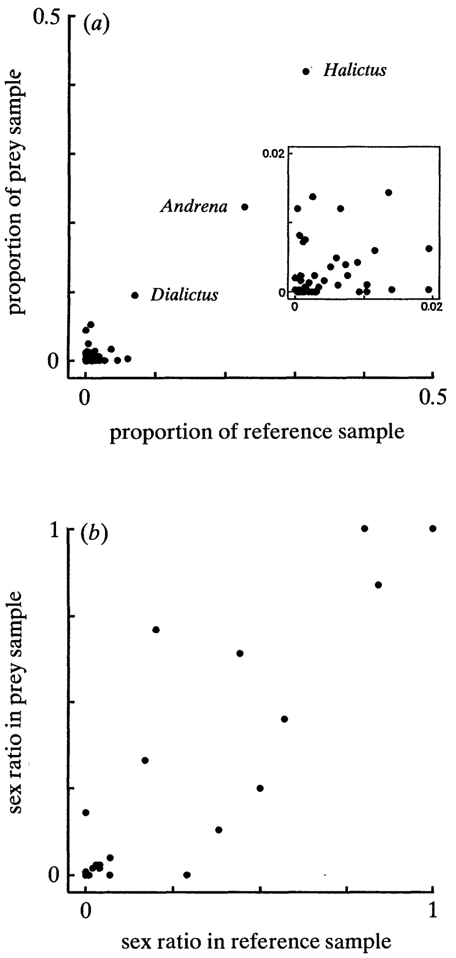

Figure 4. Relative abundances and sex ratios of genera in the prey and reference samples. Seventy-five genera of wasps and bees occur in the prey and reference samples considered together (see Appendix 2). Each point in the upper scatterplot (*a*) shows the relative abundances of a given genus in the two samples. The three main genera (*Halictus*, *Andrena*, and *Dialictus*) are strongly correlated, and most other genera are rare, making up less than 2% of each sample (inset). The correlation coefficient is $r = 0.96$ ($r_s = 0.49$, $p < 0.001$). The lower scatterplot (*b*) shows the proportion of males among the individuals of a given genus, in each of the two samples. *Apis* and *Bombus* are excluded because the samples contain only female workers; genera with fewer than five individuals in each sample are also excluded. The resulting sample size is 20, and the correlation is $r = 0.86$ ($r_s = 0.74$, $p < 0.01$).

England and known to be on the wing in July (when *P. sanbornii* is most active), we are left with a potential universe of around 260 species (figure 5*c*). Given that a few of these species are either too small (head widths below 1.6 mm) or too large (above 4.1 mm) to be taken as prey by *P. sanbornii*, there would appear to be roughly 230 bee species in the list of potential prey.

Seventy-eight species of bees appear in the prey list for our site (Appendix 1), and seven additional species appear in Evans & O'Neill's (1988) list for Bedford and Carlisle. Thus we have already seen more than one third of all the bees that could plausibly appear in the prey list, and a much larger fraction of all those that are likely to occur in the Littleton area at present. Forty-six genera of bees are known to occur in southern New England, and 26 of these (57%) appear in the prey sample described here. Given the rate at which we continue to encounter new prey species, we can expect to see most of the local early-summer bee fauna by the time we finish analysing the prey from 1984–87 (another 3000–4000 items).

The coverage of wasps is much less complete. Out of 72 genera and about 270 species of southern New England sphecid wasps, only eight genera (11%) and 18 species (7%) appear in the prey list. This is not surprising, given that *P. sanbornii* takes more than ten times as many bees as it does sphecid wasps. A typical wasp species is likely to occur at a lower population density than a typical bee, since wasps are predaceous; if so, a typical wasp is more likely to be effectively absent from any given locality. In addition, some wasp species hardly ever visit flowers, and it is our impression that relative to bees, a somewhat larger proportion of New England sphecid wasp species are either too small or too large to be taken by *P. sanbornii*.

The predominance of bees in the diet of *P. sanbornii* might seem to imply that they are 'preferred' relative to wasps, but this is apparently not so. Appendix 2 gives a taxonomic summary of the reference sample (at the genus and family levels) for 1984 through 1987, from the middle of June through late July. The relative abundances of vespid wasps, sphecid wasps, and bees are very similar to those in the prey sample. This indicates that most prey are indeed taken at flowers, and that most categories of prey are taken at frequencies roughly proportional to the rates at which they are encountered.

Some genera occur in only one of the two samples, and the samples represent different sets of years. Yet the correlation of relative abundances is high (figure 4*a*), implying that the reference sample was taken from a world much like that in which *P. sanbornii* hunts, and in particular, that a given genus tends to remain either common or rare. We have not yet identified all items in the reference sample to species, but it is clear that the species-level correlation will be lower than those at the generic and family levels. This is not surprising, given the high year-to-year variation seen in both samples (table 3, figure 10).

Some instances of apparent underutilization can be explained easily. For example, wasps of the genus *Oxybelus* and bees of the genus *Hylaeus* tend to be smaller than any items in the prey sample, while bumblebees (*Bombus*) tend to be larger. Presumably, the very small species are unprofitable and the very large ones are too dangerous to attack or too large to carry.

A few genera of intermediate size appear to be genuinely underutilized. Wasps of the genus *Philanthus* have yet to appear as prey, but they are 2.6% of the reference sample. All of the other *Philanthus* species at Littleton are smaller than *P. sanbornii*, and would therefore seem to be suitable prey, as would the males of *P. sanbornii* itself. Cannibalism of males has been documented for *P. basilaris*, a large western species closely related to *P. sanbornii* (O'Neill & Evans 1981).

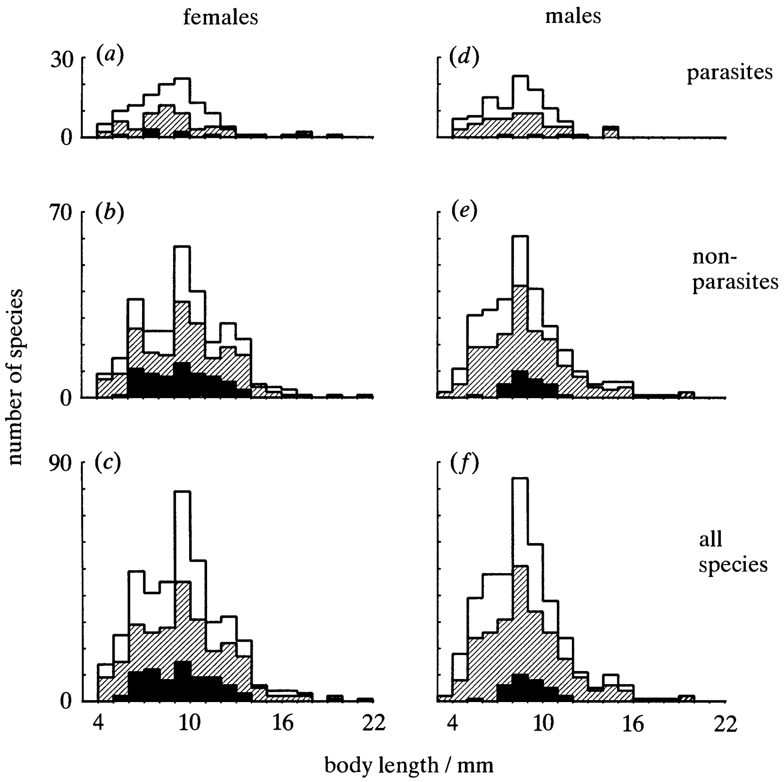

Figure 5. Body-length distributions of New England bees. Each panel shows the distribution of body lengths for three successively more restricted sets of bee species. The outer (open) histograms include species from New England, New York, and eastern Canada, at all times of year; the middle (hatched) histograms represent southern New England (Massachusetts, Rhode Island and Connecticut) during the month of July; the inner (filled) histograms include only those species actually taken by *P. sanbornii*. Body lengths are from species descriptions in the taxonomic literature; most are taken from Mitchell's (1960, 1962) survey of eastern bees, but more recent generic revisions have been consulted where available (e.g. LaBerge 1977 for several groups of *Andrena*). The sample of female cleptoparasites (*a*) includes 117 species for greater New England, 56 for southern New England in July, and 7 for *P. sanbornii* at Littleton. There is no hint of multimodality. The sample of non-parasitic females (*b*) includes 294, 198, and 68 species. There is a strong suggestion of trimodality in the two larger samples. The modes are at 6 mm, 9 mm, and 12 mm. The species taken by *P. sanbornii* show evidence of the first two peaks, but not of the third, which is noticeably underrepresented in the prey sample. The combined sample (*c*) includes all females (411, 254, and 75 species). The sample of male cleptoparasites (*d*) includes 104, 52, and 3 species. Like the other male distributions, this one shows a weak shoulder at 5–6 mm, but is otherwise unimodal. There are 293, 192, and 29 species in the sample of non-parasitic males (*e*). Note how different this distribution is from that for the corresponding set of females. The combined sample of males (*f*) contains 397, 244, and 32 species.

Bees of the genus *Ceratina* make up only 0.3% of the prey sample, but they are 5.8% of the reference sample and have probably been common since the beginning of the study.

Honeybees (*Apis mellifera*) are large-bodied and abundant, so they would seem to be ideal prey for *P. sanbornii*. The Kansas and Florida populations described above appear to take many honeybees (60% and 40% of the samples reported), and the Afro-European *P. triangulum* (which is the same size as *P. sanbornii*) takes essentially nothing but honeybees. At our site, by the middle of July, honeybees outnumber all native bees combined at most flowering plants, yet they make up only 1.9% of the prey sample. (They are the only species we purposely avoided collecting, so their 2.3% abundance in the reference sample is an extreme underestimate of their actual relative abundance.)

There are two cases of conspicuous overutilization. *Andrena brevipalpis* is the fifth most abundant prey species (177 items, 5.6%), but it is rare in the reference sample (7 items, 0.2%). Of the 15 most abundant bee species it is the only one with specialized foraging preferences, and in 1988 we easily found it at sumac (*Rhus* sp.), a plant we had previously ignored but from which *A. brevipalpis* has often been collected (LaBerge 1977). The wasp *Aphilanthops frigidus* is the eighth most abundant prey species (137 items, 4.4%), but it is completely absent from the reference sample. This case is discussed further below, in connection with prey sex ratios.

4. PREY SIZE DISTRIBUTIONS

P. sanbornii takes prey of a very wide range of sizes. The distributions shown in figure 5 use mean overall body length, because that is the measure of size most often published in the taxonomic literature. But

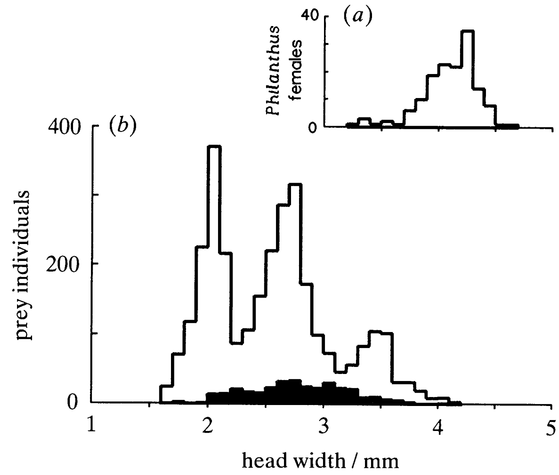

Figure 6. Head-width distributions of *P. sanbornii* females and prey. The upper panel shows the distribution of head width for 147 females of *P. sanbornii*. The range is from 3.2 mm to 4.6 mm, with a mean of 4.1 mm and a standard deviation of 0.24 mm. All are from the Littleton study site. Most were reared from excavated cocoons, but some were collected as adults that had recently died of natural causes, and a few were accidentally killed during censuses of active nests. The lower panel shows the distribution of head width for the 3034 individuals in the prey sample with intact head capsules. Bees are represented by the open area (2711 items), wasps and *Odontomyia* by the filled area (320 + 3 = 323 items). The range is from 1.6 mm to 4.1 mm, with a mean of 2.53 mm and a standard deviation of 0.53 mm (bees 2.51, 0.54; wasps 2.75, 0.42).

estimates of body length are necessarily imprecise, owing to postural differences among the specimens chosen for study. Except in figure 5, we use head width as the measure of size, because it can be determined accurately even for our reconstructed specimens.

The frequency distribution of head widths for the prey actually taken by *P. sanbornii* is strikingly trimodal for bees, but not for wasps (figure 6). Each of the three peaks in the distribution for bees receives important contributions from several major and many minor species. Figure 7*a* shows the abundances of all 78 bee species, as a function of their average female head widths. The average head widths are less uniformly distributed than the average overall lengths shown in figure 5. In particular, there is a notable absence of species at around 2.2 mm average head width, which corresponds to the trough between the first and second peaks in the overall frequency distribution (figure 6). By comparing figure 7 and table 3 to figure 6, the identities of the most important contributors to each peak can be determined.

The apparent clustering of species' sizes under the three individual-abundance peaks suggests that each cluster might simply be a group of species that are similar in size because they are closely related. This is true to a limited extent, especially for the first peak, which is dominated (in number of species) by the large and closely related halictid genera *Evylaeus* and *Dialictus*. (Appendix 1 gives the head widths of all species.) However, several species that are only dis-

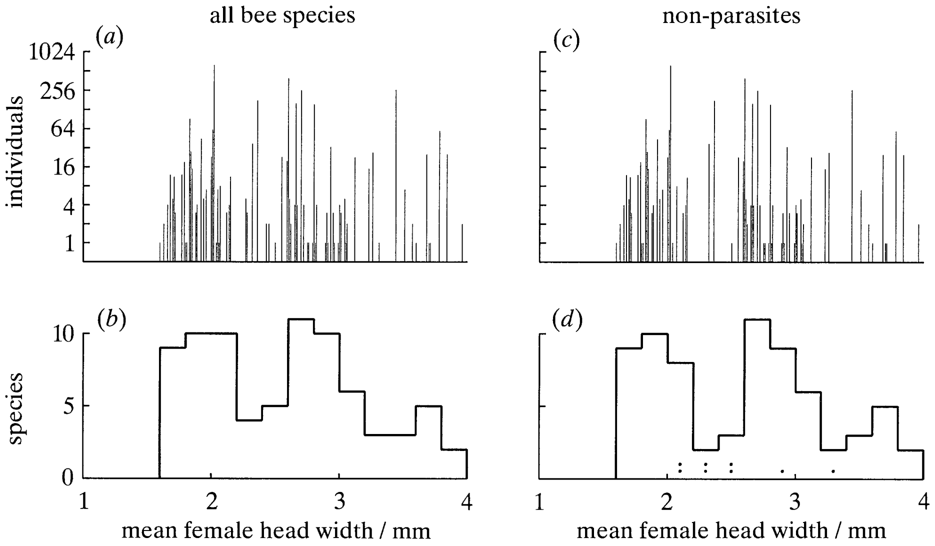

Figure 7. Abundances and frequencies of bee species by mean female head width. In the upper panels (*a*,*c*) each vertical line represents one of the bee species in the prey sample. Its height is proportional to its absolute abundance (on a logarithmic scale), and its horizontal position indicates the mean head width of its females (to the nearest 0.01 mm). For species represented only by males, the average male head width was multiplied by the average ratio of female to male head widths for other closely related species, to yield an estimated mean female head width for that species. Where two or more species had the same head width, some were moved to adjacent, unoccupied sizes; most of these cases were resolved by movements of 0.01 mm, and in no case was a species moved by more than 0.03 mm. The histograms (*b*,*d*) show the number of species falling in each 0.2 mm interval of mean head width, regardless of abundance. For example, among all species in the prey sample (*a*,*b*) there are nine species between 1.6 mm and 1.8 mm, only one of which is represented by more than 16 individuals. When the eight cleptoparasitic species are removed from the sample (*c*,*d*) the impression of trimodality is strengthened. The head-width categories from which cleptoparasites were removed are indicated by dots (*d*).

tantly related to *Evylaeus* and *Dialictus* also occur in the first peak, and one species that is closely related to them is an important member of the second peak.

Halictus, *Lasioglossum*, *Evylaeus*, and *Dialictus* all belong to the tribe Halictini. The boundaries and relationships of these genera are not well understood, but the latter three are usually viewed as a clade distinct from *Halictus*; for example, some classifications treat *Evylaeus* and *Dialictus* as subgenera of *Lasioglossum* (e.g. Michener 1974). The first peak is dominated in number of species by *Evylaeus* and *Dialictus*, but in number of individuals by *H. confusus*, the most abundant species in the prey sample. Its congeners *H. ligatus* and *H. rubicundus* are the first and second most abundant species in the middle peak. The fourth species in the middle peak is *L. coriaceum*, which is nominally more closely related to *Evylaeus* and *Dialictus* than it is to *Halictus*. Thus within the Halictini there are two cases in which the boundaries of genera (or groups of genera) fail to match the boundaries of size–abundance peaks. This indicates that there is more to the pattern than mere taxonomic affinity.

The family Megachilidae occurs in all three peaks, and several other families and genera are well distributed over two peaks. For example, *Andrena brevipalpis* is the third most abundant species in the middle peak, while *A. wilkella* is the dominant species in the last peak. Several other species of *Andrena* make smaller but significant contributions to one or the other of these two peaks. If we include rare species from the reference sample that do not yet occur in the prey sample, then both *Andrena* and *Halictus* have species in all three peaks, and both the Andrenidae and the Megachilidae have at least several representatives in each peak.

In summary, the data on size and relative abundance of bees (but not wasps) suggest a pattern of trimodality that appears to have two related but distinct manifestations. First, the most abundant species tend to be those with average female head-widths near the centres of the hypothesized peaks, and second, the average female head-widths of the species present (disregarding relative abundance) tend to cluster around these same modal sizes. In other words, both individual abundance and species abundance appear to be trimodally distributed with respect to head width.

It is possible, but unlikely, that these patterns could be artifacts created by trimodal size preferences expressed by hunting *Philanthus* females. To express such preferences, females would need to avoid bees of two presumably abundant size classes, near the middle of their preferred size range. We do not know of any arguments or evidence suggesting that different techniques of capture or handling are used on prey of different sizes. Although the independent reference sample is not yet fully analysed, we know that it and the actual prey sample contain substantially the same set of species, in generally similar relative abundances (see figure 4, Appendix 2, and further discussion below). This suggests that the size–abundance distribution of bees in the reference sample will be similar to that of bees in the prey sample. A subsequent analysis of museum collections representing greater New England and several sites in western North America has revealed essentially the same pattern, with additional peaks at sizes smaller and larger than those taken by *P. sanbornii*, while a different but also apparently multimodal pattern is seen for female bees of Australia (J. Seger, J. W. Stubblefield, J. S. Burner & V. J. Tepedino, unpublished data).

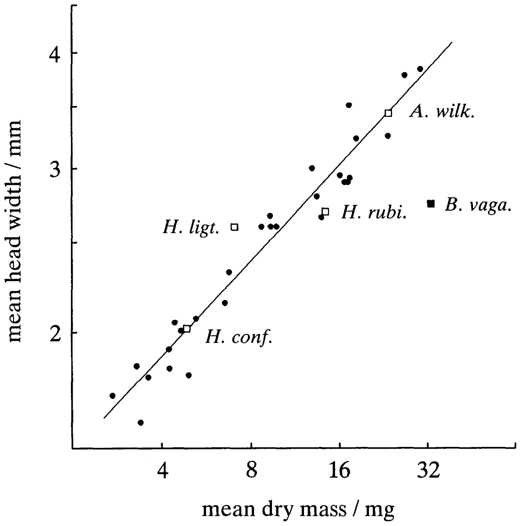

Figure 8. Relationship between dry mass and head width for the females of 33 bee species. Mean dry masses are from the 1984 reference sample; mean head widths are from the prey sample. Note that logarithmic scales of measurement are used on both axes. The straight line is a reduced major axis (slope = 0.35, $r = 0.97$) fitted to all the points except that for *Bombus vagans* (filled square), which has an extremely small head for its mass, as do most bumblebees. Four species discussed in the text are indicated by open squares.

The body-length distributions (figure 5*c*,*f*) appear at first to be unimodal. But on closer examination the female distributions show definite shoulders, suggesting smeared secondary peaks to each side of the main central peak. Such smearing might be expected even if body length were trimodally distributed, owing to the inaccuracy of body-length measurements. But if head width itself (rather than body size) were the character that tended to have discrete optima, then this smearing might appear even in body-length data of perfect accuracy. The mean dry masses of 64 species of female bees from the reference sample appear to be bimodally distributed (data not shown); the lower mode corresponds roughly to the small head-width peak, but the upper mode appears to fall between the middle and large head-width peaks. Despite these differences of shape between the two distributions, there is a high correlation ($r = 0.97$) between log mean head width (from the prey sample) and log mean dry mass (from the reference sample), for the females of 32 species that occur in both (figure 8).

Eight bee species in the prey sample are cleptoparasites. Females of these species visit flowers to feed on nectar, but they do not collect pollen for their offspring, which develop in the nests of other species. When these species are removed from the sample, the trimodality of head widths becomes more pronounced (figure 7*d*). This might be expected if size or head-width were related to methods of pollen collection and not to nectar feeding. A similar pattern is seen in the body-length distributions for all New England bees; parasites show no hint of multimodality, while females of the non-parasitic species show a stronger suggestion of trimodality than that seen in the combined distributions (figures 5*a*–*c*). Like the females of cleptoparasitic species, males do not forage for pollen, so they might be expected to show only weak multimodality, caused mainly by the tendency of male and female morphologies and sizes to be correlated. Distributions of body length for males of non-parasitic species (figure 5*e*) are in fact more nearly unimodal than those for females (figure 5*b*). Also, the correlation between mean head width and mean body length may be lower for males ($r = 0.67$, $n = 27$ species) than for females ($r = 0.92$, $n = 68$).

5. PREY SEX RATIOS

Twelve per cent of the prey are male, but there are striking sex-ratio differences among species and higher taxa. For example, the overall sex ratio of vespid wasps is near 50%, and males exceed females in 5 out of 11 species, while in sphecid wasps the overall sex ratio is 75%, and males exceed females in 12 out of 17 species. By contrast, the overall sex ratio among bees is only 5%, with males exceeding females in only 5 out of 78 species. A similar pattern appears in Evans & O'Neill's (1988) prey sample for populations at Bedford and Carlisle, and in their data for several other species of *Philanthus*. These sex ratios are similar to those in the reference sample (Appendix 2 and figure 4*b*), consistent with the idea that *P. sanbornii* females take virtually all the aculeate Hymenoptera (of suitable sizes) that they encounter at flowers.

The differences between wasp and bee sex ratios reflect basic differences of ecology. Most adult wasps and bees take their nourishment at flowers (although some wasps take honeydew, seldom if ever visiting flowers). Bees also provision their offspring with pollen and nectar, so adult female bees spend large amounts of time at flowers. Wasps provision their offspring with insects or spiders that females usually find in places other than at flowers. (*Philanthus* is a notable exceptions to this rule.) Thus a typical female wasp need make only a few brief visits to flowers each day.

Other things being equal, these differences in female behaviour would create the kinds of overall sex-ratio biases seen in the prey and reference samples (Evans & O'Neill 1988). But the amount of time that males spend at flowers also depends on many details of male behaviour, and in particular on where males search for mates. Males that find mates at flowers should be taken more often by hunting *Philanthus* females than males that find females somewhere else. At least two of our five male-biased bee sex ratios may be explained by this aspect of their biologies.

Dufourea novaeangliae (five males, no females) and *Melissodes apicata* (22 males, three females) both forage exclusively on pickerel weed (*Pontederia cordata*) (Kukuk *et* al. 1985; LaBerge 1956), an aquatic plant that occurs in several ponds and streams within a kilometer of the nesting area. Males of *D. novaeangliae* are known to patrol patches of *Pontederia* in their search for mates (Kukuk *et al.* 1985), and we have often observed this behaviour ourselves. The male behaviour of *M. apicata* has apparently not been described, and the species virtually disappeared after the first few years of the study, but we subsequently observed males patrolling *Pontederia* at the edge of a pond near the Anacostia River in Washington, D.C.

A much more strongly male-biased sex ratio is shown by the wasp *Aphilanthops frigidus* (135 males, two females). Its females provision their nests exclusively with queen ants of the genus *Formica*, and its phenology is keyed to their nuptial flights (Evans 1962). Beginning in mid-July, the females can often be found working at their burrows, but males of *A. frigidus* are completely absent from the reference collection. We have repeatedly searched for them, without success, and there appears to be no published account of their behaviour. Some individual *P. sanbornii* females have taken very large numbers of *A. frigidus* males, which suggests that the latter may be spatially concentrated at least some of the time. One possible site of concentration would be at honeydew deposits on trees (F. D. Parker, personal communication); if this were true it would imply that some *P. sanbornii* females discover and exploit prey sources not associated with flowers. The strength of the overall male bias among all sphecid wasps in the prey sample is largely a reflection of the extreme bias contributed by this most abundant wasp species (see Appendix 2).

6. HETEROGENEITY AMONG YEARS

Although the prey records are qualitatively similar from year to year, they show almost every imaginable kind of quantitative variation. Even aggregate measures such as mean head width and taxonomic diversity (table 1) are significantly heterogeneous over years. When the data are examined in detail, the extent of the heterogeneity becomes even more impressive.

The year-by-year head-width distributions (figure 9) are strongly trimodal in 1978, but less so in 1980 through 1982. In 1983 the first and middle peaks are very strong, but the last peak is virtually absent; 1983 is the year with the lowest mean head width and the lowest taxonomic diversity (table 1). Yearly abundances of the 25 most abundant prey species (and their mean head widths) are given in table 3; by comparing these numbers to the yearly head-width distributions shown in figure 9, it is possible to infer which species are the main contributors to any given peak. For example, the first peak in 1983 is mostly *Halictus confusus*, with contributions from *Dialictus cressonii* and *Augochlorella striata*, while the middle peak is dominated by *H. ligatus*, with contributions from *Lasioglossum coriaceum* and *Andrena spiraeana*.

Three of the seven most abundant bees are andrenids, and four are halictids. These seven species account for 65% of all prey, but each varies dramatically from year to year (figure 10). The least variable

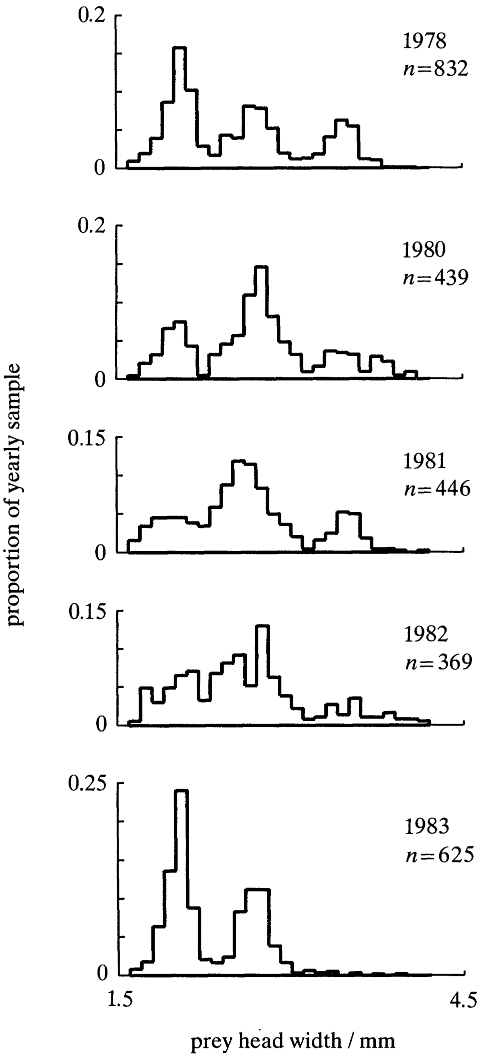

Figure 9. Head-width distributions of bees, by year. Frequency distributions of head width are shown separately for each of the five years represented in the prey sample (bees only). Sample sizes differ among the five years (table 1), so to facilitate comparisons the areas under these distributions have been equalized. The unfilled area in figure 6 is thus a weighted average of the five distributions shown here.

(*L. coriaceum*) differs fivefold between its least and most abundant years; the most variable (*A. wilkella*) differs more than 17-fold. Each of the top three andrenid species is the most abundant andrenid in at least one year; each is also the least abundant (of the top three) in at least one year. Each of the four halictids except *H. rubicundus* is the most abundant prey species of any kind at least once, and each of the four is the least abundant (of the four) at least once. In addition, each of these seven top species exceeds each of the other six at least once, though not necessarily all in one year.

Dramatic year-to-year variation in relative abundance appears to be the rule among all prey species. Only seven of the 25 species listed in table 3 fail to show significant heterogeneity, and five of these seven are borderline ($0.1 > p > 0.05$; see table 3).

The first year in which we made quantitative reference collections of potential prey was 1984, so we cannot directly assess the extent to which the yearly variation in the 1978–83 prey samples reflects the dynamics of local wasp and bee populations. For 1984–87 we will be able to compare prey samples to our own collections made throughout the flight season. We expect these comparisons to show that much of the yearly variation seen in the prey samples is caused by yearly variation in the local abundances of the prey species. This expectation is supported by several lines of evidence. First, previous long-term studies of bee communities (and their plants) have found substantial temporal variation (e.g. Tepedino & Stanton 1980, 1981). Second, our reference samples show variation similar to that seen in the prey samples; for example, two of the three most abundant species (*Andrena wilkella* and *Halictus ligatus*) have very similar standard deviations and CVs of arcsine-square-root transformed relative abundance in the two samples; (the third species, *H. confusus*, is significantly more variable in the prey sample). Additional evidence comes from the observed distributions of prey species among nests within years, and among cells within nests, as discussed in the next section.

7. HETEROGENEITY AMONG NESTS AND AMONG CELLS

Within any given year, prey are unevenly distributed by species among nests. Table 4 gives the absolute abundances of the top 20 prey species in each nest with six or more cells. The differences among years are easy to see, and the differences among nests within years are, if anything, even more striking. The overall pattern of heterogeneity is highly significant within each of the five years (see legend to table 4).

In 1980 and 1981 we followed the activities of many marked females. Nest usurpation did occur, but at a low rate. Thus a typical nest is the lifetime work of one female, and differences among physically distinct nests can be interpreted as differences among females. To the extent that individual nests sometimes contain the work of more than one female, the observed differences among nests underestimate the actual differences among females.

It is conceivable, but unlikely, that different females prefer to take different prey species. If this were the explanation for the heterogeneity among nests, then we would expect to see the strongest effect at the genus and family levels, where the prey differ more in size, appearance, and habits than they do at the species level. Instead, the pattern appears to be idiosyncratic, often involving strong differences of relative abundance among closely related prey species. A simple explanation for this pattern is that females tend to return to particular places at which they have previously been successful. Given that prey species are clumped both spatially and temporally, the habit of returning again and again to the same place as long as it continues to be profitable could explain much of the heterogeneity seen among nests.

If this explanation is correct, prey should tend to occur in runs of particular species, within a nest. A cell-by-cell prey list for nest 63 of 1980 (figure 1*a*) is given in table 5, and for nest 880 of 1982 (figure 1*b*) in

Table 3. *Yearly abundances of the 25 most abundant prey species (1978–83)*

(HW is mean head width in millimeters. Female means are given for most species, but male means (indicated by '*') are given for those represented mainly by males. '%' is per cent of the total sample of prey individuals. The 25 species shown here account for 90% of the total of 3138 individuals. The distribution of abundance is significantly heterogeneous for all but seven species (9, 15, 16, 17, 19, 21, and 22), five of which are borderline ($0.1 < p < 0.05$; chi-square or randomization tests).)

rank			HW	total	%	1978	1980	1981	1982	1983
1	HAL	Halt conf	2.02	631	20.1	242	34	28	42	285
2	HAL	Halt ligt	2.60	398	12.7	44	8	95	39	212
3	AND	Andr wilk	3.44	263	8.4	122	46	68	22	5
4	HAL	Halt rubi	2.70	257	8.2	113	62	36	38	8
5	AND	Andr brev	2.36	177	5.6	25	28	58	62	4
6	HAL	Laso cori	2.66	159	5.1	24	66	30	20	19
7	AND	Andr spir	2.80	154	4.9	45	43	20	29	17
8	SPH	Aphl frig	2.95*	137	4.4	45	47	12	8	25
9	HAL	Dial cres	1.83	92	2.9	16	18	24	14	20
10	SPH	Lest prod	2.66	74	2.4	7	11	54	1	1
11	HAL	Dial nigr	2.01	62	2.0	32	9	15	6	
12	API	Apis melf	3.78	59	1.9	17	28	4	10	
13	HAL	Agla stri	1.92	44	1.4	6	12	1	5	20
14	HAL	Agra pura	2.32	37	1.2	12	2	6	12	5
15	HAL	Agap virs	2.93	33	1.1	9	9	3	9	3
16	AND	Andr crat	3.25	28	0.9	9	8	1	7	3
17	HAL	Dial coer	1.84	28	0.9	10	4	6	4	4
18	SPH	Ecte cont	2.88*	25	0.8	1	5	18	1	
19	MEG	Mega mend	3.84	25	0.8	4	8	4	7	2
20	ANT	Meli apic	3.36*	25	0.8	19	2	3	1	
21	AND	Andr thas	3.12	23	0.7	8	7	4	3	1
22	HAL	Agps metl	2.55	23	0.7	7	6	8	1	1
23	HAL	Dial nymp	2.01	23	0.7	14	2	1	6	
24	VES	Euod fora	3.00	22	0.7			14	6	2
25	AND	Andr frag	2.60	20	0.6	10	9	1		

table 6. The clumping of any species with ten or more items is obvious, but the pattern was first called to our attention by rare species. For example, all three males of *Dialictus* sp.4 were found in two adjacent cells of nest 880. Common species also tend to be spatially aggregated within nests. These patterns can be demonstrated by plotting the prey species abundances (tables 5 and 6) on the nest maps (figure 1).

Given that there are significant differences among nests within years, and that some yearly samples contain only four nests, then some proportion of the observed year-to-year variation must be caused by sampling rather than by real differences among years in the relative abundances of prey species. We used a two-level nested ANOVA to partition the variation (in number of items of a given species per cell) into components attributable to variation among years, variation among nests within years, and variation among cells within nests. This was done separately for each of the 20 most abundant species in the prey sample (table 7).

Even after the effects of sampling and of heterogeneity among nests have been removed, there remains a significant amount of variation attributable to differences among years, for 9 of the 20 species. For three of these species (*Halictus confusus*, *H. ligatus*, and *Lestica producticollis*), the proportion of variance attributable to years is roughly 30%. The effect of nests within years is significant for 12 of the 20 species, and the average size of the effect at this level is larger than that at the level of years. There appears to be no relationship (over species) between the size of the effect of years and the size of the effect of nests within years. This is reassuring, since we would not expect the two effects to be related. Overall, the results of this analysis confirm our impression that the differences among years and among nests within years are both larger than would be expected on the null hypothesis that females are sampling from an effectively homogeneous and unchanging pool of prey individuals.

8. DISCUSSION

The prey recorded here were taken from one location, in five out of six consecutive years, by a wasp that takes most species of wasps and bees that visit flowers. This sample reveals the composition and dynamics of the local early-summer wasp and bee communities, as seen through the eyes of a highly skilled collector. Some of the most interesting results to emerge from this study concern the structure of the bee community.

Within years, the sample is aggregated into nests representing the lifetime production of individual females, and within nests it is aggregated into cells. This hierarchical organization has allowed us to analyse the variance in relative abundance of particular prey species, in ways that give some insight into the hunting behaviour of *P. sanbornii*. In addition, the

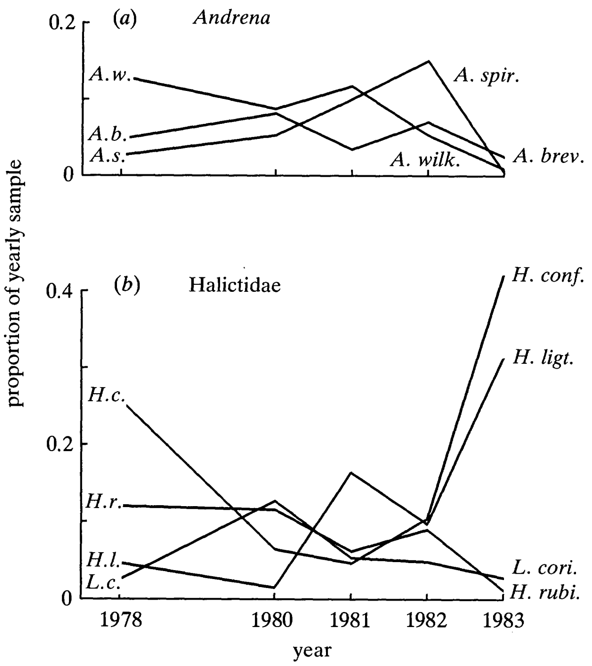

Figure 10. Yearly relative abundances of the seven bee species most abundant overall. The height of each curve shows the proportion of the prey sample comprised of individuals of the indicated species, in the year indicated on the horizontal axis. Yearly absolute abundances of the 25 most abundant prey species are given in table 3. Each of the three dominant species of *Andrena* (*a*) exceeds both of the others at least once. All three species of *Halictus* (*b*) in the prey sample are very abundant on average, but all three also appear to fluctuate wildly. *Lasioglossum coriaceum* has been less variable than the other dominant halictids, but even so it varies by a factor of seven between its smallest and largest years.

independent reference sample provides a rough baseline against which a few apparent instances of biased prey selection can be seen.

In this section we first discuss what *P. sanbornii* has shown us about the structure of its prey community. Then we discuss what the prey reveal about the hunting habits of *P. sanbornii* and its congeners in New England and North America. Finally, we briefly discuss some ways in which plant–bee–beewolf systems are different from most plant–herbivore–predator systems.

(*a*) *Prey diversity and population dynamics*

Most prey species show dramatic changes of relative abundance, within the few years covered by the prey sample. Even the two most abundant genera (*Andrena* and *Halictus*) undergo large fluctuations. For example, *Andrena* is nearly 22% of all prey for the five years combined, and it is by far the most important genus nutritionally, owing to the relatively large body size of typical individuals. Yet in 1983, *Andrena* virtually disappeared, dropping to less than 5% of all prey. We know from the reference collections and from casual inspection of prey remains for 1984–87 that this hiatus was only temporary. In particular, we expect *A. wilkella* to return in force. This species was 13% of all prey in 1978 (122 items), second only to *H. confusus*, and then declined more or less steadily to 0.7% (five items) in 1983. *H. confusus* suffered almost as large a decline through 1981 and then made a spectacular comeback in 1983.

If the abundances of bees at flowers are a fair reflection of their actual abundances, then the Littleton community would appear to have rather lively dynamics. It is not clear, however, whether the striking changes in apparent abundance mainly reflect intrinsic dynamics of the plant–bee–wasp system or extrinsic factors such as weather and disturbance. For example, most bees visit a variety of plants and move quickly among them in response to changes in the foraging opportunities they present. Thus even fairly minor year-to-year shifts in the phenologies of particular plant species could cause large shifts in the plants visited most frequently by many bee species (see Tepedino & Stanton 1980, 1981). The relative abundance of a given bee species might therefore fluctuate wildly within any small area with a restricted set of plants, while showing little variation over larger spatial scales that include a broader diversity of foraging opportunities.

Changes in local abundance can also arise from spatial variation in the level of disturbance or the stage of succession. During the four years that we made reference collections (1984–87) there was only minor change in the apparent status of most stands of flowering plants at which we collected. One major stand and its associated nesting area were destroyed in 1985, and this is likely to have affected subsequent years, but we were aware of only minor human disturbance within a kilometre of the nesting area in the years covered by the prey sample described here (1978–83). However, certain kinds of disturbance would not have been noticed, such as pesticide usage by property owners. And because bee nests tend to be patchily distributed, very restricted disturbances could conceivably have striking consequences.

Both *Philanthus* and its prey are creatures of open, early-successional habitats. Decades of sand-and-gravel operations in the vicinity of our site may thus be directly responsible for its great abundance and diversity of aculeate Hymenoptera. Much of the area is already returning to brush and forest, and other parts are being taken over by various forms of intensive human development. These changes are undoubtedly affecting both the composition and the dynamics of the wasp and bee communities, and it is possible that the full data set (spanning 10 years) will show at least hints of such secular trends. Biogeographic studies of wasp and bee communities in regions such as eastern Massachusetts could directly address the factors affecting long-term patterns of diversity and abundance, if designed to exploit historical changes in land use.

(*b*) *Bee size distributions*

The most intriguing pattern to emerge from the prey data is the multimodal size-abundance distribu-

Table 4. *The 20 most abundant prey species in nests with six or more cells (1978–83)*

(The prey species are arranged in order of increasing mean head width, except that 'other' includes roughly 90 minor species of all sizes. (Mean head widths are given in Appendix 1.) The species are partitioned into groups corresponding to the three modes of the overall head-width distribution. This table gives a nest-level summary of the data used in the nested analysis of variance (NANOVA) described in the text, except that it omits a few small nests with three to five cells. Nest identifiers are written vertically (e.g. the first nest under 1978 is 'p3'). Under each identifier is the total number of complete cells in the nest that were produced during the year to which the nest is assigned (usually the current year, but in two cases the previous year); these cells are assumed to be the work of a single female, and they are the ones from which the prey summarized in this table were taken. The data for each year take the form of a contingency table. A heterogenous distribution of prey species over nests could be demonstrated, in principle, by a significant contingency chi-square, except that many cells in each table (species i in nest j) have expected frequencies of less than one item (see Lewontin & Felsenstein 1965). As a consequence, the sampling distribution of X^2 may not be adequately approximated by the chi-square distribution with $(r-1)\times(c-1)$ degrees of freedom, so we approximated the sampling distribution of X^2 by Monte Carlo simulation. For each year, we generated 1000 random contingency tables having the same marginal totals as the actual data, and calculated X^2 for each. We then compared X^2 for the real table to the distribution of X^2 for the simulated tables. In every year X^2 for the real table is much larger than the largest of the 1000 simulated values. In four of the five years, it is two to three times as large, and in the least heterogeneous year (1982) it is 1.7 times as large ($X^2 = 199.8$; simulated values range from 117.7 to 45.6, with a median of 75.7). Thus for each year the null hypothesis (random distribution of prey species over nests) can be rejected at $p \ll 0.001$.)

year	*1978*										*1980*					*1981*						*1982*				*1983*			
nest I.D.	p3	p5	p6c	p6d	p6e	p6f	p6g	p6h	p6i	p6j	63	171	173	174	334	x6	x18	309	615	49	x82	880	903	873	y5c	y4	y5a	y5b	y8
cells	21	8	8	12	7	12	11	7	6	9	15	7	8	12	6	6	10	7	16	14	6	21	11	9	9	6	16	24	19
Dial cres		2		6	1	1	3		1		8			3	1	2		1	7	5		6	1	4	2		2	9	9
Dial coer			1	1		1	2	3			2			1				1	2	3		1		3					2
Agla stri	1					2	1		1	1	4	4	1						1		3		2			5	11	4	
Dial nigr			3	3	1	5	3	4	3	6	2		3	3		2			7	3	1	4		2					
Halt conf	54	12	7	23	9	20	36	4	10	6	3	5	2	9	2	1	6		9	10		13	8	14	5	21	91	109	64
Agra pura				3			1	2	1	1		1		1						3		2	2	5	2		2		1
Andr brev			2	1		4		7	2			6	10	6		3	2	2	12	32	2	54	2	1	5		1	2	1
Halt ligt	19	1		2		10	1			1		1	4	1			21	15	10	5		27	4	1	4	33	44	112	23
Lest prod					1		1			2		1	2	1		4	5	3	9	22	4			1		1			
Laso cori	2		3	3	2	2	4		2	3	19	14	5	10	2	6	3		10	3	3	2	1	11	4	1	2	2	15
Halt rubi	10	7	19	12	1	9	4	21	2	8	2	3	16	7	1	6	8	2	11	5	3	20	3	1	12	1	2		5
Andr spir	10		8	2		3	9		1	4	13	4	5	3	1	1	1		10	1	2	13	1	9	6		5	6	6
Ecte cont						1						3				5		1	1	8	1				1				
Agap virs		1		1	2		1		1	1	3			3	1		1			2		4	3		2	3			
Aphl frig	24	6		1		1	4	1		1	10		1	16	13	5	1		3	2				7	1	1	10	1	13
Andr crat			3				1			3	2	2	2	1							1				4		1	2	
Andr wilk	29	19		23	4	18	4		2	5	3	3	2	2	2	1	21	13	7	3	17		21	1					5
Meli apic		2			10		2			3											3	1							
Apis melf	7				2		2	1		1	5	1		3	6		1		1			2	2	3					
Mega mend		1					2						1	2	1				2	1	1		4	2	1		2		
other	19	3	5	8	16	5	22	7	18	11	23	2	8	12	5	12	8	9	17	31	6	25	16	8	17	8	7	14	13

Table 5. *Distribution of prey species in cells of nest 63 (1980)*

(Species and cells are both sorted in order of increasing mean head width. The species are partitioned into groups corresponding to the three principal modes of the overall head-width distribution (as in table 4). Note that large and small species frequently occur in the same cells. Totals for species and for cells are given on the right and bottom margins, respectively.)

	cell I.D.															
	28	19	17	34	29	27	35	21	30	25	26	37	7	13	23	
Dial vrsn	1															1
Dial sp. 3	1															1
Dial coer		1											1			2
Dial line			1		2	1	1									5
Dial cres	1	2	1	1					1	1		1				8
Agla stri	2	1									1					4
Dial nigr		1			1											2
Noma pygm			1		1											2
Halt conf						1					2					3
Myzi macu								1								1
Cera cadu			1													1
Cerc arel					1								1			2
Anci unif														1		1
Agps metl											1					1
Laso cori	5	4		4					2			3			1	19
Andr frag						1	2									3
Halt rubi		1													1	2
Andr spir									6	6	1					13
Cerc clyp			1													1
Agap virs							2								1	3
Aphl frig								4					3	3		10
Andr thas										1					1	2
Andr crat															2	2
Mega mend					1											1
Andr wilk						1						2				3
Andr niva		1														1
Apis melf			1		1	1					2					5
	10	11	6	5	6	6	5	5	9	8	7	6	5	4	6	99

tion of female bees (figures 5–9). Griffiths (1986) describes qualitatively similar distributions for bird species, and reviews several other studies on birds, fish, bovids, insects, and marine plankton, that seem to reveal multimodal size–abundance distributions. Griffiths uses log-transformed average body-length estimates as the index of size, and he argues that body mass is probably the ecologically relevant variable. He finds that individual abundances and species abundances both tend to be multimodally distributed, as do we. But here the pattern appears to be stronger for head widths than for body lengths, and it is shown only by the females of non-parasitic species (figures 5 and 7). The body-length distributions shown in figure 5*b* suggest that the pattern is as strong for greater New England at all times of year, as it is for southern New England in July, or for Littleton as seen by *P. sanbornii*. Holling (1992) has recently described multimodal distributions of species mean body masses for North American birds.

There are two ways to interpret the possible ecological meaning of the patterns described here. First, head width might simply be an index of overall body size. In that case, its trimodality would reflect an underlying trimodality of body size, presumably caused by size-related ecological interactions. Second, head width itself (or more precisely, a set of dimensions closely tied to head width) might be the character directly involved in the relevant ecological interactions. In this case, body size might show only a hint of multimodality, or none at all.

Halictus confusus (2.02 mm mean head width, 4.9 mg dry mass) is the dominant member of the first head-width peak. *Andrena wilkella* (3.44 mm, 23.7 mg) is the dominant member of the third peak. Both of these species have average head widths close to those expected for bees of their respective masses. *H. ligatus* (2.60 mm, 7.1 mg) is the dominant member of the middle head-width peak, but compared to most bees in the sample, it has a very large head for its mass (figure 8). Thus *H. confusus* and *H. ligatus* are much more similar in mass than would be expected on the basis of their head widths. Their dry-mass distributions overlap broadly, but their head-width distributions overlap only slightly.

This observation is consistent with the idea that head width itself (or some variable closely tied to head width) may tend to have discrete optima. Why this should be so is not obvious. Few bees in the prey and reference samples are highly specialized foragers; most

Table 6. *Distribution of prey species in cells of nest 880 (1982)*
(For details see legend to Table 5.)

	cell I.D.																				
	12	11	23	8	27	19	21	9	10	18	24	5	26	25	16	15	17	6	22	14	7	
Dial sp. 4			2											1								3
Dial rohw	2			1															1			4
Dial cres	4															1	1					6
Dial sp. 3				1			1															2
Dial coer													1									1
Agla stri											1		2									3
Dial nigr				1	1			1			1											4
Dial nymp	2	3																				5
Halt conf	2	4		4			2									1						13
Andr brev				1	8	10	2	8	7	3		8			4	1			1	1		54
Agra pura									1	1												2
Halt ligt			4	1						3	7		2	5				2			3	27
Cerc arel			1																			1
Ecte macl																	1					1
Halt rubi			1	2				2	1		1	2			2		3	2	3	1		20
Laso cori															1				1			2
Euod fora											1		1				1	1				4
Andr spir				2		1		1				1					3		1	4		13
Coll bank														1								1
Agap virs													3	1								4
Andr thas																1						1
Mega relt		1																				1
Meli apic																1						1
Zeth spin																					1	1
Mega mont																			1			1
Apis melf	1						1															2
	11	8	8	13	9	11	6	12	9	7	11	11	9	8	7	5	9	5	8	6	4	177

visit many plant species, depending on which are most abundantly in flower. To the extent that we know of active preferences, they seem to be determined more by taxonomic affinities than by size. For example, megachilids seem to show a preference for legumes (especially *Lotus*), but large and small species can often be taken at the same time from the same individual plant. If head width is related to foraging specializations, it seems likely to have as much to do with methods of pollen and nectar collection as with choices of particular flower sizes or types. One possibility is that pollen-collecting species tend to organize themselves into 'size guilds', for which a given flower is, in effect, different resources. On this hypothesis, the members of such guilds would find themselves in direct competition with fewer species (and individuals) than would bees on the boundary between two guilds, who would tend to compete with the members of both guilds. This idea (and others) will be discussed at length elsewhere, in connection with a statistical analysis of several morphometric data sets (J. Seger, J. W. Stubblefield, J. S. Burner & V. J. Tepedino, unpublished data).

(*c*) ***Prey selection in the genus* Philanthus**

In New England, *P. sanbornii* is univoltine with a flight season that extends from late June through July. A much smaller univoltine species, *P. politus*, is also on the wing at this time, which corresponds to the first of two major temporal peaks of bee abundance and diversity that occur each summer. Most of the reference sample was taken during June and July, but we have collected in all months from late April through October. Bee abundance and diversity both increase rapidly in late June, reach a maximum in early July, and decline into early August. This temporal peak in the abundance and diversity of potential prey species parallels a similar temporal peak in the abundance and diversity of plants in flower. The number of plants in flower declines sharply during the second half of July, prior to the flowering of the late-summer plant community which is dominated by *Solidago* and *Aster*. A new set of univoltine bee species appears at that time, as does a new set of univoltine *Philanthus* species (*bilunatus*, *lepidus*, *solivagus* and *ventilabris*, of which only *lepidus* is common at our site). In broad terms, then, the summer can be divided into two peaks of abundance and diversity for flowers, bees, and beewolves.

There are also many bee species, including all social species and some non-social halictids, that have two or more generations and that participate in both peaks. *P. gibbosus* is the only beewolf known to exhibit a similar pattern in New England. The bi- and multivoltine bees tend to become more abundant as the season progresses, and this may explain why the late-

Table 7. *Components of the variance of number of items per cell, for the 20 most abundant prey species*

(Entries under years and nests are the proportions of the variance of number of items per cell (x) explained by variation at that level; the remainder is variation among cells within nests, which is viewed formally (if not biologically) as 'error'. Similar results were obtained using the transformed variables $\log(1+x)$ and x/n, where n is the total number of items in the cell. There are 5 years, 39 nests (having three or more cells), and 364 cells in the data set used here (d.f.: 4, 34, 325). Similar results were obtained using only those nests with five or more cells (d.f.: 4, 27, 306), although a few of the variance components that are significant here at the 0.05 level (*) failed to reach significance, and one of the components that is significant here at the 0.01 level (**) fell to the 0.05 level. The analysis was performed using the nested ANOVA procedure for unequal sample sizes described by Sokal & Rohlf (1981, pp. 239–308). When sample sizes are unequal, it is possible to obtain apparently 'negative' variance components. In the few cases in which this happened, these 'negative' components were rounded up to 0.00.)

species	n	years	nests
Ecte cont	22	0.08*	0.19**
Lest prod	61	0.29**	0.13**
Aphl frig	130	0.00	0.11**
Andr brev	167	0.08*	0.15**
Andr crat	25	0.00	0.02
Andr spir	143	0.01	0.05*
Andr wilk	255	0.02	0.30**
Agra pura	27	0.03*	0.01
Agla stri	43	0.07**	0.00
Agap virs	31	0.01	0.00
Halt conf	603	0.32**	0.04*
Halt ligt	379	0.27**	0.21**
Halt rubi	242	0.00	0.31**
Laso cori	149	0.09*	0.10**
Dial coer	23	0.00	0.01
Dial cres	85	0.00	0.01
Dial nigr	57	0.03	0.04
Mega mend	23	0.01	0.03
Meli apic	25	0.00	0.29**
Apis melf	43	0.05*	0.05*
other	389	0.00	0.12**

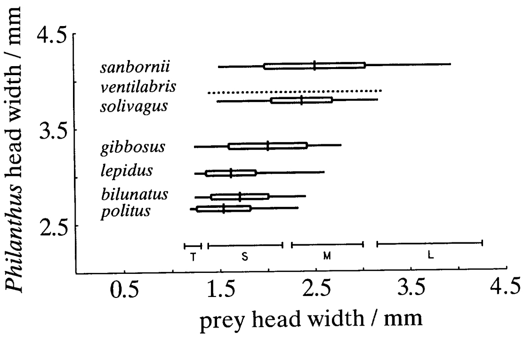

Figure 11. Prey sizes of New England *Philanthus* species. Each box-and-whisker diagram shows the mean, standard deviation, and range of head widths for bees recorded as prey of *Philanthus* species that occur in New England. The vertical position of each box-and-whisker shows the species' mean female head width. Approximate ranges of the major bee head-width peaks are indicated above the horizontal axis ('tiny', which is not taken by *P. sanbornii*, 'small', 'medium', and 'large'). Wasps recorded as prey are not included, but none of these *Philanthus* species takes many wasps, so their omission has little effect on the resulting distributions of prey head width. The three *Philanthus* species most abundant at our study site in early summer are *politus*, *gibbosus*, and *sanbornii*, which are very well separated in size. In late summer we see *lepidus*, *gibbosus* (which is bi- or multivoltine), *solivagus*, and *ventilabris*. Prey records (for sites in New England and New York only) are from Evans & O'Neill (1988), Evans & Lin (1959), and this study. No northeastern records exist for *ventilabris*, which is represented here by an estimated range based in part on a small number of western prey records (dotted line). Sample sizes are 378 (*politus*), 34 (*bilunatus*), 209 (*lepidus*), 203 (*gibbosus*), 233 (*solivagus*) and 2937 (*sanbornii*). Most prey head widths are from our database for North American bees, but some are estimated from family-and-sex-specific regressions of species' mean head widths (our measurements) on body lengths (from the taxonomic literature).

summer period is less diverse than the early-summer period.

In many respects *Philanthus* species are the insect equivalents of bird-eating hawks, which were used by Schoener (1984) in a biogeographical test for competitive exclusion. There is a strong correlation between the sizes of hawks and the average sizes of their prey (Schoener 1968), and sympatric hawk species tend to be more different in size than would be expected if communities were assembled at random from the world-wide species pool. In *Philanthus* it is feasible to look in detail at the prey actually taken by each member of a sympatric association, as was done by O'Neill & Evans (1982) at a site where four species are active at the same time of year. We have not studied prey utilization in the other *Philanthus* that occur at our site, but figure 11 shows head-width distributions of the prey so far recorded for all seven New England species. Although the data are very limited, they show three potentially interesting patterns.

First, the species cover the full range of potential sizes; few North American *Philanthus* are smaller than *politus* or larger than *sanbornii*. Second, species active at the same time of year tend to be more different in size than might be expected; this is clearest for the three early-season species (*politus*, *gibbosus*, and *sanbornii*). Third, there is more variation in maximum prey size than there is in minimum prey size; large *Philanthus* take prey that smaller species presumably cannot take, and they also take many or most of the prey taken by their smaller congeners. This last observation suggests that sympatric *Philanthus* species should tend to be involved in densely connected, 'rigid-circuit' food webs (see Cohen 1978; Cohen *et al.* 1990; Pimm 1991). For all pairwise comparisons among the six species with New England prey records, the mean proportion of shared prey in the shorter of the two lists is 0.6

Table 8. *Family-level summary of prey taken by North American* Philanthus *species*

(The prey families are Ichneumonidae, Scelionidae, Chrysididae, Tiphiidae, Mutillidae, Pompilidae, Vespidae, Formicidae, Sphecidae, Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae, Anthophoridae, Apidae. Prey records are from Evans & O'Neill (1988) and this study. Female mean head widths are unpublished data of J.S. and J.W.S.)

	HW	ICH	SCE	CHR	TIP	MUT	POM	VES	FOR	SPH	COL	AND	HAL	MEL	MEG	ANT	API
zebratus group																	
basilaris	3.72	+			+		+	+	+	++	++	+	++		+	++	+
zebratus	3.76	++					+	++		++	++	++	++		++	+	+
sanbornii	4.14			+	+			++		++	+	+++	+++	+	++	++	++
bicinctus	5.65									++		+			++	+	+++
gibbosus group																	
multimaculatus	2.70									+			+++				
gibbosus	3.31									+	+	+	+++				
crabroniformis	3.40									+	+	+	+++		+		
inversus	3.60										+		+++				
barbatus	4.26				+			+		+		+	+++				
pacificus group																	
pacificus	2.62	+[a]		+				+		++	+	++	+++				
pulcher	2.74	+	+	++				+		++	++	++	+++		++	+	
barbiger	3.05	++[b]			+			+		++	+	+	+++			+	
politus group																	
parkeri	2.04									+		+++	++				
psyche	2.32	++[a]		++		+	+			++	+	+++	+++				
serrulatae	2.42					+				+		++	+++				
politus	2.66									+	++	++	+++				
albopilosus	3.32	+						+		++	++	+	+++	+	+		
ventilabris	3.87				+			+		+	+	+	+++				
other																	
bilunatus	2.78										+	+	+++				
lepidus	3.03											+	+++				
solivagus	3.78							+		++	++	++	+++			+	

+ Present but unimportant (less than 2% of items and low diversity).

+ + Moderate importance and/or diversity.

+ + + Major to overwhelming importance in the diet, and high diversity relative to sample size.

[a] Ichneumonidae + Braconidae.

[b] Ichneumonidae + Braconidae + Perilampidae.

(range: 0.3–0.9), even though some species are active at different times of year and the data come from various sites in different years.

Not all North American *Philanthus* communities appear to be as broadly connected as those in New England, but caution should be used in interpreting apparent prey specificities from limited data. A species may appear to hunt differently at different sites (O'Neill & Evans 1982; Evans & O'Neill 1988), or even in different years at the same site (*P. sanbornii*). Thus much of the apparent variation in prey specificity and diversity among North American *Philanthus* probably reflects simple size restrictions and sampling error rather than genuine taxonomic preferences. Nonetheless, a family-level comparison of prey records for all North American species studied to date reveals some interesting patterns (table 8). Most species take a variety of different families and can plausibly be characterized as opportunistic generalists. The importance of halictid bees for most species is hardly surprising as these are among the most common small to middle-sized bees almost everywhere in temperate North America. However, long-tongued bees (Melittidae, Megachilidae, Anthophoridae, and Apidae) appear to be under-represented in the diets of most species except those in the *zebratus* species group (which includes *P. sanbornii*) and *P. pulcher* in the *pacificus* group. Most long-tongued bees are large, as are members of the *zebratus* group, so to some extent this pattern would be expected on the null hypothesis that *Philanthus* species do not discriminate taxonomically among bee and wasp flower visitors. There are, however, many megachilids and anthophorids of small to moderate size, and *P. pulcher* (itself a small species) takes them at significant rates (5.8% in a sample of 588 prey).

The relative scarcity of long-tongued bees can be subjected to an approximate statistical test for the better-studied New England species. From the frequencies of small long-tongued bees in the *P. sanbornii* prey sample and in the reference sample, we estimate that long-tongued bees of suitable size comprise at least 1.5–2% of the prey potentially available to *gibbosus* and *solivagus* (both of which are larger than *pulcher*). This suggests that seven to nine long-tongued bees should have been found among the 453 prey recorded for *gibbosus* and *solivagus*, but in fact there is only one such item. This outcome is significantly unlikely on the null hypothesis of taxonomically random sampling (p roughly 0.01–0.001). Thus it would appear that long-tongued bees are for some reason less attractive than short-tongued bees to most species outside of the *zebratus* group. Another interesting pattern is that sphecid wasps occur almost as regularly, although never as abundantly, as do short-tongued bees among the prey recorded for most species.

The picture that emerges, especially for New England, is one in which opportunistic generalist predators take almost any flower-visiting bee or wasp of suitable size, with certain broad but mild taxonomic biases. However, there are a few cases of conspicuous underutilization of particular prey taxa. For example, *Ceratina* is far more common in the reference collection than it is among the prey of *P. sanbornii*, and it has not been reported as prey for any other New England *Philanthus*. This is puzzling because *Ceratina* is common throughout the summer and is about the same size as *Halictus confusus*, which is taken by almost all *Philanthus* species. *Ceratina* may be better defended structurally than most bees, and there is evidence that it produces defensive chemicals (J. H. Cane 1986, and personal communication). Also puzzling is the scarcity of honeybees among the prey of *P. sanbornii* at our site. Honeybees were introduced in colonial times and have been spectacularly successful in New England. In Littleton they are abundant by the middle of June and extremely so by the end of July, when their biomass may well exceed that of all native bees combined. Why does *P. sanbornii* not take more of them? Is *Apis* defended in some way that presents difficulty for the 'naive' American wasp? If so, the other populations discussed above may have overcome this difficulty (Evans 1955; Kurczewski & Miller 1983), although there are too few prey records to support any strong conclusions. In any case, we are witnessing an unplanned experiment in evolutionary ecology. Will *Apis* eventually come to comprise a much larger fraction of the prey taken by *P. sanbornii*? The Afro-European *P. triangulum* is almost exactly the same size as *sanbornii*, and it takes honeybees exclusively.

Almost all prey species tend to be nonrandomly aggregated among cells within nests, and among nests within years. This suggests that females develop the habit of returning again and again to the same location, as long as they continue to have success there. This foraging strategy has been documented in other kinds of animals, especially birds (see, for example, Royama (1970); Grundel (1990)), and is reminiscent of the 'win–stay, lose-shift' strategy often seen in animal learning experiments (e.g. MacIntosh 1974). But we are not aware that anyone has yet considered its possible effects on the dynamics of the prey species. In the early 1980s, the Littleton *P. sanbornii* population could have taken as many as 20000 bees from a fairly circumscribed area over a period of only four weeks, and the smaller *Philanthus* species would have augmented this toll at the smaller end of the size range. It seems possible that these predators could significantly affect the dynamics of some of their prey species. If so, the patchiness of their hunting might be important. For example, if social bees tend to forage on plants near their nests, then some colonies are likely to suffer much heavier predation than others, depending on which colonies are accidentally discovered by hunting *Philanthus* females.

(*d*) ***Flowers, bees, and beewolves***

This study together with the cumulative results of many others allows us to begin to formulate a general picture of the community ecology of flower–bee–*Philanthus* systems that might serve as a framework for further research. Opportunism is a major feature at each trophic level. Many plants are opportunistic generalists that can be pollinated by wide diversity of bees; many bees forage opportunistically on an even greater diversity of plants; and most *Philanthus* species are willing to take virtually any bee or wasp they may encounter. Why should all these species show so little discrimination? One obvious benefit is the predictability to be realized by depending on a diverse suite of species rather than on only a few, any one of which may be highly unreliable as a resource; to the degree that the fluctuations of a set of species are independent, their average abundances will vary far less than the abundance of any one component species. There are many factors that might tend to make species abundances roughly independent of each other. These include intrinsic population dynamics of a chaotic character, local outbreaks of disease or parasites that affect different sets of species, and differential success in local patches, with consequent differences in rates of movement between patches.

That there are advantages in depending on a diverse resource base is not a new idea, but the received view of flower–pollinator interactions strongly emphasizes the subset of highly coevolved systems that attract our attention because they are so wondrously complex and peculiar. These specialized relationships between plants and bees certainly deserve the intensive study they have received, but they are not typical. At least in temperate North America, most flowers are available to, and used by, a broad spectrum of visitors. There are some plants with restricted sets of visitors, and some bees that visit restricted sets of plants, but neither the plants nor the bees are thereby ecologically isolated. For example, two species in the prey list (*Dufourea novaeangliae* and *Melissodes apicata*) are restricted to *Pontederia cordata*, a locally common aquatic plant that produces dense spikes of small flowers. But while *Pontederia* supports these two specialists, it also attracts many generalists. Similar patterns have been documented in extensive surveys of bees visiting *Larrea* (Hurd & Linsley 1975) and *Helianthus* (Hurd *et al.* 1980), two widespread genera that attract large and diverse sets of bee species. Each of these plants supports a relatively small set of highly specialized foragers and a substantially larger set of more generalized foragers that harvest pollen from several to many other plant species. At the next trophic level, coexisting secondary consumers such as *Philanthus* prey on broadly overlapping sets of primary consumers. Thus the entire system is one in which most of the actors are connected to many others through their interactions with adjacent trophic levels.

Although many bees ‘cheat’ plants by taking nectar or pollen without acting as pollinators, and some plants ‘manipulate’ their pollinators, the basis of the overall relationship between bees and plants remains mutualistic because both parties stand to benefit from interaction. Indeed, the beauty of flowers is a direct consequence of competition among plants for pollinators. In contrast, the interaction between plants and herbivores is qualitatively different; it readily gives rise to escalating warfare because any gain by one party necessarily entails a loss by the other.

Ecological communities based on the two modes of interaction are likely to be very different as well. For example, different plant structures such as stems, leaves, and seeds are typically exploited by very different means, and herbivores often require specific adaptations to overcome particular plant defensive strategies. For both sides, the outcome tends to favour specialization. Similarly, plants tend to hide from herbivores (not advertise to them), and this offers scope for specialization on both sides as specific adaptations may be required to locate a suitable host plant. Perhaps not surprisingly, phytophagous insects are extremely diverse, with at least one-third of a million species (Strong *et al.* 1984). The specialization of phytophagous insects is paralleled by that of their predators and parasites, whose diversity is also very great. Thus a typical phytophagous insect appears to be specialized to a particular anatomical part of a restricted set of plants, and is likely to be victimized by a restricted set of similarly specialized predators and parasites. This is in striking contrast to a typical bee, which is likely to visit a diverse suite of plants, and to be victimized by opportunistic generalist predators and parasites. Although it is relatively easy for a bee to become specialized on a particular plant, it is much harder for a plant to become specialized on one or a few bees, since most improvements in floral value for one bee are likely to be improvements for other bees as well.

The number of *Philanthus* species that can coexist in any given region may well be limited by their tendency to have similar diets that include many of the same species. The bee-hunting Philanthini (*Philanthus* + *Trachypus*) are much less diverse than the closely related beetle-hunting Cercerini (*Cerceris* + *Eucerceris*). For the eastern U.S. we estimate that there are eight species in the first group (P + T) and 29 species in the second (C + E); the corresponding numbers for all of North America, Central America and the Carribean are 37 and 178. This difference in diversity of these otherwise similar predators may reflect differences in the ecologies of their prey taxa. Beetles occupy a wide variety of niches. By hunting one kind of beetle, a predator is inevitably pulled away from others. Species of *Cerceris* and *Eucerceris* should therefore tend to specialize along a number of different niche dimensions, and this diversity of opportunities for specialization should permit the coexistence of many species, each exhibiting a relatively low level of prey diversity. In fact, many species of *Cerceris* and *Eucerceris* prey on only one or two genera of beetles (Scullen & Wold 1969). But all bees must visit flowers, and most are generalists. At least with respect to their foraging they occupy a relatively limited number of distinct niches, and a predator on any one is inevitably brought into contact with many others. Thus despite their diversity and abundance, bees may constitute a relatively homogeneous and unitary resource that is not easily divisible along niche dimensions other than phenology and size.

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APPENDIX 1

Prey species (1978–83) with codes, abundances, and mean head widths

(n_T = total number of items; n_F = number of females; n_M = number of males; HW = mean head width (in millimetres); s.d. = standard deviation of HW.)

				n_T	n_F	HW	s.d.	n_M	HW	s.d.
STR	Odnt	pleb	*Odontomyia plebeja* Loew	3				3	3.28	0.126
CHR	Hedy	conf	*Hedychrum confusum* du Buysson	1	1	2.15				
TIP	Myzi	macu	*Myzinum maculatum* (Fabricius)	6				6	2.12	0.104
		quin	*Myzinum quinquecinctum* (Fabricius)	1				1	2.75	
VES	Panc	pdst	*Parancistrocerus pedestris* (Saussure)	8	5	2.31	0.075	3	2.15	0.150
		pens	*Parancistrocerus pensylvanicus* (Saussure)	4	4	2.22	0.144			
	Euod	fora	*Euodynerus foraminatus* (Saussure)	22	11	3.00	0.125	11	2.66	0.207
	Anci	antl	*Ancistrocerus antilope* (Panzer)	3	1			2		
		cats	*Ancistrocerus catskill* (Saussure)	1	1	2.90				
		unif	*Ancistrocerus unifasciatus* (Saussure)	3				3	2.63	0.058
	Symm	cana	*Symmorphus canadensis* (Saussure)	1	1					
	Zeth	spin	*Zethus spinipes* Say	1				1	3.65	
	Vesp	cons	*Vespula consobrina* (Sladen)	1	1	3.70				
SPH	Asta	leut	*Astata leuthstromi* Ashmead	1				1	3.25	
		unic	*Astata unicolor* Cresson	3	1	3.05		2	3.38	0.460
	Oxyb	subl	*Oxybelus subulatus* Robertson	1	1	2.45				
	Ecte	ceph	*Ectemnius cephalotes* (Olivier)	4	1	3.60		3	3.22	0.301
		cont	*Ectemnius continuus* (Fabricius)	25	9	3.32	0.180	16	2.88	0.327
		lapi	*Ectemnius lapidarius* (Panzer)	2	2	2.60	0.071			
		macl	*Ectemnius maculosus* (Gmelin)	11	3	3.30	0.283	8	2.51	0.175
	Lest	conf	*Lestica confluenta* (Say)	3				3	2.03	0.257
		prod	*Lestica producticollis* (Packard)	74	42	2.66	0.142	32	2.13	0.111
	Gory	atri	*Gorytes atricornis* Packard	6	6	2.52	0.140			
		simi	*Gorytes simillimus* Smith	1				1	2.65	
	Pspl	phal	*Pseudoplisus phaleratus* (Say)	1	1	2.40				
	Aphl	frig	*Aphilanthops frigidus* (Smith)	137	2	3.40	0.354	135	2.95	0.334
	Cerc	arel	*Cerceris arelate* Banks	9	2	2.55		7	2.49	0.080
		clyp	*Cerceris clypeata* Dahlbom	7	1	3.00		6	2.71	0.235
		comp	*Cerceris compar* Cresson	1				1	2.30	
		fumi	*Cerceris fumipennis* Say	2				2	2.63	0.106
COL	Coll	bank	*Colletes banksi* Swenk	3	1	2.95		2	2.80	
		lati	*Colletes latitarsis* Robertson	1				1	2.75	
		prod	*Colletes productus* Robertson	1	1	2.80				
	Hyla	mode	*Hylaeus modestus* Say	1	1	1.80				

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APPENDIX 1 (*contd.*)

				n_T	n_F	HW	s.d.	n_M	HW	s.d.
AND	Andr	brev	*Andrena brevipalpis* Cockerell	177	168	2.36	0.095	9	2.24	0.147
		cean	*Andrena ceanothi* Viereck	1	1	3.05				
		corn	*Andrena cornelli* Viereck	1				1	3.30	
		crat	*Andrena crataegi* Robertson	27	27	3.26	0.089			
		frag	*Andrena fragilis* Smith	20	13	2.60	0.097	7	2.47	0.212
		imit	*Andrena imitatrix* Cresson	5	5	2.60	0.127			
		kalm	*Andrena kalmiae* Atwood	1	1	2.80				
		mirn	*Andrena miranda* Smith	4	4	3.00	0.041			
		naso	*Andrena nasonii* Robertson	1	1	2.50				
		nigr	*Andrena nigrifrons* (Cresson)	4	4	2.72	0.189			
		niva	*Andrena nivalis* Smith	2	2	3.57	0.035			
		spir	*Andrena spiraeana* Robertson	154	152	2.80	0.099	2	2.55	
		thas	*Andrena thaspii* Graenicher	23	22	3.12	0.090	1	3.15	
		wilk	*Andrena wilkella* (Kirby)	263	246	3.44	0.107	17	2.94	0.205
HAL	Dufo	nova	*Dufourea novaeangliae* (Robertson)	5				5	1.75	0.035
	Agps	metl	*Augochlorposis metallica* (Fabricius)	23	23	2.55	0.119			
	Agra	pura	*Augochlora pura* (Say)	37	36	2.32	0.154	1	2.25	
	Agla	stri	*Augochlorella striata* (Provancher)	44	43	1.92	0.067	1		
	Agap	texa	*Agapostemon texanus* Cresson	4	3	2.82	0.058	1	2.45	
		virs	*Agapostemon virescens* (Fabricius)	33	33	2.93	0.093			
	Halt	conf	*Halictus confusus* Smith	631	626	2.02	0.081	5	1.87	0.076
		ligt	*Halictus ligatus* Say	398	376	2.60	0.148	22	2.19	0.106
		rubi	*Halictus rubicundus* (Christ)	257	245	2.70	0.133	12	2.49	0.124
	Laso	acum	*Lasioglossum acuminatum* McGinley	4	4	2.65	0.058			
		cori	*Lasioglossum coriaceum* (Smith)	159	159	2.66	0.078			
	Evyl	cinc	*Evylaeus cinctipes* (Provancher)	3	3	2.12	0.029			
		divg	*Evylaeus divergens* (Lovell)	1	1	1.60				
		foxi	*Evylaeus foxii* (Robertson)	2	2	1.63	0.035			
		pctn	*Evylaeus pectinatus* (Robertson)	1	1	2.05				
		pect	*Evylaeus pectoralis* (Smith)	4	4	1.89	0.063			
		queb	*Evylaeus quebecensis* (Crawford)	7	7	1.96	0.093			
	Dial	brun	*Dialictus bruneri* (Crawford)	4	4	2.15	0.108			
		coer	*Dialictus coeruleus* (Robertson)	28	26	1.84	0.088	2	1.75	0.000
		cres	*Dialictus cressonii* (Robertson)	92	92	1.83	0.080			
		line	*Dialictus lineatulus* (Crawford)	15	15	1.84	0.071			
		nigr	*Dialictus nigroviridis* (Graenicher)	62	60	2.01	0.080	2	1.70	0.000
		nymp	*Dialictus nymphaearum* (Robertson)	23	23	2.01	0.095			
		pilo	*Dialictus pilosus* (Smith)	11	11	1.71	0.092			
		rohw	*Dialictus rohweri* (Ellis)	19	19	1.79	0.093			
		vrsn	*Dialictus versans* (Lovell)	12	12	1.68	0.050			
		zeph	*Dialictus zephyrus* (Smith)	3	3	1.72	0.029			
		sp. 1	*Dialictus* (undetermined species 1)	5	5	1.71	0.042			
		sp. 2	*Dialictus* (undetermined species 2)	4	4	1.66	0.075			
		sp. 3	*Dialictus* (undetermined species 3)	12	12	1.77	0.078			
		sp. 4	*Dialictus* (undetermined species 4)	3				3	1.70	0.000
	Sphe	runc	*Sphecodes ranunculi* Robertson	2	2	2.45	0.071			
		styg	*Sphecodes stygius* Robertson	1	1	2.05				
MEL	Mlta	amer	*Melitta americana* (Smith)	5	5	3.04	0.131			
		mltd	*Melitta melittoides* (Viereck)	1	1	3.00				
MEG	Heri	cari	*Heriades carinata* Cresson	1	1	1.80				
	Hopl	cyli	*Hoplitis cylindrica* (Cresson)	1	1	2.90				
		prod	*Hoplitis producta* (Cresson)	11	11	2.15	0.135			
		trun	*Hoplitis truncata* (Cresson)	1	1	2.75				
	Osmi	atrv	*Osmia atriventris* Cresson	4	4	2.67	0.119			
		crls	*Osmia coerulescens* (Linnaeus)	2				2	2.90	0.424
		dist	*Osmia distincta* Cresson	3	3	3.00	0.000			
		pumi	*Osmia pumila* Cresson	2	2	2.60	0.071			
	Mega	brev	*Megachile brevis* Say	7	5	3.51	0.119	2	3.22	0.389
		cent	*Megachile centuncularis* (Linnaeus)	1				1	3.40	
		gemu	*Megachile gemula* Cresson	2				2	3.78	0.177
		mend	*Megachile mendica* Cresson	25	14	3.84	0.279	11	3.53	0.228
		mont	*Megachile montivaga* Cresson	1	1	3.70				
		relt	*Megachile relativa* Cresson	15	14	3.23	0.097	1	2.80	
	Chal	camp	*Chalicodoma campanulae* (Robertson)	3	1	2.90		2	2.93	0.035
	Coel	octo	*Coelioxys octodentata* Say	1				1	3.15	
		sayi	*Coelioxys sayi* Robertson	1	1	2.95				

APPENDIX 1 (*contd.*)

ANT	Epeo	bifa	*Epeolus bifasciatus* Cresson	2	2	2.43	0.035			
	Noma	cune	*Nomada cuneata* (Robertson)	5	5	2.27	0.241			
		depr	*Nomada depressa* Cresson	3	3	2.28	0.029			
		pygm	*Nomada pygmaea* Cresson	7	5	2.05	0.141	2	2.07	0.035
	Meli	apic	*Melissodes apicata* Lovell & Cockerell	25	3	3.68	0.076	22	3.36	0.119
	Cera	cadu[a]	*Ceratina calcarata* Robertson or *dupla* Say	8	8	2.07	0.120			
API	Bomb	vaga	*Bombus vagans* Smith	1	1	2.75				
	Apis	melf	*Apis mellifera* Linnaeus	59	59	3.78	0.109			

[a] Females of *Ceratina calcarata* and *C. dupla* cannot be distinguished reliably, so they are lumped into the synthetic species 'cadu'.

APPENDIX 2

Comparison of prey and reference samples

(Number of individuals, per cent of the sample, and sex ratio (as per cent males) are given for families and for selected genera in the prey and reference samples. Where some minor genera have been deleted, numbers in parentheses following the family name give the number of genera in the prey sample, the number in the reference sample, and the number in both combined. Diptera and non-aculeate Hymenoptera have been eliminated, as have two minor families that occur in only one sample (melittid bees with six items in one genus in the prey sample, and pompilid wasps with four items in two genera in the reference sample). We consciously avoided honeybees; their true relative abundance is far greater than indicated by the reference sample. Bumblebees may also be underrepresented. The reference sample is restricted to dates between 17 June and 25 July, when *P. sanbornii* females are actively hunting. Few females live beyond 25 July, and at about that time a distinctive late-summer bee fauna begins to appear, mainly on *Solidago* which is just beginning to bloom. Some social bees begin to produce large numbers of males in late July and early August, so the inclusion of late collections could bias their sex ratios and relative abundances.)

family	*n*		% of sample		% males	
Genus	prey	ref	prey	ref	prey	ref
Chrysididae (1, 4, 4)	1	12	0.03	0.32	0	17
Tiphiidae	7	27	0.22	0.72	100	100
Myzinum	7	27	0.22	0.72	100	100
Vespidae (6, 10, 12)	44	64	1.40	1.71	45	36
Parancistrocerus	12	26	0.38	0.69	25	50
Euodynerus	22	4	0.70	0.11	50	0
Ancistrocerus	7	10	0.22	0.27	71	20
Sphecidae (8, 26, 27)	288	342	9.18	9.12	75	73
Ectemnius	42	9	1.34	0.24	64	44
Lestica	77	14	2.46	0.37	45	57
Philanthus		98		2.61		77
Aphilanthops	137		4.37		99	
Cerceris	19	69	0.61	1.84	84	84
Colletidae	6	167	0.19	4.45	50	22
Colletes	5	3	0.16	0.08	60	67
Hylaeus	1	164	0.03	4.37	0	21
Andrenidae	683	841	21.79	22.41	5	8
Andrena	683	807	21.79	21.51	5	7
Calliopsis		33		0.88		36
Perdita		1		0.03		100
Halictidae	1909	1548	60.89	41.26	3	5
Dufourea	5	15	0.16	0.40	100	80
Augochloropsis	23	5	0.73	0.13	0	0
Augochlora	37	1	1.18	0.03	3	0
Augochlorella	44	48	1.40	1.28	2	2
Agapostemon	37	23	1.18	0.16	3	4
Halictus	1286	1118	41.02	29.80	3	3

APPENDIX 2 (*cont.*)

family *Genus*	*n* prey	 ref	% of sample prey	 ref	% males prey	 ref
Halictidae (*cont.*)						
Lasioglossum	163	25	5.20	0.67	0	0
Evylaeus	18	41	0.57	1.09	0	29
Dialictus	293	250	9.35	6.66	2	4
Sphecodes	3	22	0.10	0.59	0	50
Megachilidae	81	308	2.58	8.21	27	17
Anthidiellum		9		0.24		22
Heriades	1	69	0.03	1.84	0	28
Hoplitis	13	32	0.41	0.85	0	0
Osmia	11	18	0.35	0.48	18	0
Megachile	51	131	1.63	3.49	33	17
Chalicodoma	3	37	0.10	0.99	67	11
Coelioxys	2	12	0.06	0.32	50	42
Anthophoridae (4, 6, 6)	50	247	1.59	6.58	48	11
Nomada	15	21	0.48	0.56	13	38
Melissodes	25	2	0.80	0.05	88	100
Ceratina	8	216	0.26	5.76	0	7
Apidae	60	192	1.19	5.12	0	5
Bombus	1	102	0.03	2.72	0	8
Psithyrus		3		0.08		67
Apis	59	87	1.88	2.32	0	0
	3135	3752	100.00	100.00		