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BEHAVIOR AND PHENOLOGY OF A SPECIALIST BEE (*DIEUNOMIA*) AND SUNFLOWER (*HELIANTHUS*) POLLEN AVAILABILITY¹

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Abstract. The phenological relationships between nesting behavior of a specialist, solitary bee, *Dieunomia triangulifera*, and the flowering of its primary pollen source, *Helianthus annuus*, were studied for 3 yr at a site in northeastern Kansas, which contained between 50 000 and >150 000 nests. Activity patterns of *D. triangulifera* are closely synchronized with pollen availability on nearby sunflower plants in three ways: (1) each year, *D. triangulifera* became active within days of the beginning of the local sunflower bloom, and the emergence schedule of the entire population at the nest site was timed such that all females had constructed nests and were collecting pollen at peak bloom; (2) over a season the greatest numbers of provisioning females were active at peak bloom, when pollen was most abundant; and (3) over the day, females made more trips, each of which took less time when pollen was most abundant on nearby flowers than when it was scarce. Between seasons, female reproductive success varied positively with the availability of *H. annuus* pollen. When pollen was abundant, and the population at the nest site was low, ≈ 3 times more cells were provisioned than the following year when the bee population was high and pollen abundance declined. Furthermore, 20 pollen-collecting bee species (10 specialists and 10 generalists), besides *D. triangulifera*, used an estimated 68% of the available sunflower pollen at this site. These data suggest that resource limitation is important in shaping patterns of provisioning behavior in *D. triangulifera*. Other behaviors presumably related to reproductive success were variable and suggest resources were not limiting: (1) all females did not forage on each day, even at peak bloom; (2) variance in both trip durations and the numbers of trips made per day was large; and (3) females produced far fewer eggs in their lifetime than apparently possible. We suggest that the apparently conflicting evidence for resource limitation may be explained by a physiological limit on the rate of egg production; in such a case, the effects of resource limitation, while clearly important, might not be the primary factor limiting reproductive output.

Female *D. triangulifera* benefit by being synchronized with their resource. Daily and seasonal synchrony enable females to collect a greater amount of pollen during shorter foraging trips. This translates into higher mean reproductive success and, at the population level, allows more females to be supported by the pollen produced from nearby plants. In short, those females that are synchronized with the sunflower bloom effectively increase their own resource availability. This phenomenon may be general, especially in short-lived organisms, i.e., the evolution of specialization may be associated with fitness benefits based on synchrony with a preferred food source.

Key words: *Asteraceae*; *demography*; *Halictidae*; *Helianthus annuus*; *Hymenoptera*; *oligolecty*; *phenology*; *plant–pollinator interactions*; *resource limitation*; *resource specialization*; *solitary bees*.

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INTRODUCTION

More than 16 000 species of bees collect nectar and pollen or oil, and several thousand others are parasites (e.g., Linsley 1958). Among the pollen collectors, specificity ranges from bees that collect pollen from plants of a single species (monolecty) to others that collect it from plants of a narrow range of closely related species

or genera (oligolecty), to still others that visit a wide variety of plants (polylecty) (e.g., Robertson 1928, Linsley and MacSwain 1957, 1958, Engel and Dingeman-Bakels 1980, Westrich and Schmidt 1987). Many monolectic and oligolectic bees have special morphological features that correspond to peculiar morphologies of the plants from which they collect pollen (Linsley 1958, Thorp 1979), nectar (Laroca et al. 1989) or oil (Vogel 1974, Neff and Simpson 1981, Buchmann 1987, Steiner and Whitehead 1988). Modified floral morphologies are thought to restrict the array of pollinators that visit the flower, thereby increasing pollinator fidelity (Stebbins 1970, Feinsinger 1983). Other specialist bees visit plants with relatively generalized floral morphologies and are often not or little modified for their host plant. Such plant species, including creosote bush (*Larrea*; Hurd and Linsley 1975), mesquite (*Prosopis* spp.; Simpson et al. 1977), *Tamarix* spp., and various members of the Asteraceae, can attract many species of both generalist and specialist bees.

Evolutionary advantages of pollen specialization in bees are inadequately understood. The relative role of resource limitation as a factor promoting the evolution of oligolecty has been debated since early in this century. Robertson (1914, 1925) contended that pollen was often limiting and that specialists were better competitors for the available pollen than were generalists. Lovell (1913), in contrast, contended that pollen was rarely limiting and that pollen specialists were able to provision more cells than generalists. Both authors seem to have agreed that specialists collect more pollen per foraging effort, which has since been demonstrated experimentally (Strickler 1979, Cane and Payne 1988, Laverty and Plowright 1988). Robertson (1914, 1924, 1925, 1929, and references therein) also discussed other features pertaining to oligolectic bees that have been little studied since, including the importance of synchrony between the active period of the bees and the flowering period of the plants. Synchrony in ecological relationships has been discussed in other contexts (Thompson and Willson 1979, Price 1980, Wcislo 1987, Bailey and Ridsell-Smith 1991), and numerous studies demonstrate that asynchrony reduces fitness.

We investigated the possible factors involved in the maintenance of pollen specialization on annual sunflower, *Helianthus annuus* L. (Asteraceae), by a solitary, oligolectic halictid bee, *Dieunomia* (*Epinomia*) *triangulifera* (Vachal). Over 280 pollen-collecting bees visit the annual sunflower in the United States; of these, 131 species (49%) are reportedly oligolectic (Hurd et al. 1980). Its open discs allow almost any insect visitor to be an effective pollinator, whether foraging for nectar or pollen (e.g., Neff and Simpson 1990, 1991) or pouncing on potential mates (Parker 1981), and most of the bees specializing on this plant lack obvious morphological modifications associated with foraging on this plant. Our study investigated: (1) the relationship of *H. annuus* pollen availability to *D. triangulifera* re-

productive success and population size; (2) the potential importance of resource limitation; and (3) diel, seasonal, and yearly synchronization between bee activity and pollen presentation. We then discuss the possible evolutionary importance of synchrony to specialization by *D. triangulifera*.

MATERIALS AND METHODS

Study site

Dieunomia triangulifera nests were in large aggregations on a farm on a floodplain of the Kansas River near Eudora (Douglas County), Kansas (38°57'30" N, 95°7'30" W). In the fields crop plants [corn (*Zea mays*), soy beans (*Glycine max*), and alfalfa (*Medicago sativa*)] were grown, or fields were left fallow. *D. triangulifera* have been nesting at this site at least since 1972 (Mr. Gregory Shipe, *personal communication*), and at least one of us has worked there since 1984. Bees nested both in bare open fields and between rows of crops that were short or not densely planted. Consequently, the precise location on the farm of the bee aggregation varied from year-to-year, depending on land use patterns.

Helianthus annuus

H. annuus is an early successional, herbaceous, self-incompatible annual common in agricultural areas and roadsides throughout its range in the United States and México. It is native to North America, and probably was distributed widely by people as a "weedy camp species" (Heiser 1976), though its present abundance is probably much higher than in the past, due to disturbance. The apparent flower (or capitulum) is composed of 50–400 individual disk florets surrounded on the periphery by conspicuous, elongate, yellow, sterile, ray florets (McGregor 1976). Individual florets are functionally monoecious due to strong protandry, and the male phase typically lasts 1 d (Putt 1940). Nectar secretion occurs only in the male phase (Neff and Simpson 1990). Plants begin growing in May and usually are several metres tall by early August, when they begin flowering in our area. Peak bloom is ≈ 2 wk after initial bloom, and capitula of isolated plants sometimes bloom as late as October or early November. *H. annuus* produces large quantities of pollen and nectar (≈ 60 mg of sugar per capitulum [Neff and Simpson 1990]).

Dieunomia triangulifera

Throughout its range (mainly west of the Mississippi River in the Great Plains, from Minnesota to Utah and southern New Mexico [Cross 1958]) *D. triangulifera* (hereafter referred to as *Dieunomia*) is a primary oligolecte (sensu Hurd et al. 1980) on yellow composites (Asteraceae) in the sunflower genus *Helianthus*. Pollen is carried primarily on the hind legs and metasomal (abdominal) sterna and is collected by tapping the heads of the disc flowers with the ventral surface of the meta-

soma. Based on examination of pollen loads and field observations, other composites (e.g., *Heterotheca*) were not visited by *Dieunomia* for pollen. Voucher specimens of all bees (and associated parasites) are deposited in the Snow Entomological Museum, University of Kansas.

Emergence phenology

Information on patterns of *Dieunomia* emergence phenology was obtained in 1988 by making 20 sweep samples through the nest site each day and tallying the percentages of male and female bees caught. More precise emergence data were obtained in 1989–1991 by placing three 0.9×0.3 m and one 1×1 m emergence traps over areas where bees nested the previous year. Traps were usually checked daily, and the numbers and sexes of emerging bees and parasites counted.

Nest establishment and longevity

Phenology of nest establishment was determined by randomly establishing 1-m^2 "longevity quadrats" throughout the nesting site ($n = 16$, 1988; $n = 17$, 1989; $n = 14$, 1990). Each day, or rarely once in several days, new nests were individually marked by placing color-coded tags in the soil next to each nest. To estimate nest longevity in 1988 and 1989, we noted during each visit whether nests tagged on earlier days were still active. Open burrows with mounds (tumuli) were considered active and closed burrows without mounds were inactive. Although females typically fill in the burrow entrance when they leave to forage, and some females may spend an entire day inactive within a closed nest, subsequent observations revealed such occurrences.

More precise estimates of nest longevity and other parameters were obtained in 1990 by direct observation of a 2-m^2 plot containing 63 marked nests, hereafter referred to as the Observation Plot. Detailed records of activity within this plot were made on 26, 28, 31 August and 2, 5, 7, 10, 12, and 15 September, and longevity was measured as the interval between the first and last time a female was seen in a nest.

We assume that females only excavate a single nest in their lifetime, though females were not marked. There was little discrepancy between numbers of females emerging and numbers of nests initiated in the quadrats, though some females may have dug second nests when they were unable to relocate their first nest. Individuals do not appear to skip poor seasons by remaining as inactive prepupae or adults underground, as do some other bees (e.g., Rust 1987). At the end of the 1989 season, the driest year, we excavated below the emergence traps (where bees nested in 1988 but not 1989) and found no living stages of bees.

Unless stated otherwise data are presented as means ± 1 SE.

Dieunomia population size

In 1988 the total female population size was esti-

mated by extrapolating from nest densities in "longevity quadrats" to the area covered by nesting bees. We obtained more precise estimates of population size by censusing 79 (2 September 1989) or 96 (3 September 1990) 1-m^2 quadrats taken every five paces along a transect over the entire nesting site.

Nest excavations

We obtained estimates of the numbers of cells provisioned per nest from nest excavations made of entire 1-m^2 quadrat plots where the numbers of nests were known (see *Nest establishment and longevity* above). We excavated three quadrats in both 1988 and 1989, and two in 1990, and from these we recorded the total numbers of cells and their contents in each plot. This method gives a realistic estimate of average productivity (numbers of cells per nest) because it includes nests that fail (published estimates often exclude failed nests, inflating productivity), but it does not permit us to associate cells with specific nests and obtain estimates of the variance in productivity. Cells could not be associated with individual nests because of the close proximity of nest tunnels.

Diel activity of bees

Limited observations of provisioning by individual bees were made in 1988 and 1989. In 1990, on 7 d (with two additional days of less complete observations) we monitored all observable activity in the Observation Plot and recorded provisioning trip duration (in minutes) and whether the bees returned with or without pollen. On 1 d near peak bloom (5 September 1990) we watched the Observation Plot for an entire day (0650 to 1930), and recorded all provisioning activity. For the analysis of trip durations, time intervals used were 15 min, or a group of however many such intervals was required to attain a minimum sample size of five trips per interval. Invariably a single female resident occupied a given marked nest, allowing for individual-level analyses. Times of day are reported as Central Daylight Time.

Numbers of pollen grains per foraging trip

To determine the amounts of pollen carried by females, we collected a total of 38 individuals throughout the season as they returned to their nests. Returning foragers were delayed by plugging the nest entrances with loose soil and captured in clean glass vials (without noticeable loss of pollen). Subsequently we added 70% ethanol to the vial with the bee. Pollen grains were individually counted in the laboratory (see *Pollen analysis* below).

Numbers/types of pollen grains per larval cell

The number of pollen grains used to produce offspring was determined by three methods. In the first method, we excavated intact pollen balls and eggs, re-

moved the egg and any soil particles, and then dried and weighed the pollen ball. We then calculated the relationship between dry mass and number of pollen grains, by counting the pollen grains in a single subsample from each of 10 of these pollen balls. This yielded a linear regression of $y = 6042 + 36\,512x$ (y = pollen count and x = dry mass in milligrams; $r = 0.98$), which was used as our conversion factor for all analyses. In the second method, complete pollen counts were made of six provision masses. In the third method we counted all of the pollen grains from 10 complete fecal deposits of natal cells. Bee larvae defecate the entire larval provision into their natal cell just before eclosion and the outer pollen shell (exine) passes intact. All samples were prepared as described by O'Rourke and Buchmann (1991). Adult *Dieunomia* females are larger than males on average (Wcislo et al. 1992), but may or may not be reared on larger pollen balls; in this paper we pooled pollen provision counts for both sexes.

Other sunflower bees

Females of numerous bee species collect or feed on pollen or nectar from sunflowers in our area; males also visit the plants to feed and search for females. To determine the relative abundance of these bees near the *Dieunomia* nest site, on 3 d bracketing peak flowering (26 August, 2 and 8 September 1990), we collected all bees landing on sunflowers during a 15-min period for nearly every hour of flight activity ($n = 25$ collections; see Hurd et al. 1980). We collected at a large ($\approx 300\text{ m}^2$) patch of sunflowers, $\approx 2\text{ km}$ southeast of the aggregation. On 2 September, we also made hourly 15-min collections at a smaller ($\approx 20\text{ m}^2$) patch of sunflowers 500 m northwest of the aggregation ($n = 5$ collections). Estimates of the seasonal flight periods of all the represented nonparasitic bee species (see Fig. 12) are based on label data associated with specimens from northeastern Kansas in the Snow Entomological Museum, University of Kansas.

Diel flowering phenology

Changes in pollen availability over the course of the day were estimated on 8 and 12 September 1990 from hourly collections of 25 florets from five capitula. Each floret was detached with dissecting forceps and quickly dipped three times into a clean vial filled with 70% ethanol to remove pollen, and pollen grains were counted (see *Pollen analysis* below).

Seasonal flowering phenology

The phenology of newly opened capitula was determined from 15 individually marked plants in 1988 that we checked usually every 3rd d. To determine how long individual heads remained open, we chose two plants and placed uniquely marked tags on all newly open heads each day. Total number of capitula produced per plant was counted on all plants after flow-

ering was complete ($n = 15, 20,$ and 22 capitula per plant in 1988, 1989, and 1990, respectively). In 1989 and 1990 we noted the first and last dates capitula were open and then assumed the shape of the flowering phenology curve to be the same as for 1988.

Seasonal resource availability

We measured total pollen production in 1988 by counting every sunflower plant growing in an area of 0.5 km radius from the nest site, excluding the area north of the Kansas river. We categorized the relative densities within plant patches as "sparse," "intermediate," and "dense," and then calculated an average density for each category by dividing total number of plants by total area, yielding the following values: "sparse" (0.067 plants/m²), "intermediate" (0.164 plants/m²), and "dense" (0.26 plants/m²). Plant populations between 0.5 and 1.5 km radii were estimated by mapping the areas and categorizing the densities of sunflower patches, then multiplying each mapped area by its estimated density. In 1989 and 1990 we censused all sunflower patches for a 2.5 km radius in a similar manner. Total seasonal pollen production was calculated as: pollen/unit area = (pollen/floret) \times (florets/capitulum) \times (capitula/plant) \times (plants/square kilometre).

Minimum daily foraging area

The size of the active female bee population varied through the season. Therefore, we estimated the number of active females for each day of the season by dividing the numbers of nests that were established in our quadrats the previous 13 d (see *Results: Seasonal provisioning activity and longevity* below) by total nests active in the quadrats over the season (giving the proportion of the population active at that time) and multiplying by the total numbers of nests at the nest site. We then multiplied this value by the amount of pollen collected per female per day, giving an estimate of the daily pollen requirements of the entire population.

Pollen analysis

Pollen from pollen-laden females in alcohol was removed and dispersed with 60-s exposure to a sonicator micro-tip (Ultrasonics model W-220F). Pollen ball/fecal samples examined microscopically appeared to consist exclusively of *H. annuus* pollen. Sunflower pollen grains measure 26.5 μm in equatorial diameter (Buchmann and O'Rourke 1991, O'Rourke and Buchmann 1991). Accordingly, pollen grains within a size range of 20–50 μm diameter were counted and scored as *H. annuus* pollen, although some other composites fall within this range. Pollen grains were counted by a HIAC-ROYCO model PS-320 particle size analyzer (Pacific Scientific).

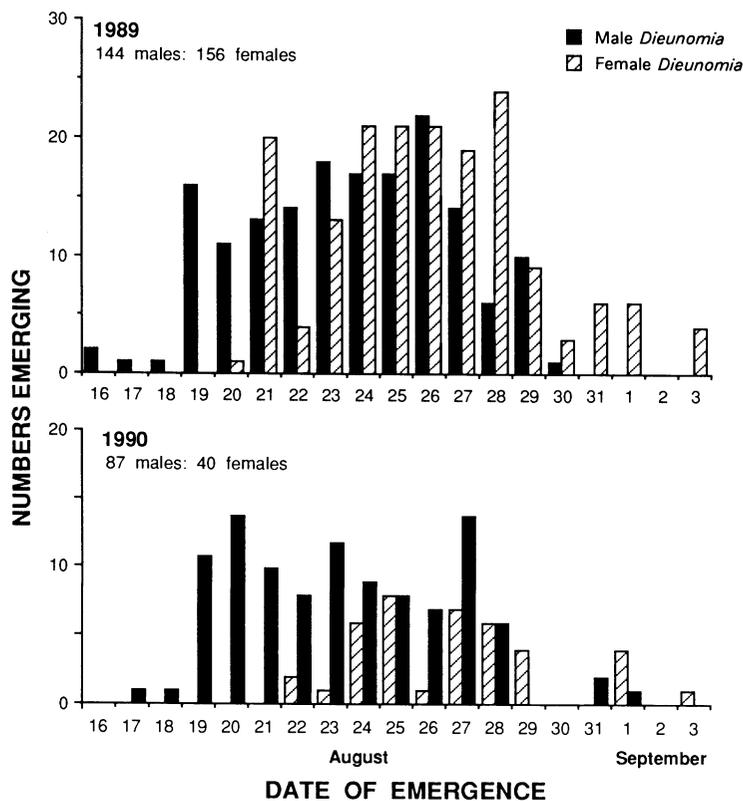


FIG. 1. Emergence phenologies of female and male *Dieunomia triangulifera* in 1989 and 1990.

RESULTS

Bee emergence and sex ratio

Dieunomia emerges in early- to mid-August (Fig. 1), and females provision nests through mid- to late-September (or rarely into early October). The population is usually protandrous: males began emerging on 7, 17, 16, and 17 August 1987–1990, respectively; corresponding dates for females were 12, 17, 20, and 19 August 1987–1990.

Nest establishment

Females began establishing nests within a day after emergence if soil was sufficiently moist to support excavations. In drier years, many females postponed nest construction apparently until rains moistened the soil. Some nest construction was induced by artificially wetting the soil. Females began excavating nests on 19, 21, and 19 August 1988–1990, respectively. The seasonal peak dates of nest establishment were 28, 28, and 29 August 1988–1990.

Features of nest architecture did not qualitatively differ from nests illustrated by Cross and Bohart (1960), except that cells were at up to twice the depth (40–90 cm) of the deepest cells reported by those authors and, on average, had fewer cells (Table 1). Nests were often densely aggregated (40 nests/m²) and less often isolated

by up to 10 m. Soils at the nest site have been described by Cane (1991).

Diel patterns of provisioning

At temperatures above 18°C females first left their nests between 0730 and 0800. Provisioning trips were shortest in the morning and gradually increased in duration until mid-afternoon, when trip times again began to decrease as sunset approached (Fig. 2). Mean values for the five fastest trips for each time period are also presented in Fig. 2. More females left their nests between 0830 and 0930 than at any other time of the day (Fig. 3) and trips during this period were of the shortest duration (Fig. 2). The fewest trips were made between 1230 and 1330 (Fig. 3), and these were among the longest in duration (Fig. 2). Foraging trip durations decreased in the late afternoon (after 1700) relative to mid-afternoon (Fig. 2). A few more females left their nests during this period than during midday (Fig. 3), suggesting that some *Dieunomia* females might also respond to the late afternoon pollen presentation by the sunflowers.

The numbers of pollen grains carried per trip by foraging females decreased from mid-morning to early afternoon but increased in the last hour of daylight (Fig. 4), whether corrected for body size or not. This pattern also corresponds closely to the reduced standing crop of pollen seen on nearby sunflower capitula

TABLE 1. Summary of population parameters and usage of *Helianthus annuus* pollen by *Dieunomia triangulifera* (ND = no data).

	1987	1988	1989	1990
<i>D. triangulifera</i>				
Number of bees	ND	52 660	154 961	116 383
Total cells/nest site	ND	310 690	274 271	523 723
Number of cells per nest	ND	5.9	1.8	4.5
Pollen per pollen ball (mg)	77.7 ± 4.3 (n = 10)	91.8 ± 6.8 (n = 9)	ND	≈64.0 ± 3.4 (est.; n = 6)
Estimated total pollen collected by aggregation (kg)	ND	28.5	(≈21.8)	33.5
Female mass (mg)	26.7 ± 0.9 (n = 15)	32.9 ± 0.7 (n = 32)	ND	24.3 ± 0.8 (n = 21)
Foraging trip durations during 0900–1100 (min)	ND	27.45 ± 1.72 (n = 23*)	67.75 ± 5.98 (n = 29)	62.2 ± 3.0 (n = 112)
Time in nest when provisioning (min)	ND	6.96 ± 0.33 (n = 24)	8.14 ± 0.75 (n = 29)	6.83 ± 0.26 (n = 70)
No. of pollen grains carried per trip	788 891 (n = 15)	418 627 (n = 33)	ND	596 647 (n = 23)
<i>H. annuus</i>				
Capitula/plant	ND	176.6 ± 12.4 (n = 17)	40.0 ± 6.4 (n = 29)	80.2 ± 13.2 (n = 20)
Plants/km ²	ND	3011.2	2293.1	4222.9
Estimated pollen/km ² (kg)	ND	137.2	23.7	87.4

* During 1045–1245.

and is inversely related to the aforementioned variation in trip durations.

The numbers of trips made per day and trip durations were highly variable among individuals. For an entire day in the Observation Plot, the numbers of pollen-carrying trips varied from 0 to 8 ($\bar{X} = 3.44 \pm 0.3$ trips, $n = 44$; Fig. 5) and the range of trip durations was 19–188 min ($\bar{X} = 67.3 \pm 3.3$ min, $n = 136$; Fig. 6). Except near dusk, the occasional very long trips occurred throughout the day (Fig. 2) and it is unlikely females were collecting pollen or nectar for the entire 2 or 3 h involved; for this reason we also indicate in

Fig. 2 the five fastest trips per foraging interval, as the minimum trip duration is more likely to accurately reflect changes in pollen availability over the day. Females occasionally entered nests that were not their own, but always left these nests quickly without depositing pollen and soon relocated their own nests.

The number of pollen trips needed to make a pollen ball was estimated by dividing total mass of a pollen ball ($n = 25$ actual counts; converted from pollen counts in some cases) by the average numbers of pollen grains (converted to milligrams) in a scopal load (mean = $672\,537 \pm 35\,309$ grains; average of 30 samples from

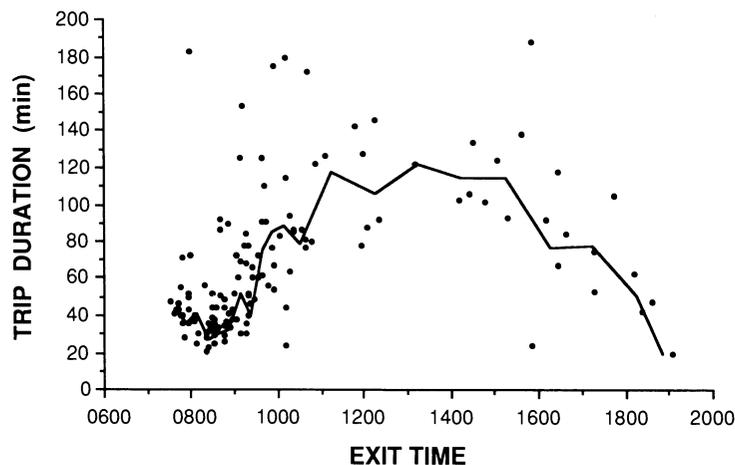


FIG. 2. Durations of all foraging trips made on 5 September 1990 in the Observation Plot vs. time trip was initiated. The line indicates the mean of the five fastest trips per period.

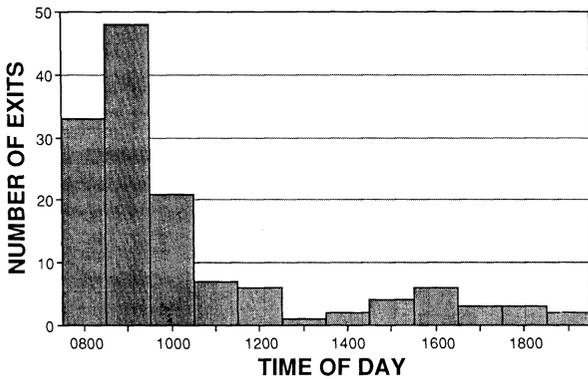


FIG. 3. Numbers of exits of females from the Observation Plot for each hour on 5 September 1990.

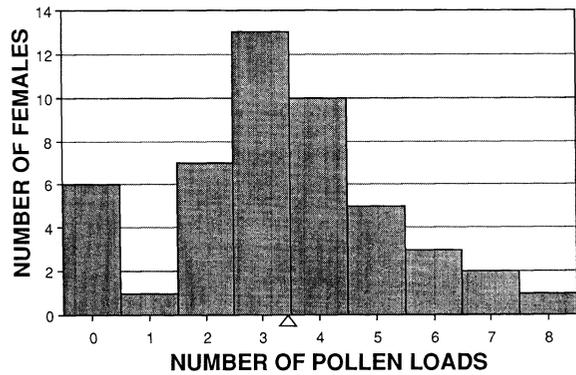


FIG. 5. Total numbers of pollen loads brought back by active females (excluding 6 nonprovisioning females) in the Observation Plot on 5 September 1990. Mean number of loads (3.44) indicated by Δ beneath scale.

before 1200, eight samples after 1200). Calculated in this way, females require, on average, 4.35 trips to provision a larval cell. The variation in trips per day (Fig. 5) indicates that females can provision a cell (or more) in 1 d, but often do not, even at peak bloom.

Seasonal provisioning activity and longevity

The total numbers of provisioning trips and the numbers of trips per active female in the Observation Plot (Fig. 7) show peaks of activity corresponding to peak *H. annuus* bloom. Mean trip times between 0900 and 1000 were not significantly different on 28, 31 August and 2, 7 September (multiple comparison of means, GT2 method, no significant differences [Sokal and Rohlf 1981]; we do not have comparable data for the very early and late parts of the season). Averaged over the entire 1990 season, females returned to their nests with pollen on 92% of 691 foraging trips. Returns without pollen were more frequent early and late in the season, e.g., in 1990 over 50% of the trips after 10 September 1990 were not pollen trips.

On any given day there were also always some in-

active females which did not fly (Fig. 8). No dissections were made to ascertain ovarian states of such females, but most provisioned on later dates, indicating they could still produce eggs. Together with active females collecting no pollen loads (Fig. 8), some 25% of the population may not provision on any given day, even at peak bloom.

The life-span of females was estimated to be 14 d, using nest establishment data from marked quadrats; direct observations in the Observation Plot gave a mean longevity of 13.2 d ($n = 63$).

Seasonal and diel patterns of pollen production

The mean number of capitula per plant varied as much as four-fold between years (Table 1). The number of capitula per plant is significantly correlated with flowering longevity ($r = 0.77, P < 0.01, n = 10$). A capitulum had 353 ± 13.1 florets ($n = 17$ capitula). Flowering longevity in 1988 averaged 27.6 ± 4.38 d (range 19–36 d) with individual capitula offering pollen

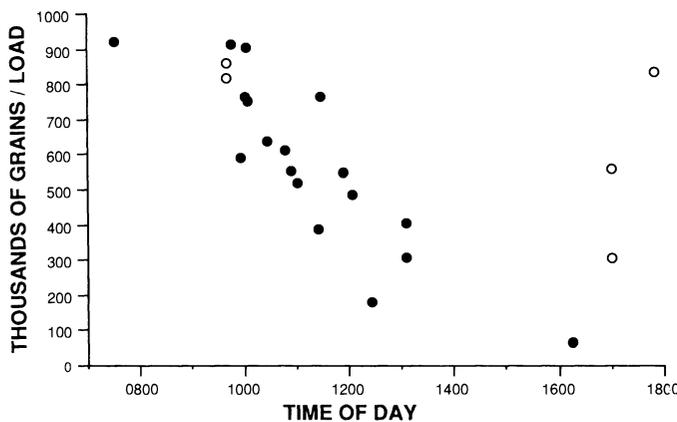


FIG. 4. Numbers of pollen grains in scopal loads from females returning to their nests during the day ($n = 23$, from 2, 5, 11, 12 September 1990). O, samples from dates near peak bloom.

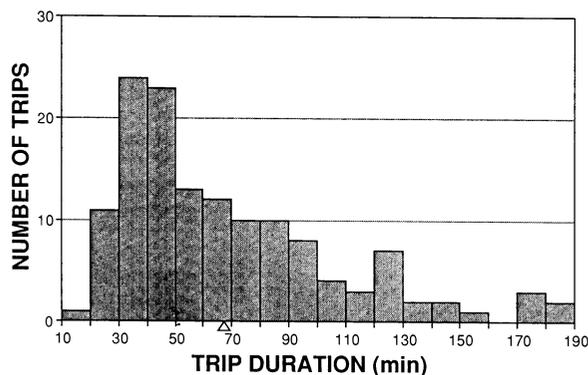


FIG. 6. Foraging trip durations ($n = 136$) in the Observation Plot on 5 September 1990. Mean trip duration (67.3 min) indicated by Δ beneath scale.

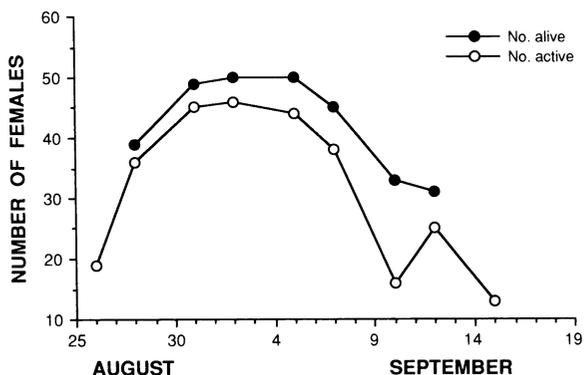


FIG. 8. The numbers of bees active (flying) in the Observation Plot on given dates in 1990 compared with the total numbers that were known to be alive (based on subsequent observation).

for only 8.6 ± 0.15 d (range 6–11 d). Per capitulum, the mean number of florets shedding pollen per day is 41.0 florets/d (353 florets/8.6 d). The quantity of sunflower pollen on plants was greatest between 0900 and 1030 (Fig. 9), which is the period of the day when bees made rapid provisioning trips (Fig. 2) and carried the largest pollen loads. Pollen standing crop decreased rapidly, such that by 1100 very little or none remained on florets, but after 1600 pollen increased approximately twofold from the early afternoon levels. In other areas of its range *H. annuus* also has a secondary late-day presentation of pollen (Fell 1986, Neff and Simpson 1990). Pollen produced per disk floret was 0.73 mg (range 25 000–43 000 grains). When extrapolated to daily pollen production per capitulum, the 41 disk florets produced 30 mg pollen (41 mature disk florets per day per capitulum \times 0.73 mg pollen per disc floret = 30 mg pollen). Thus, over its 8.6-d lifetime, a capitulum produced 258 mg pollen (30 mg pollen per day \times 8.6 d \times 0.73 mg pollen per disc floret per day = 258 mg pollen).

Foraging area and pollen availability

The minimum foraging distance required to supply

the population with sufficient pollen varied through the nesting season (Fig. 10), as well as between years. Our estimates of foraging area assume the following as constants: (1) females live on average 13.2 d; (2) each makes 3.44 pollen collecting trips per day; (3) a female carries 18.25 mg of pollen per trip; (4) *Dieunomia* females collect 32% of pollen produced; (5) there are 353 florets per capitulum, and 41 offer pollen on a given day, for a total of 30 mg/capitulum/d of pollen; and (6) females are as likely to utilize resources from distant plants as from nearby plants. Assumption number 2 is likely an overestimate, since varying proportions of females did not forage on any given day of the season (the mean is based on a single day's complete observations, including zeroes, from a date near peak bloom; Fig. 5); assumption number 3 is based on samples reflecting more active foraging when pollen loads are larger (Fig. 4); assumption number 4 is a probable underestimate; assumption number 6 probably overestimates utilization of more distant plants (see Roubik 1989).

The minimum area needed to support the females at the nest site for each day of the flight season was

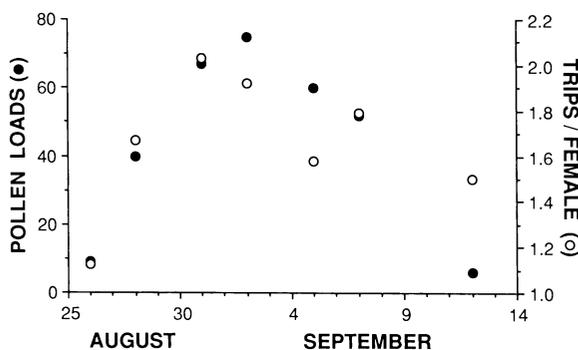


FIG. 7. Total numbers of pollen loads (●) brought to nests and numbers of trips per provisioning female (○) in the Observation Plot during the peak foraging period of the day (0900–1100) in 1990.

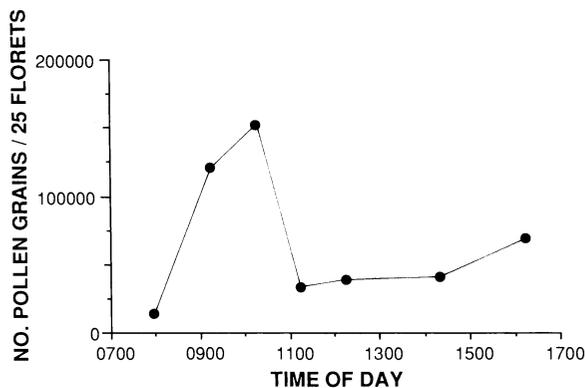


FIG. 9. Numbers of pollen grains found on florets of *Helianthus annuus* throughout the day on 8 and 12 September 1990.

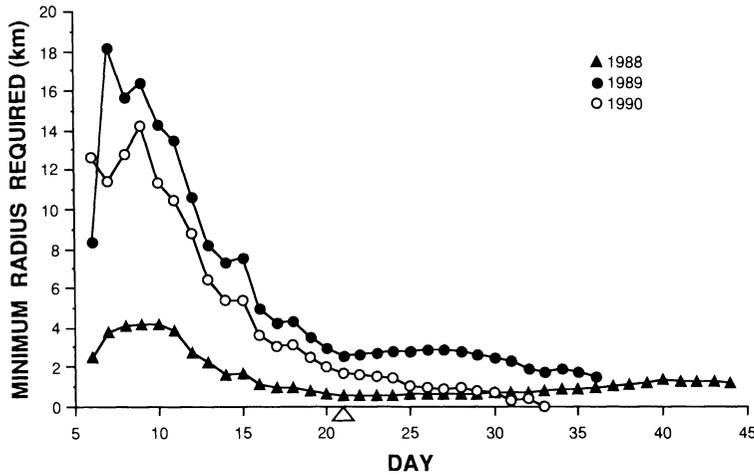


FIG. 10. Minimum estimated radius of foraging area needed to supply the pollen requirements of the entire *Dieunomia* aggregation during 1988, 1989, and 1990. Flowering phenology was recorded only in 1988, and this phenological pattern (Fig. 11) was used for all 3 yr, standardized so day 1 = first day of flowering period. The date of peak bloom is indicated by Δ beneath horizontal axis.

calculated by first estimating the mass of pollen required to supply the population on a given day: pollen required = (number active females) \times (amount of pollen collected per trip [18.25 mg]) \times (pollen trips per day [3.44]); then calculating the mass of pollen available per unit area on this same day: pollen available per square kilometre = (plants per square kilometre) \times (capitula/plant) \times (proportion of capitula open) \times (pollen per capitulum per day [30 mg]) \times (proportion of pollen collected by *Dieunomia* [0.32]). From these estimates the area needed to support the nesting aggregation equals: minimum area = pollen required/ (pollen available per square kilometre).

These calculations for 1988, 1989, and 1990 were then converted to radii yielding the appropriate areas, allowing us to compare resource availability within and between years.

The minimum area measure is sensitive to both changes in the numbers of females and open capitula,

and the profiles in Fig. 10 are essentially the inverse of pollen availability. Thus, little pollen is available early in the season, and if all active females were to forage, it would take a large area to supply the required pollen. At this time, however, females make few or no provisioning trips (Figs. 7 and 8). In 1988, the pollen requirements of the aggregation at peak bloom could be satisfied within a ≈ 1 km radius of the nest site. In 1989, numbers of capitula per plant decreased so that at peak bloom some females must have flown as far as 3.0 and 3.5 km from the nest site or more. Pollen foraging trip durations, taken at times near peak bloom (7 September 1988, 5 September 1989, and 5 September 1990) were much shorter in 1988 than the other years (Table 1), despite the fact that the 1988 observations were from later in the day (1045–1245 vs. 0900–1100), when foraging trips became longer. These differences in trip duration probably relate to a combination of the greater distances females had to fly to find sunflower plants and the need to visit more plants per trip in the drier years of 1989 and 1990, when plants produced fewer capitula (Table 1).

Population size

Summary data for 3 yr (Table 1) show changes in population size, provisioning behaviors, productivity, and total dry mass of female *Dieunomia* at the nest site. Years of reduced provisioning success occurred when sunflowers had fewer capitula and when plants were less abundant near the nest site (Table 1), suggesting that female provisioning behavior and success was influenced by changes in pollen availability. In 1988, pollen was abundant relative to the number of provisioning females, and bees required less time to collect a load of pollen, provisioned more cells per nest, and presumably foraged over a relatively small area at peak bloom (Fig. 10). Probably as a consequence, the

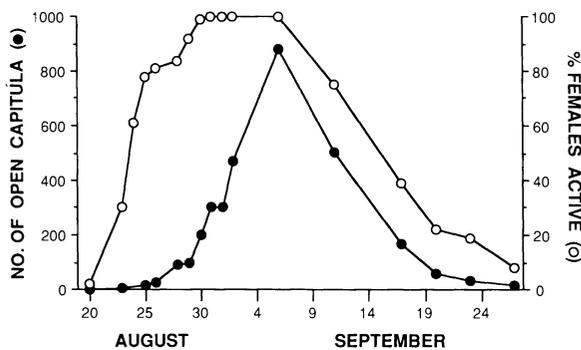


FIG. 11. Percentages of nesting females estimated to be alive in marked study quadrats (○) and total numbers of open capitula on 15 *H. annuus* plants growing near the nesting site (●) in 1988.

TABLE 2. Bee species and numbers of males and females collected on native *Helianthus annuus* near the nest site, 26 August–8 September 1990. O = primary *Helianthus* oligolege, O' = secondary *Helianthus* oligolege, P = polylege (sensu Hurd et al. 1980), * = parasitic taxa. Numbers to the left of the names indicate that samples included pollen-collecting females and correspond to the numbers of Fig. 12.

Taxa	Males	Fe- males	Pollen usage
Apidae (+ "Anthophoridae")			
1 <i>Apis mellifera</i>	0	4	P
2 <i>Bombus pennsylvanicus</i>	115	114	P
3 <i>Bombus griseocollis</i>	12	8	P
4 <i>Bombus faternus</i>	0	4	P
5 <i>Bombus bimaculatus</i>	3	0	P
6 <i>Svastra obliqua</i>	4	27	O'
7 <i>Melissodes bimaculata</i>	0	1	P
8 <i>Melissodes agilis</i>	38	70	O
9 <i>Tetraloniella helianthorum</i>	1	0	O?
<i>Psithyrus variabilis</i>	4	0	*
<i>Nomada adducta</i>	0	1	*
<i>Triepeolus concava</i>	1	5	*
<i>Triepeolus distincta</i>	4	1	*
Megachilidae			
10 <i>Megachile fortis</i>	0	6	O'
11 <i>Megachile brevis</i>	1	0	P
Melittidae			
12 <i>Hesperapis carinata</i>	1	0	O
Halictidae			
13 <i>Lasioglossum zephyrum</i>	3	6	P
14 <i>Agapostemon texanus</i>	3	0	P
15 <i>Halictus ligatus</i>	0	3	P
16 <i>Dieunomia triangulifera</i>	109	111	O
17 <i>Dufourea marginata</i>	2	12	O
<i>Sphecodes</i> sp.	0	1	*
Andrenidae			
18 <i>Pseudopanurgus aethiops</i>	0	5	O
19 <i>Perdita albipennis</i>	5	63	O
20 <i>Andrena helianthi</i>	0	29	O
21 <i>Andrena accepta</i>	9	26	O
<i>Pterosarus</i> sp.	0	2	?
Total no. individuals	315	499	

bee population increased almost threefold. In that year (1989) resources per bee were scarce (Table 1), and bees took more time to collect each pollen load, provisioned 31% fewer cells per nest, and probably foraged over greater distances. This decline in pollen availability presumably explains the decrease in the population size the next year, when resource availability was intermediate; associated with intermediate pollen availability, the numbers of cells per nest, and estimated foraging distances were also intermediate (Table 1, Fig. 10). A feedback effect occurred, that pollen availability in one season partially determined pollen availability the following season. Overall mortality due to parasitism was relatively constant throughout all years of our study, accounting for the destruction of 11% of all brood cells (Wcislo et al. 1994). In summary, each season could be characterized by the combined effects of bee population size (itself a result of the pre-

vious season), plant density, and plant productivity (capitula per plant).

Seasonal bee-plant synchronization

Dieunomia nest activity (from sample quadrats), and floral phenology of *H. annuus* ($n = 15$ plants), in 1988 are shown in Fig. 11. Once flowering starts (20, 24, and 21 August in 1988–1990, respectively), there is a rapid increase in mature capitula up to peak bloom, followed by a more gradual decrease in their numbers. In this year all nests in our quadrats were established before peak bloom of *H. annuus*. The same pattern was also observed in subsequent years, though not quantified.

Total pollinator activity

Twenty bee species other than *Dieunomia* visited *H. annuus* for pollen (Table 2) and 8 of the 20 species have flight seasons that coincide primarily with sunflower flowering (Fig. 12), though none as closely as *Dieunomia*. Most of the 814 individual bees we caught were nectar foragers ($n = 612$). Female *Dieunomia* comprised 10.6% of the total numbers of bees caught and 32% of the pollen collecting individuals. The other dominant taxa were *Bombus pennsylvanicus* and *Melissodes agilis* (Apidae). We did not identify the pollen on the scopa of individual bees other than *Dieunomia* but presumably much was from *H. annuus*. It is our impression that the typical *Dieunomia* pollen load is relatively large because most other species have a smaller body size and/or carry pollen only on their hind legs.

DISCUSSION

Many theoretical discussions concerning the evolution of specialization have proposed that selection for specialization is strongest when resources are predictable and abundant (Emlen 1966, Levins 1968, Levins

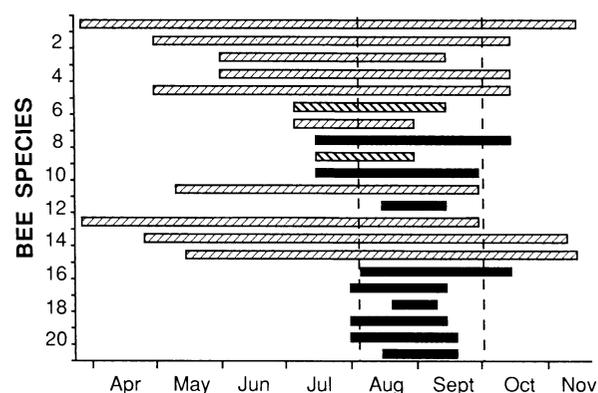


FIG. 12. Seasonal flight periods of 21 nonparasitic bee species collected at *H. annuus* flowers. For identities of numbered species, see Table 2. ▨, polyleges, ■, strict sunflower oligoleges, ▩, secondary oligoleges/potential oligoleges. Vertical dashed lines indicate beginning and end of typical *H. annuus* flowering period.

and MacArthur 1969, Real 1980, Real and Caraco 1986, but see Futuyma 1976), and many known food specialists, including one social and numerous solitary bees (e.g., Løken 1950, Hurd and Linsley 1975, Laverty and Plowright 1988), exploit abundant or superabundant resources (for other taxa see, Otte and Joern 1975, Futuyma and Moreno 1988, Jaenicke 1990).

Helianthus annuus possesses characteristics that logically might promote specialization: it is abundant and widespread; it predictably begins flowering within a 2–3 wk period each year, and the flowers bear large amounts of pollen and nectar (*Results*; Simpson and Neff 1987). Although we lack comparative data on the amount of pollen different plants produce, *H. annuus* is doubtlessly on the upper end of a scale of production. Over the 1988 season, an average plant at our study site produced enough pollen in its lifetime to provision between 545 and 620 *Dieunomia* brood cells (42 350–48 800 mg). These features, as well as the open, accessible capitulum, might explain why sunflowers have such a remarkable number of bee species that visit it for pollen and nectar, many of which are oligoleges (see Table 2 for one site; Hurd et al. 1980).

The importance of synchrony

Neff and Simpson (1990) have shown that bee visitation patterns to sunflowers in Texas were strongly influenced by the schedule of pollen and nectar presentation. Our observations of *Dieunomia*, demonstrate that it, too, closely tracks sunflower pollen abundance daily, seasonally, and between years. Those periods (day or season) during which sunflower pollen was most abundant correspond to periods with the highest numbers of provisioning trips, the highest rate of foraging by individual females, and the greatest amounts of pollen collected per trip. Although daily sunflower usage patterns by the bees are potentially learned behaviors (Thorp 1979, Dukas and Real 1993), the seasonal timing involves features of the bees' life history that are evolved traits.

When a specialist uses a relatively short-lived resource that varies in abundance through a season the degree of synchrony may be a powerful selective factor. Synchrony theoretically decreases environmental uncertainty (i.e., increases predictability) with respect to resource availability (Roff 1983) and decreases the between-generation variation in fitness (see Yoshimura and Clark 1991). For *Dieunomia*, the energy advantage associated with synchrony to host plants may be substantial. Some females active at the nest site early in the season must have used an area of >8 km radius (1050 km²), while those active at peak bloom foraged over an area of only 3 km radius (30 km²). Flight distances for *Dieunomia* are unknown, but average flight distances for worker honey bees (*Apis mellifera*), which are slightly smaller than *Dieunomia* females, are 2.25 km with a maximum of 12 km (Visscher and Seeley 1982). If poorly synchronized females do not forage

and wait until resource availability increases, then the cost incurred is a shortened foraging season. We can estimate this cost based on the information concerning honey bee foraging distances. Assuming that few *Dieunomia* females fly farther than 10 km, then from Fig. 9, the provisioning season is truncated from 30 to 24 d. In general, carrying capacity is a function of the way the environment is utilized by organisms (Allen 1976). If many females emerge prior to peak bloom, they will effectively reduce the carrying capacity of the local environment, forcing some females to fly prohibitively long distances, postpone foraging until more resources become available (as they appear to do in *Dieunomia*), disperse, or switch to other resources (if available). Synchrony, therefore, may be very important in the selective maintenance of specialization.

The role of resource limitation

Periods when resources are limited presumably are when selection on provisioning behavior is strongest. For *Dieunomia*, some observations strongly suggest that resources are limited. Pollen was completely removed from capitula within several hours after anthesis, probably because foraging by other specialists and generalist species of bees was greatest during this period. *Dieunomia* were much less likely to initiate foraging trips when pollen abundance was low. Similarly, variation in foraging trip durations also suggests that pollen-collecting females are responding to changes in daily and seasonal pollen availability, a phenomenon that occurs in other bees (Strickler 1982, Buchmann and Cane 1989, Neff and Simpson 1991). We also found that all females broke diapause, emerged, mated, excavated a nest, and were ready to collect pollen by peak bloom despite yearly variation in the starting date of sunflower bloom. Finally, there appears to be a correspondence between resource abundance and reproductive success; numbers of cells per nest in "poor" years were lower than numbers in "good" years.

In contrast, other individual behaviors suggested that resources were not limiting. Among active bees, the number of pollen trips per day ranges from zero to eight even though females can provision an entire cell in approximately four trips. Some bees do not leave their nests even on days when flight conditions are excellent, yet they collect pollen on subsequent days. There was large variance in foraging trip durations (10 to >190 min), whether pollen was plentiful or scarce. Females produce, on average, 2–6 offspring, far fewer than theoretically possible given that they live nearly 14 d and can provision approximately one cell per day on average. Low fecundities such as this are typical for solitary apoid Hymenoptera (other than some Megachilidae), which usually do not exceed 20 cells per nest (e.g., Michener and Rettenmeyer 1956, Michener and Lange 1958, Michener 1960, Stockhammer 1966, Danforth 1989, 1990). Low fecundity in many solitary bees is probably related to the fact that each egg is large

relative to body size, in comparison with social and parasitic species (Iwata 1955, Iwata and Sakagami 1966, Alexander and Rozen 1987). Females metabolize fat body or proteins from pollen to synthesize egg proteins (vitellogenins) for these large eggs. The observation that some females did not forage during the middle of the season, even though conditions were excellent, may relate to physiological conditions associated with vitellogenesis. We hypothesize that females which foraged at reduced intensity did not have a mature egg ready to deposit.

We further suggest that the physiological costs associated with construction and provisioning of a cell may influence vitellogenesis to the point at which the rate of egg production is no more than an egg every 2–3 d. If so, any reduction in pollen availability could also indirectly affect fecundity, as it would potentially reduce both the energy efficiency of foraging as well as a female's nutritional status (reducing the rate of egg production even further). In essence, the rate of reproduction is dependent on how much time and energy it takes to produce a single offspring (Danforth 1990). If these nonforaging reproductive activities are also costly, a trade-off may exist between these activities, and this would explain how there can be strong evidence for resource limitation at the population level, even though females do not appear to behave as if resource levels were limiting.

Synchrony and pollen specialization

Our argument assumes that the synchrony observed is a result of a change of phenology by the bee and not the plant, and as such is contrary to the "pollinator tracking" hypothesis (see Rathcke 1983, Paige and Whitham 1985, for an alternative viewpoint, Robertson 1924, Kochmer and Handel 1986). In the *D. triangulifera*–*H. annuus* study we have no direct data bearing on this question, although the flowering phenology of *H. annuus* would presumably shift in response to the suite of taxa that go to this plant, rather than just *Dieunomia* (cf. Herrera 1988, Thompson and Pellmyr 1992).

Traditionally, the hypotheses concerning specialization in bees (Lovell 1913, 1914, Robertson 1914, 1925, Michener 1954, Strickler 1979, Thomson 1980, Schaffer et al. 1983, Roubik and Buchmann 1984, Laverty and Plowright 1988) have strongly emphasized interspecific competition. Social (intraspecific) competition is underemphasized in discussions of food specializations (cf. West-Eberhard 1983). The effective increase in resource availability gained by an organism with its resource relative to less synchronized conspecifics is possibly an important aspect of the evolution of specialization in general, especially among short-lived organisms. There are many examples of ecological relationships where asynchrony reduces fitness, such as: (1) individuals of flowering plants that bloom too early/late have reduced seed set (Augsburger 1981), and this

can also adversely affect specialist pollinators, as in the pollination ecology of *Yucca* sp. and yucca moths (Powell and Mackie 1966, Kingsolver 1984); (2) aphids that emerge too late cannot feed on the older, tougher plant tissues and die (Dixon 1976); (3) socially parasitic bumble bees that attack host colonies after the latter have grown too large cannot invade the colony (Fisher 1984).

Such studies strongly suggest that synchronized activity translates into increased reproductive success of synchronized individuals over those that are poorly synchronized. While the relative importance of intra- and interspecific interactions may not always be clear, this may be important in understanding pollen specialization in *Dieunomia*.

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