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Nesting Behavior of Four Species of *Perdita* (Hymenoptera: Andrenidae)

BRYAN N. DANFORTH
Department of Entomology, Snow Entomological Museum,
University of Kansas, Lawrence, Kansas 66045

ABSTRACT: Observations on a nesting aggregation of *Perdita* (*Perdita*) *difficilis* in southeastern Arizona indicate that this species is solitary, provisions two cells per day during two foraging periods (0700–1000 and 1700–1930 hr) and requires only three trips (two with pollen and one with nectar, in that order) to provision a cell. Nests are occupied for less than 5 days and bees most likely occupy several nests during their lifetimes. *P.* (*Perdita*) *luciae,* a bee similar in appearance to *P. difficilis,* was studied at the same locality. Like females of *P. difficilis,* females of *P. luciae* completely provision a cell with three trips (two with pollen and one with nectar, in that order), however, unlike *P. difficilis, P. luciae* provision cells between 0800 and 1300 hr. Nest architecture of both *P. difficilis* and *P. luciae* is described. *Perdita* (*Cockerellia*) *coreopsidis,* studied in southeastern Arizona, has up to three generations a year, is facultatively communal (with up to 14 females per nest), requires six to eight pollen trips to provision a cell and is capable of provisioning up to two cells per day. Communal nests appear to arise in this species because emerging females remain in their natal nests. No obvious agonistic or cooperative behavior was observed among nest-mates. A study of *P.* (*Cockerellia*) *albipennis* in the vicinity of Lawrence, Kansas indicated that this species is solitary, requires five pollen trips to provision a cell and provisions only one cell per day. There was no indication of more than one generation per year. Information on the behavior of the parasites of all four species is provided. The costs and benefits and possible causes of communal nesting in *P. coreopsidis* are discussed.

The genus *Perdita* contains over 500 species of small to minute bees found primarily in the arid western United States and northern Mexico. In spite of the size of the genus, the nesting behavior of only 11 species has been studied in any detail (review by Rozen, 1967; Eickwort, 1977; Torchio, 1975; Bennet and Breed, 1985). More importantly, of the 11 species studied so far, the majority (eight) are placed in only one of the 21 subgenera recognized by Timberlake (1954–1968), the subgenus *Perdita.* We are far from an understanding of the total range of nesting behaviors exhibited by members of this genus.

This paper presents observations on the nesting behavior of two more species within the subgenus *Perdita* (*P. difficilis* Timberlake and *P. luciae* Cockerell; both in the *Sphaeralceae* group) and of two species within the subgenus *Cockerellia* (*P. coreopsidis* Cockerell and *P. albipennis* Cresson). Communal nesting appears to be a fairly common feature of *Perdita,* found in four of the five subgenera studied so far (*Cockerellia, Cockerellula, Macrotera* and *Macroteropsis*), and the work presented here on *P. coreopsidis* is the first detailed study of communal nesting in this genus.

The bees referred to below as *P. difficilis* may actually include specimens of another species recognized by Timberlake (1964): *P. exclamans* Cockerell. Although the males of these two species are easily distinguished based on the shape of the hind femora, females are indistinguishable (Timberlake, 1964, p. 323). Timberlake admitted that these two "species" may be a single species with di-

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morphic males. Because only males of *P. difficilis* were collected at the study site, and because there was no morphological or behavioral evidence to suggest that the females observed comprise two species, I will refer to these bees as *P. difficilis.*

Although Timberlake (1954) recognized four geographically distinct subspecies of *P. coreopsidis,* the range of color pattern variation observed in specimens collected at the study site includes three of Timberlake's subspecies (*c. coreopsidis, c. collaris* Cockerell and *c. kansensis* Timberlake). Because of the wide variation in color pattern at one locality, the validity of these subspecies is doubtful and I will refer to the species simply as *P. coreopsidis.* Voucher specimens of bee and fly species discussed in this paper are in the Snow Entomological Museum, University of Kansas, Lawrence.

Materials and Methods

In the studies of *P. coreopsidis* and *P. albipennis,* females were marked on the mesoscutum with two spots of enamel paint. Using four colors this gave a total of 16 potential individual labels. There was no evidence of interchange of bees among nests so redundancy in labels did not lead to any confusion. No redundancy in labeling was necessary in the *P. albipennis* study because only 12 females were marked. Because of their small size, individual marking was impossible for *P. difficilis* and *P. luciae.* But based both on nest excavations ($n = 12$ for *P. difficilis*; $n = 13$ for *P. luciae*) and on foraging data, there was no indication that more than one female occupied a nest in either species.

Foraging behavior of individual bees was observed by covering nest entrances with 15 dram opaque plastic pill bottles which had one side replaced with a fine mesh screen. Whenever a bee appeared in a vial, or flying around outside, the bee was identified, pollen loads noted, and the vial removed to allow departure or entrance. This method appeared not to interfere greatly with the normal timing of departures and returns of the bees and allowed me to follow many more nests than would otherwise have been possible.

The volume of nectar in the crop was determined by gently squeezing the metasoma of freshly killed bees and collecting the nectar exuded from the mouthparts in 5 μl capillary tubes.

Nests were excavated by blowing a fine mist of dry plaster of Paris powder into tunnels and then following the powder-lined tunnels by scraping soil away with a pen-knife. Because of the depth and complexity of *P. coreopsidis* and *P. albipennis* nests, and because lateral tunnels leading to completed cells are closed tightly with soil, it was often difficult to determine which completed cells belonged to the nest being excavated. Data on number of cells per nest, therefore, should be considered approximations. Cells currently being provisioned, on the other hand, could be unambiguously identified because of open burrows leading to them.

In the results given below means are given with the standard error of the mean.

Results

Perdita (*Perdita*) *difficilis*

HABITAT: *Perdita difficilis* ranges from Texas to southern California and northern Mexico, and adults have been collected from March to early June (Timberlake, 1964). The nesting aggregation studied was approximately 20 km north of Rodeo, Hildago Co., New Mexico, in the vicinity of the San Simon cienaga. Although *P.*

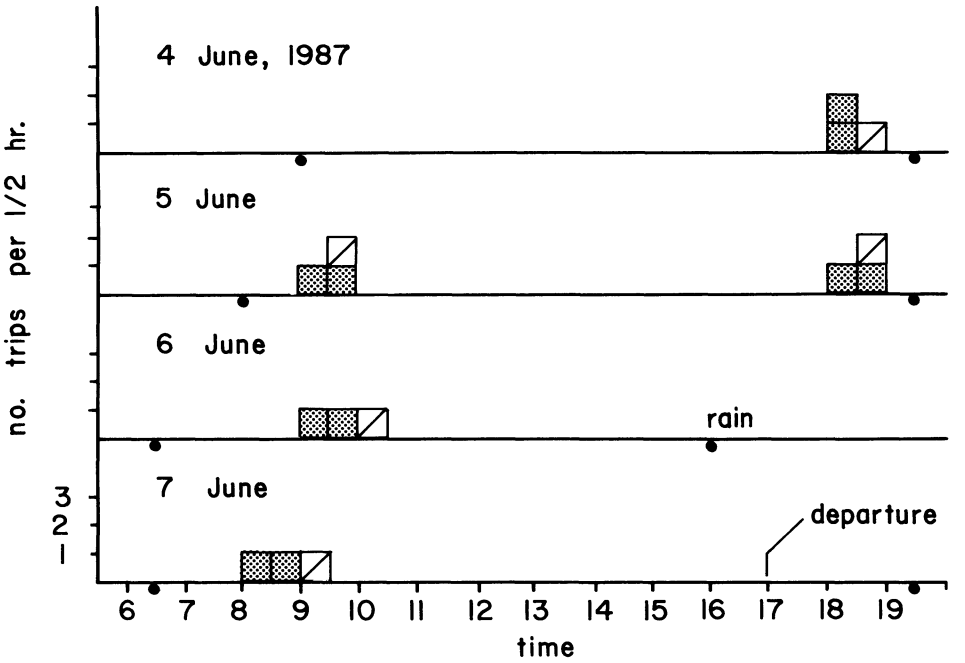

Fig. 1. Typical foraging behavior of *P. difficilis*. Data from nest #36 on 4–7 June 1987. Stippled boxes indicate returns with pollen; cross-hatched boxes indicate returns without pollen—presumably nectar trips. When a box is on top of another, the upper box represents a later trip. Closed circles along the x-axis indicate beginning and end of observation period.

difficilis could be collected on *Prosopis juliflora* at many localities both in the San Simon valley and in the vicinity of Willcox, Arizona, the study site chosen had a particularly large and dense nesting aggregation. The data presented below are based on observations of approximately 80 nests, in a 50 square meter area, studied from 25 May to 12 June 1987, and 26 May to 9 June 1988.

The dominant vegetation at the site is *Larrea tridentata* (Xygophyllaceae) and *Prosopis juliflora* (Leguminosae), which is the sole source of pollen, and possibly also nectar, for both *P. difficilis* and *P. luciae.* The soil consisted of very fine-grained, almost clay-like, sand.

Other members of the *Sphaeralceae* group were also present at the study site (e.g., *P. punctosignata* Cockerell and *P. luciae,* see below) but only nests of *P. difficilis* and *P. luciae* were found.

FORAGING AND PROVISIONING BEHAVIOR: The typical foraging pattern for *P. difficilis* is shown by the bee in nest #36 on 5 June 1987 (Fig. 1): two bouts of foraging per day (one between 0700 and 1000 hr and the other between 1700 and 1930 hr), with each foraging bout consisting of two pollen trips (shaded boxes) followed by one trip with small or no pollen loads visible on the legs (cross-hatched box). A foraging "bout" is defined as a series of closely spaced foraging trips, temporally discrete from other foraging trips. Of the 30 foraging bouts observed in 1987, 27 (90%) consisted of three trips, as described above, but three (10%) consisted of only two pollen trips. Measurements of crop contents in 1988 indicated that 21 out of the 23 (91%) bees carrying "full" pollen loads (as judged

visually) had no nectar in their crops, while the remaining two bees had detectable amounts of nectar (0.17 and 0.22 μl). All six bees captured returning to nests with "small" loads or no pollen on their legs had detectable amounts of nectar in their crops (range 0.22–0.73 μl; $\bar{x} = 0.45 \pm 0.08$ μl). Therefore, the last trip of the foraging bout, on which small pollen loads are carried, is a nectar trip.

Both mean trip duration and mean time spent in the nest between trips decreased slightly during a foraging period, though differences between the means are not statistically significant: mean duration first trip = 30.3 ± 9.5 min (n = 30); mean duration of second trip = 21.3 ± 6.2 min (n = 30); mean duration of third trip = 13.8 ± 5.5 min (n = 27); mean duration of first period between trips = 8.2 ± 5.6 min (n = 34); mean duration of second period between trips = 6.31 ± 4.39 min (n = 32).

By catching bees at specific points during a foraging bout and excavating the nest, it is clear that each bout of foraging provides the provisions necessary for the completion of one cell. In *P. difficilis,* and many other species of *Perdita,* when the pollen loads (two/trip) are deposited in the cell, they remain discrete and one can count how many trips worth of pollen have been deposited. When bees were collected returning to the nest on the second trip, having completed one previous trip (n = 2), a single cell was being provisioned and it contained one trip worth of pollen. In three out of four cases, when bees were collected returning on the third trip, having completed two previous trips, the single cell being provisioned had two trips worth of pollen. These findings hold for bees collected during either the morning or the afternoon foraging periods. Finally, in one nest excavated at 1500 hr, all cells had completed pollen balls and the female was in the process of building a new cell, apparently to be provisioned during the afternoon foraging period. These observations indicate that (1) a cell is completely provisioned with the two to three loads of pollen brought in during each foraging bout and (2) the cell for the morning foraging period is apparently constructed during the previous night and the cell for the afternoon foraging period is constructed during the day (between 1000 and 1700 hr).

However, in one case (nest #71), when the bee was collected returning with small pollen loads from the third trip during the morning foraging period (two previous trips with pollen), the cell currently being provisioned contained only one trip worth of pollen. The first trip worth of pollen had apparently been used to complete another cell which must have been partially provisioned the previous afternoon. This bee, therefore, had to shape the pollen ball for the completed cell, lay an egg and close off the lateral with loose soil during the time she was in the nest between trip one and two. The fact that this interval (18 min) was about twice as long as the average time spent in the nest between trips one and two (8.2 ± 5.6 min, see above) is consistent with this explanation. The important point is that bees are capable of beginning to provision a cell during one foraging period and completing it during the next, although this appears to be a rare occurrence.

As in other species of *Perdita* (Rozen, 1967), female *P. difficilis* coat the pollen ball in a shiny hydrophobic material, detectable when pollen balls are immersed in water.

Mating pairs of *P. difficilis* were observed exclusively on *Prosopis* inflorescences, and pairs remained in copula for very brief periods (<20 sec). No males were seen at the nest site and no adult males were ever found within a nest.

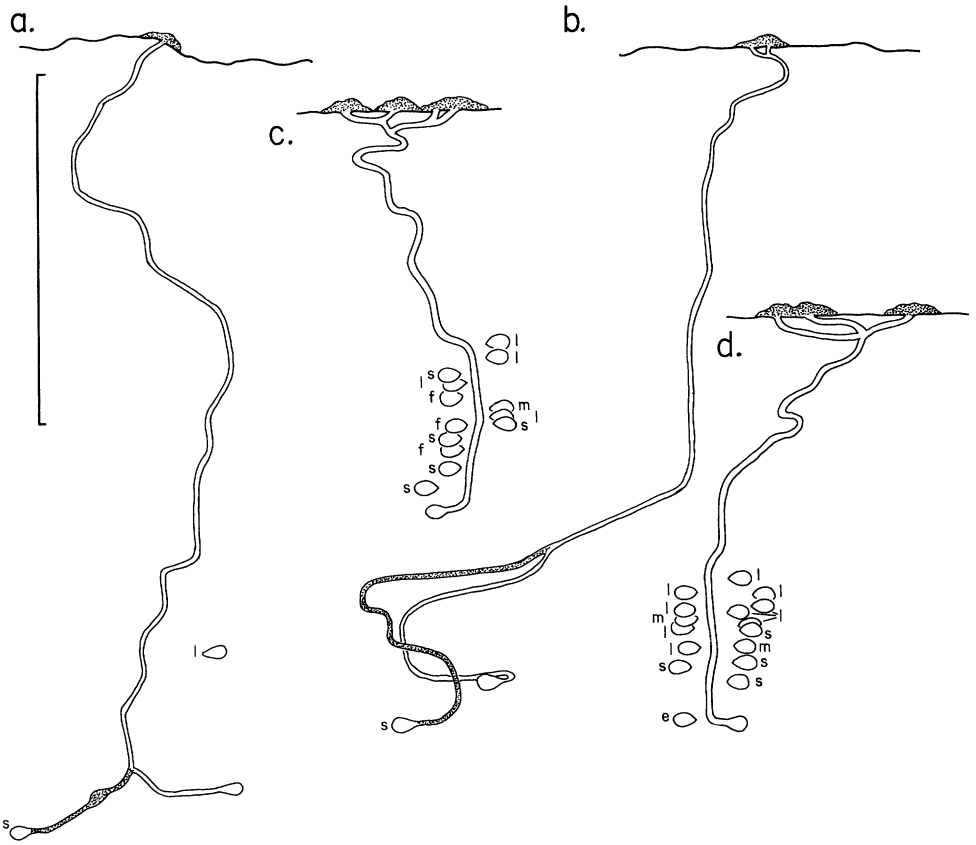

Fig. 2. Nests of *P. difficilis* (a, b) and of *P. luciae* (c, d). Letters indicate cell contents: o = old, empty cell, f = fungal-infected cell, s = small larva, m = medium larva, l = large larva, p = pupa. Unlabelled cells are those being provisioned when bees were captured. Dirt-filled laterals are stippled. Scale bar is 10 cm.

NEST OCCUPANCY AND STRUCTURE: Of the more than 80 nests studied all contained only one female. Nests of *P. difficilis* were occupied for fairly short periods of time. Most nests were inactive the day after they were located, but, of those that persisted for at least one foraging period, maximum nest occupancy was 5 days. No nest was followed from initiation through to abandonment so these data only estimate the true length of nest occupancy. Bees apparently left nests permanently during the afternoon foraging period (e.g., nest #36 on 7 June; Fig. 1) and this is the time that I observed new nests being initiated. No obvious nest closure behavior was observed. Because of the short duration of nest occupancy, female *P. difficilis* most likely occupy more than one nest per lifetime, although, since bees were not individually marked, there were no direct observations of bees occupying more than one nest. There was no indication that bees were provisioning cells in two separate nests during the same time period. Nests were either active (the resident foraging during all potential foraging periods while under observation) or inactive (no bee seen either entering or leaving the nest). If bees occupied more than one nest simultaneously, one would expect nests to alternate between active and inactive states.

P. difficilis nests (Fig. 2a, b) almost always had symmetrical tumuli. The main tunnel generally entered the ground at an angle of 30–45° to the horizontal, and the diameter of the tunnel was roughly 2 mm. After some initial meandering in the upper 3–5 cm the tunnel went essentially straight down. Laterals ranged from 1.0 to 6.0 cm in length, branched horizontally off the main tunnel and differed from the main tunnel in having a slightly smaller diameter and in following a more contorted path. Laterals leading to completed cells were tightly filled with soil and those leading to cells currently being provisioned were either filled loosely with soil or were open. Cells ranged in depth from 10–30 cm, were all subhorizontal and lacked a shiny lining, which is present in other panurgine species (Rozen, 1967). Nests contained from 1–20 cells ($\bar{x} = 4.7 \pm 1.5$; $n = 12$).

PARASITES AND PREDATORS: *Neolarra californica* Michener (Anthophoridae) and two undescribed species of *Sphecodes* (Halictidae) were common over the nest site. *Sphecodes* were observed to enter both *P. difficilis* and *P. luciae* nests. In most cases observed, *Sphecodes* would quickly depart after entering a nest, possibly due to defensive behavior of the resident, but in one case (nest #22 on 26 May) the *Sphecodes* remained in the nest (not determined whether of *P. luciae* or *P. difficilis*) for over 5 hours. During this time the host bee was in her nest, and she was not killed by the *Sphecodes*. No data were collected on entrances by *Neolarra*. Approximately 1 month after all *Perdita* species visiting *Prosopis* ceased activity, I dug up 150 *Perdita* larvae (most likely *P. difficilis* and *P. luciae*) from approximately 0.25 square meters adjacent to the study site, but no *Sphecodes* or *Neolarra* larvae were found. Rozen (pers. comm.) dug larvae from the same locality in 1986 and found 304 *Perdita* larvae and 8 *Neolarra*. These low rates of parasitism are surprising considering the ubiquity of adult parasites when cells are being provisioned.

The larvae of *Brachynemurus* near *hubbardi* Currie (Neuroptera: Myrmeleontidae) were occasionally seen moving over the nest site for a brief distance before burying themselves just beneath the surface of loose soil. On two occasions female *Perdita* entering their nests with pollen loads were killed by larvae of this species, which were buried in the bees' tumuli. There was no indication that *B.* near *hubbardi* larvae were selecting *Perdita* tumuli over other areas of loose soil.

Perdita (*Perdita*) *luciae*

HABITAT: *Perdita luciae* occurs from Sonora, Mexico, as far south as Guaymas, north to southern Arizona and southern California, and has been collected from April to early June (Timberlake, 1964). As mentioned earlier, *P. luciae,* apparently a close relative of *P. difficilis,* was studied at the same time and in the same locality as *P. difficilis* in 1987 and 1988. As in *P. difficilis,* females appeared to collect pollen exclusively from *Prosopis juliflora* and mating was restricted to *Prosopis* inflorescences. The data presented below are based on observations of 23 *P. luciae* nests.

FORAGING AND PROVISIONING BEHAVIOR: In 1987 an effort was made to gather data on cell provisioning behavior in *P. luciae* similar to the data gathered for *P. difficilis,* however, the records of nest departures and returns were inconsistent and confusing. For example, it was common to record two departures in a row and no returns, or three returns with pollen and no departures. At the time the confusion was assumed to have resulted either from nests with multiple, widely

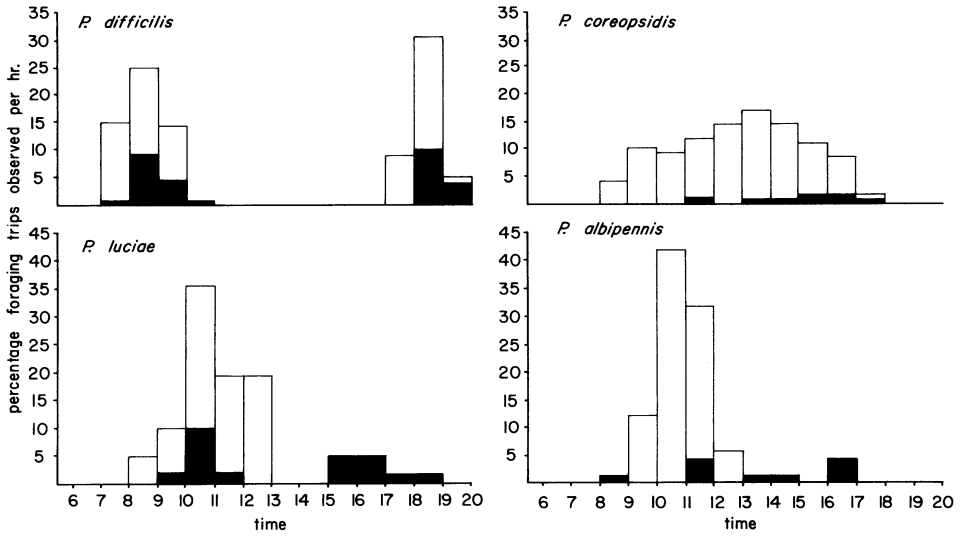

Fig. 3. Flight activities of the four species studied. Open bars correspond to returns to the nest with pollen; closed bars indicate returns to the nest without pollen (*P. luciae,* $n = 59$ returns observed; *P. difficilis,* $n = 84$; *P. coreopsidis,* $n = 743$; *P. albipennis,* $n = 96$).

separated, entrances or communal nesting. Nevertheless, the data on nest departures and returns are useful for comparison with the foraging activity of *P. difficilis.* Figure 3 shows the frequency of returns per hour throughout the day (data from several days) for *P. difficilis* and *P. luciae.*

In 1988, in order to determine the number of trips required to provision a cell in *P. luciae,* females were captured returning to their nests. The volume of nectar carried in their crops was measured and the presence or absence of pollen loads noted. The nest was then excavated to determine the number of prior pollen trips that had been made for the cell currently being provisioned. Of the four bees caught returning on the first ($n = 2$) or the second ($n = 2$) trip, all had apparently full pollen loads and three out of the four had no detectable nectar in their crops. Of the four bees caught returning on the third trip all had detectable amounts of nectar in their crop and none had full pollen loads. These results indicate that *P. luciae* females require three trips to provision a cell: two pollen trips and a third trip on which nectar and, in some cases, a small amount of pollen are carried. Nectar loads ranged from 0.17–0.56 μl ($\bar{x} = 0.36 \pm 0.06$ μl; $n = 5$). Pollen balls were coated with a hydrophobic material.

Mating pairs of *P. luciae* were observed on *Prosopis* inflorescences, which were surrounded by clouds of hovering males throughout the day.

NEST OCCUPANCY AND STRUCTURE: None of the 13 nests completely excavated had more than one female to a nest. No data are available on the duration of nest occupancy, however, assuming one cell is provisioned per day, the number of completed cells per nest may give an indication of the number of days the nest was occupied. The number of cells per nest ranged from 2–21 ($\bar{x} = 12 \pm 1.5$; $n = 13$). Therefore, nests may be occupied, on average, 12 days—more than twice as long as nests of *P. difficilis.*

Like *P. difficilis* nests, *P. luciae* nests had symmetrical tumuli over the nest entrances. However, unlike nests of *P. difficilis,* most (80%) of the nests had up to five entrances which were separated by as much as 4 cm (Fig. 2c, d). The existence of multiple nest entrances is the most likely explanation for the anomalous foraging data collected in 1987. Tunnels entered the ground at an angle of less than 45° to the horizontal and followed a meandering pathway downward. At the depth of the cells, the main tunnel straightened out and became vertical. Tunnel diameter ranged from 1.8–2.0 mm. Unlike *P. difficilis* nests, *P. luciae* build very short horizontal laterals usually 0.25–0.5 mm but rarely reaching 2.5 cm. This made it possible to identify all the cells associated with a given nest. Cells ranged from 7–17 cm in depth (n = 152), were all subhorizontal and lacked a shiny hydrophobic lining. Data on the number of cells per nest are given above.

Parasites and predators of *P. luciae* are discussed in the section on *P. difficilis.*

Perdita (*Cockerellia*) *coreopsidis*

HABITAT: *Perdita coreopsidis* occurs from northern Mexico (Coahuila and Chihuahua) to Kansas, and from Galveston, Texas to eastern Arizona, and has been collected from May through September (Timberlake, 1954). The study site was located in Cochise Co., Arizona, 3.2 km east of Apache in the center of the San Simon valley, and the data presented below were gathered from 15 June to 4 July (19 nests, 25 females studied) and from 10 August to 10 September (23 nests, 87 females studied) 1987. The area is mixed Chihuahuan desert/grassland with abundant *Gaillardia pulchella* (Compositae), apparently the sole source of pollen and nectar for *P. coreopsidis* at this site. The soil consisted of fine sand which formed a very hard layer 5–15 cm below the surface. Below 15 cm the soil became moist and softer, remaining a uniform consistency to at least 1 meter. No other species of *Perdita* occurred at this site during the course of my work but other bees (*Agapostemon, Halictus, Melissodes, Triepeolus* and *Bombus*) were common on *Gaillardia.* A small herd of cattle grazed in the vicinity.

FORAGING AND PROVISIONING BEHAVIOR: Two discrete periods of adult activity were observed: from late May (and possibly earlier) until early July, and again from early August until early to middle September. These two periods probably represent two discrete generations because nests excavated during late July, when adults were not seen on flowers, contained only quiescent last instar larvae and no adults. The presence of pupae in nests excavated in mid-September suggests that a third generation of adults was about to appear (the *Gaillardia* was still in full bloom and many inflorescences had yet to open).

Figure 4 shows the pattern of foraging activity commonly observed in this species. Typically, bees made from six to eight closely-spaced pollen-gathering trips usually beginning at about 0830 hr. Pollen-collecting trips averaged 13.2 ± 0.4 min (n = 565 trips; range = 3–75 min) and time spent in the nest between pollen-collecting trips averaged 8.1 ± 0.3 min (n = 483; range = 1–56 min, data from second generation). The initial trips of the day tended to be the longest. After the completion of this series of pollen trips (referred to below as a "bout" of foraging) bees remained in the nest for 1 to 2 hours ($\bar{x}$ = 106.2 ± 43 min; n = 68) and then either made one trip, returning without pollen on the legs (cross-hatched boxes), or began another series of six to eight pollen trips (e.g., R; Fig. 4). Up to 70% of the females provisioned two cells per day but, as described

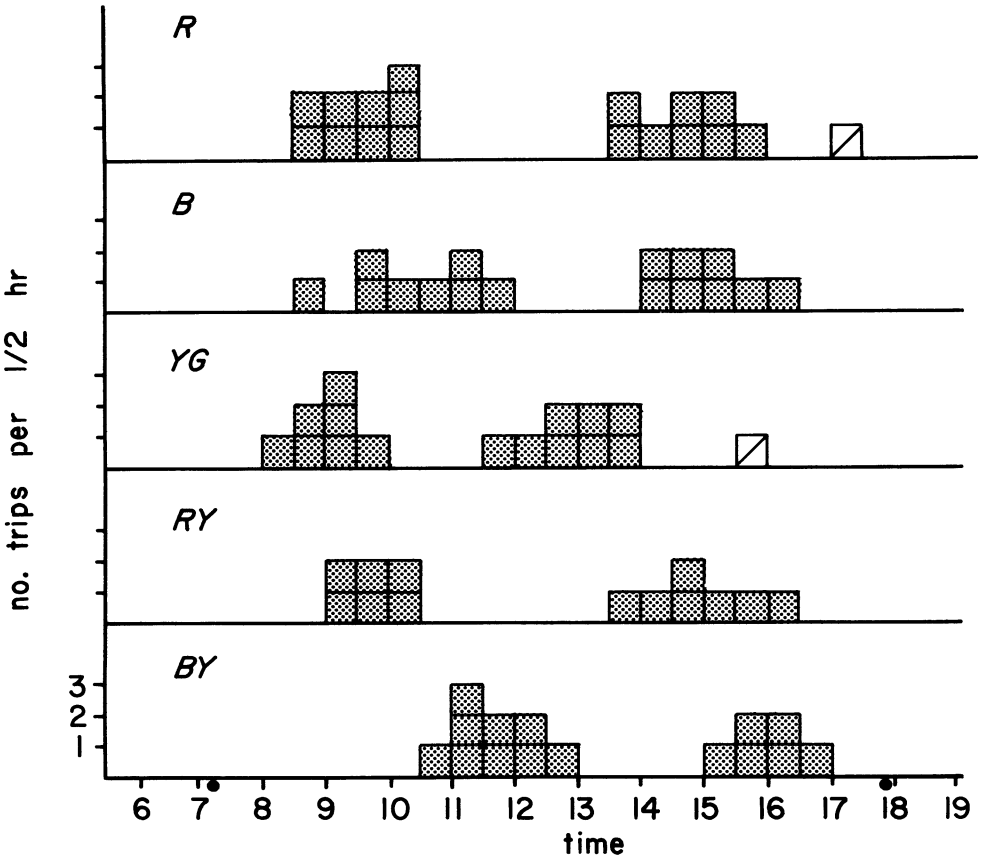

Fig. 4. Typical foraging behavior of *P. coreopsidis*. Data based on individuals in a communal nest (#16) on 3 September 1987. Symbols are the same as those used in Fig. 1. Letters (e.g., RY) indicate the colors of individually paint-marked bees.

below, this value changed over time (cf. Fig. 5). Between 1 and 2 hours after the completion of the second bout of foraging some bees appeared again and made one final trip of the day, returning without pollen (e.g., R, cross-hatched box; Fig. 4). Dissections of bees returning to nests without pollen on the legs indicated that the bees had been feeding since their crops were full of pollen grains and nectar. Bees in the process of provisioning a cell (i.e., those returning with pollen-filled scopae) did not have pollen in their crops. After making a feeding trip, bees almost never began foraging again on the same day. All foraging ended by 1800 hr (Fig. 3). Nest entrances remained open while the bees were foraging but soon after foraging stopped, entrances were loosely plugged with fine soil and remained so until foraging began again later in the day or on the following day.

From excavations of solitary nests or nests with only a few females, it is apparent that each bout of foraging represents all the pollen and nectar necessary for the provisioning of one cell. When a bee was collected leaving the nest on the first trip of the day ($n = 1$) and the nest was then excavated, I found only empty cells. When bees were collected in the middle of a series of foraging trips (e.g., after

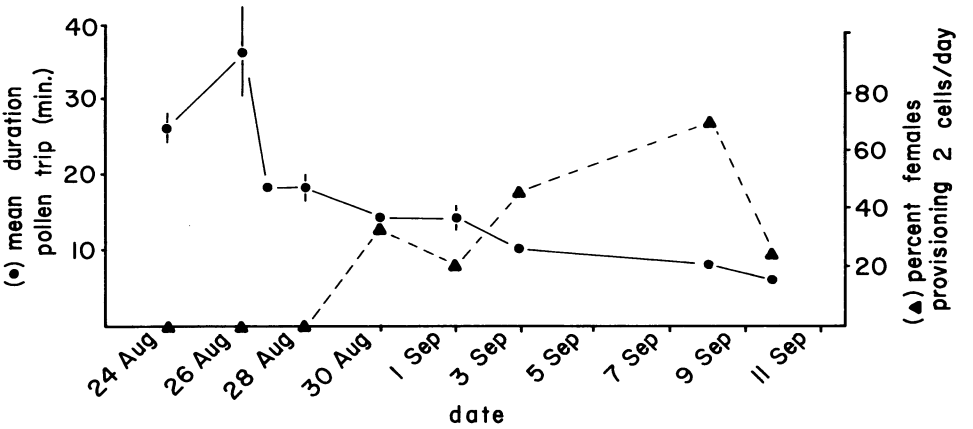

Fig. 5. Relationship between mean duration of pollen trips (closed circles, left-hand axis) and the percentage of females provisioning two cells per day (closed triangles, right-hand axis) for *P. coreopsidis* from 24 August to 11 September 1987. Standard error bars for mean duration pollen trips are shown for those means with standard errors greater than 1.0 min.

four pollen trips [$n = 2$], after five pollen trips [$n = 1$] and after six pollen trips [$n = 1$]) and the nest was dug, I found a pile of loose, relatively dry pollen in a single cell. However, nests excavated 1–2 hours after the resident had completed a bout of foraging ($n = 8$) contained only an empty cell and/or fully completed cells, each containing a spherical pollen/nectar ball. Therefore, each bout of six to eight pollen trips represents the entire provisioning of one cell; nectar must be added to the pile of dry pollen on the last or nearly last trip of the bout; at least 1–2 hours are required for pollen ball formation, egg laying and the closure of the lateral and, in some cases (see below), new cell construction; and, based on foraging behavior of individually marked females, an individual can completely provision up to two cells per day (see Fig. 4).

That six to eight pollen trips/bout provide all the provisions necessary for the provisioning of one cell was confirmed by counting the number of pollen grains per completed pollen ball ($\bar{x} = 417{,}496 \pm 34{,}935$; $n = 10$) and the number of pollen grains carried by a female returning to her nest with full scopae ($\bar{x} = 63{,}879 \pm 5665$; $n = 11$) using a HIAC/ROYCO particle counter model PC:320. Dividing pollen grains per pollen ball by pollen grains per foraging trip indicates that 6.5 pollen trips are needed for the completion of a cell.

Why did some bees, after completing a cell, begin another bout of foraging while others made only a feeding trip? Possession of a mature oocyte is one prerequisite for the provisioning of a second cell. In bees known to be provisioning a cell, the largest oocyte ranged in length from 1.1–1.28 mm ($\bar{x} = 1.20 \pm 0.05$, $n = 11$). In bees that had completed cells earlier in the day and later made feeding trips (rather than beginning to provision a second cell) the largest oocyte ranged from 0.6–1.1 mm ($\bar{x} = 0.96 \pm 0.06$; $n = 7$). The mean oocyte length of bees which provisioned a second cell of the day is significantly larger than those that did not and, therefore, the availability of a mature oocyte may limit the number of cells completed per day. Another related factor appears to be average trip time. Foraging data collected from 24 August to 10 September indicate a gradual decrease in

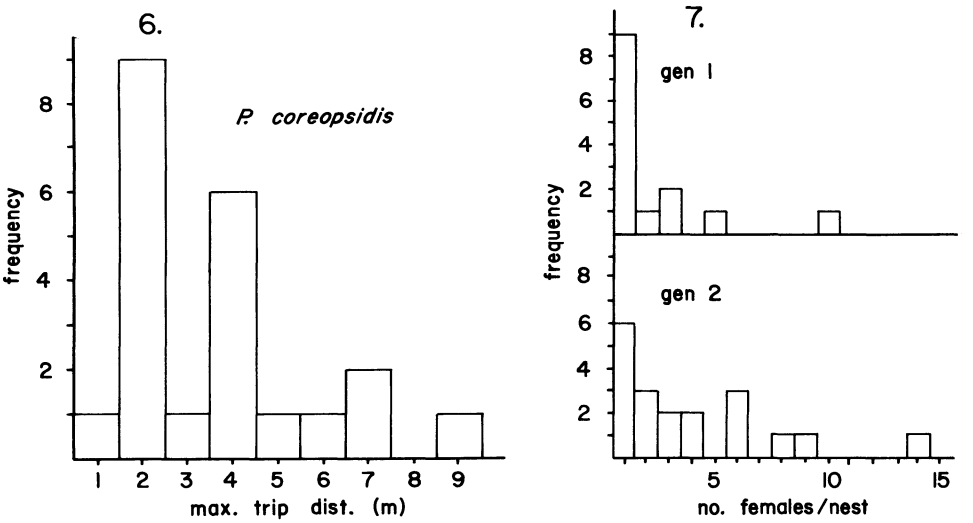

Fig. 6. Flight distances (nest to flower) for marked female *P. coreopsidis* ($n = 22$ observed flights).
Fig. 7. Distribution of number of females/nest for *P. coreopsidis* during generations one and two ($n = 33$ nests censused).

mean pollen trip time ($r = -0.84$) with a simultaneous increase in the percentage of observed bees provisioning a second cell per day (Fig. 5). The decline in trip time is most likely due to an increase in the number of flowers in bloom. Apparently, shorter foraging trips make the time required to complete the first cell brief enough that a second cell can be completed the same day.

Cell construction most likely occurred in the late afternoon or at night, as in many bees (Michener, 1974), because nests excavated early in the morning contained empty, unprovisioned cells, while nests excavated later in the day, after foraging began, did not. There is also suggestive evidence that when a bee provisioned a second cell of the day, the cell was constructed during the 1–2 hours that the bee remained in the nest following the first foraging bout. The mean time spent in the nest between the end of the first foraging bout and a feeding trip was 96.4 ± 3.8 min ($n = 42$) while the time spent in the nest between the end of the first foraging bout and a second foraging bout was 140.9 ± 9.3 min ($n = 17$)—a statistically significant difference at the 0.01% level. Therefore, when bees provisioned a second cell they stayed in the nest, on average, an extra 45 min, presumably reflecting the time needed to construct the second cell of the day.

Data on foraging distances of marked bees (Fig. 6) indicate that most females foraged less than 5 meters from the nest. There was no indication that bees returned repeatedly to the same flowers or that nest-mates forage in the same direction.

Mating was observed exclusively on *Gaillardia* inflorescences, where males aggressively pounced on foraging females. Adult males were observed leaving nests on five occasions, but, because males were never seen entering nests, it is likely that these departing males had recently eclosed and were leaving the natal nest for the first time.

NEST OCCUPANCY AND NEST STRUCTURE: *P. coreopsidis* is a facultatively communal species at the locality studied. Figure 7 shows the number of nest occupants

during the first and second generations. The majority of nests contained one adult female but as many as 14 active adult females per nest was recorded.

The proportion of single-female nests in the first generation (64%) is significantly greater than the proportion of single-female nests in the second generation (32%). Whether this difference is biologically meaningful or due to sampling bias is unclear. It is possible that a greater proportion of females in the first generation initiate new nests rather than re-use their natal nest.

Early in the second generation 11 out of a total of 87 females observed made only one feeding trip per day, rather than making repeated pollen-collecting trips. This behavior was suggestive of a reproductive division of labor or intraspecific cleptoparasitism. However, in all cases these non-foragers eventually foraged normally. All subsequent observations supported the idea that the females in a communal nest are all reproductively active.

No tumuli were observed at any nests. Rarely nests were found to have more than one entrance but all entrances were close together. In all nests excavated the main tunnel (3.5–4.0 mm diameter) entered the ground at an angle of less than 10° to the horizontal for the first 2–4 cm (Fig. 8). After the initial subhorizontal section, the tunnel followed a meandering pathway downward. Laterals branched more or less horizontally off the main tunnel, were slightly smaller in diameter and followed a more contorted path than the main tunnel, often going upward in places. Laterals leading to completed cells were always tightly filled with dirt. Laterals leading to cells currently being provisioned were open. Nests contained from 1–34 cells which ranged from 18–65 cm in depth with most cells located below 35 cm (14 nests excavated). Pollen balls were spherical and covered with a clear hydrophobic coating. Cells are apparently unlined.

Unlike many other communal bees (e.g., *Lasioglossum* [*Sphecodogastra*] *galpinsae,* as *Evylaeus,* Bohart and Youssef, 1976; *Anthophora peritomae,* Torchio, 1971), *P. coreopsidis* cells were not clustered in a way that would indicate that each female occupied and constructed cells in a different, widely separated, region of the nest. Commonly the cells currently being provisioned by the occupants of a communal *P. coreopsidis* nest were all clustered in the same region of the nest, as in *Agapostemon virescens* (Abrams and Eickwort, 1981).

PARASITES AND PREDATORS: Adults of an undescribed species of *Sphecodes* roughly equal in size to *P. coreopsidis* were collected at the study site. One *Sphecodes* was observed entering a communal *P. coreopsidis* nest at 0911 hr on 24 June, the same day a female phorid fly (*Phalacrotophora halictorum* Melander and Brues) was collected leaving the nest. The residents continued foraging as usual. For most of the following morning (25 June), the females in the nest foraged normally and five of the 10 females had completed an entire bout of foraging. However, when the two bees still foraging at 1145 hr (BR, YG) entered the nest (one with and one without pollen loads), they both shortly left the nest, one still carrying pollen. During the following 45 min these two bees repeatedly entered the nest (six and eight times). Eventually, the one with pollen groomed it off and continued trying to enter. I captured one of these bees and the other disappeared. When this nest was excavated on 27 June three dead (paint-marked) females were found in the nest, presumably killed by the *Sphecodes.* One cell contained a minute *Sphecodes* larva. Seven of the 30 cells had small fly larvae (up to three per cell), most likely the offspring of the female caught leaving the nest on 24 June. On

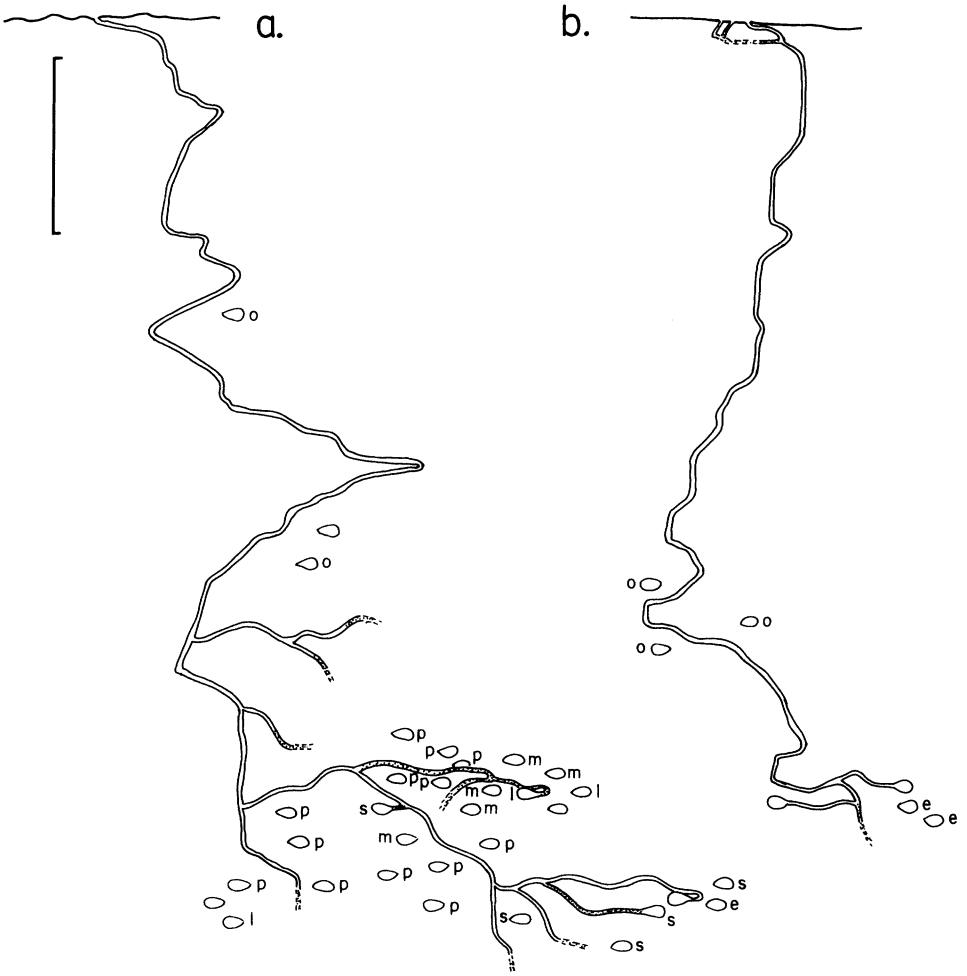

Fig. 8. Nests of *P. coreopsidis.* Symbols are the same as those used in Fig. 2.

another occasion, the resident of a solitary nest, who had foraged normally for three consecutive days, ceased foraging on the fourth day (17 June) and was not seen again. Late in the same morning a *Sphecodes* was collected leaving the nest. On 30 June the nest was excavated and another adult *Sphecodes* was found inside. Unfortunately, the tunnel was lost before cells were found, so no rate of parasitism could be calculated. These observations suggest that this species of *Sphecodes,* after entering the host nest, kills the residents and oviposits in cells with available pollen balls. It was not possible to determine whether adult or first instar *Sphecodes* kill the host egg or larva.

Perdita (*Cockerellia*) *albipennis*

HABITAT: *P. albipennis* ranges from west Texas to New Mexico and north to Idaho, Wyoming and Nebraska, and has been collected from July to September (Timberlake, 1954). Twelve nests were found along the edge of a mixed soybean/

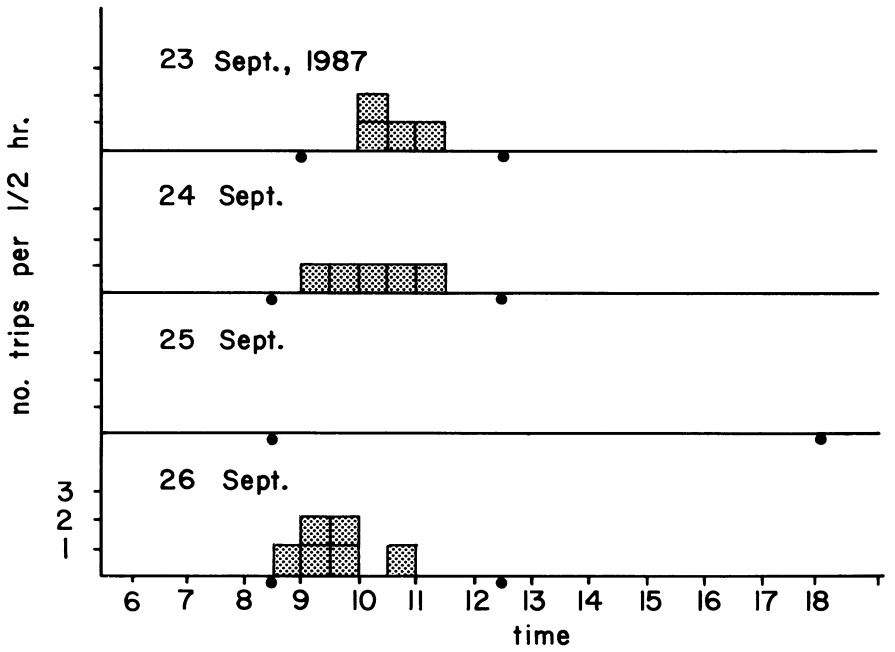

Fig. 9. Typical foraging behavior of *P. albipennis*. Data are from a single bee (GY) occupying nest #21 from 23 September to 26 September. Symbols are the same as those used in Fig. 1.

sunflower (*Helianthus annuus* and *H. tuberosa* [Compositae]) field 4 miles NW of Lawrence, Kansas, and were studied intensively from 17 September to 30 September 1987. The soil at this site consists of fine, loosely packed sand deposited as a result of flooding of the Kansas River in 1951 (Michener, 1963, gives details).

FORAGING AND PROVISIONING BEHAVIOR: Females of *P. albipennis* were observed collecting pollen and nectar and mating both on *Helianthus annuus* and *H. tuberosa*. Occasionally bees were seen on *Heterotheca* (Compositae) but did not collect pollen from this plant. Foraging typically began between 0800 and 0900 hr (Fig. 3) and consisted of four to six closely-spaced pollen trips (Fig. 9). On average, pollen-collecting trips lasted 17.6 ± 1.2 min (n = 60; range = 4–58 min) and bees spent 5.3 ± 0.5 min (n = 55; range 2–17 min) in the nest between trips. Some bees were observed to make a single trip late in the day (usually after 1700 hr) returning to the nest without pollen. This is most likely a feeding trip as in *P. coreopsidis*. Two feeding trips observed lasted 46 and 63 min.

Nest excavations indicate that each bout of foraging provides the pollen and nectar necessary to provision one cell and that the pollen is loosely piled in the cell after each trip, as in *P. coreopsidis*. Nest entrances are closed with loose soil approximately 5 min after the last return to the nest. This is the time it takes a bee to crawl down to her cell, unload the pollen and return to the nest entrance. One bee was collected when she returned to the nest entrance for closure and excavation of the nest indicated that she had deposited all the pollen in one cell and had not yet added nectar. Therefore, all the nectar added to the pollen ball is carried into the nest on the last return, and pollen ball formation occurs after nest closure.

Females of *P. albipennis* did not provision a cell on approximately one out of every three days (e.g., nest #21 on 25 September; Fig. 9). Typically the female would make just one trip, returning without pollen on her legs. Dissection of one female collected returning without pollen on a "day off" indicated that she had an apparently mature oocyte and a small amount of pollen in her crop. When the nest was excavated no empty cell was found (Fig. 10a). Why females take "days off" is unclear and apparently unrelated to weather. This behavior was very rarely observed in *P. coreopsidis* except in what appeared to be young females with undeveloped ovaries (see above).

NEST OCCUPANCY AND STRUCTURE: All 12 nests contained a single female per nest. However, one nest excavated (Fig. 10a) had at least 34 cells, suggesting that it may have been occupied by more than one female during the summer. The three other nests excavated had three to nine cells, values consistent with these nests having been entirely solitary. No new nests were observed being started during this study.

No tumuli were observed over nest entrances (Fig. 10). As in *P. coreopsidis,* tunnels (3.5–4.0 mm diameter) usually entered the ground at a small angle to the horizontal. This initial section of the tunnel could remain subhorizontal and just beneath the surface for up to 10 cm. Thereafter the tunnel followed a fairly straight path downward. Laterals typically branched horizontally off the main tunnel but were often shorter and more easily followed than in *P. coreopsidis.* Only laterals leading to cells being provisioned at the time the occupant was caught were open. Laterals to finished cells were tightly filled with soil. In the four nests excavated, cells ranged in depth from 30–76 cm with the majority located below 60 cm. Pollen balls and cells were as described for *P. coreopsidis.*

During excavation of the four *P. albipennis* nests no old cells were encountered, suggesting that, unlike *P. coreopsidis,* females of *P. albipennis* do not re-use their natal nests.

PARASITES AND PREDATORS: Female *Sphecodes manni* Cockerell and *S.* near *autumnalis* Mitchell began flying over the nest site between 1000 and 1100 hr. Entrances of *Sphecodes* into *P. albipennis* nests were observed twice (nests #10, 11). Both nests entered had been inactive for 2 days and thus presumably did not contain females inside. One nest entrance was open (#10) and the other closed with loose soil. On both occasions the parasite entered the nest around 1130 hr. A female *S. manni* was collected leaving each nest between 1100 and 1130 hr the following day and one female *S.* near *autumnalis* was collected leaving nest #11 on the next day. Nest #10 was excavated 5 days later and two cells contained a *Sphecodes* larva (the third cell of this nest had a moldy pollen ball). In another nest one nomadine larva and 18 *P. albipennis* larvae were found. No adult nomadines were observed at the study site but it is likely this larva is *Neolarra,* reported to be a parasite of other species of *Perdita* (Rozen, 1967).

Discussion

A summary of the data presented here and of published data on other species of *Perdita* is given in Table 1. The behavior of *P. difficilis* and *P. luciae* differs little from what has been reported for other members of the subgenus *Perdita* (Custer, 1929; Michener and Ordway, 1963; Rozen, 1967; Torchio, 1975; Eickwort, 1977). As far as is known, all species of *Perdita* sensu strictu are solitary,

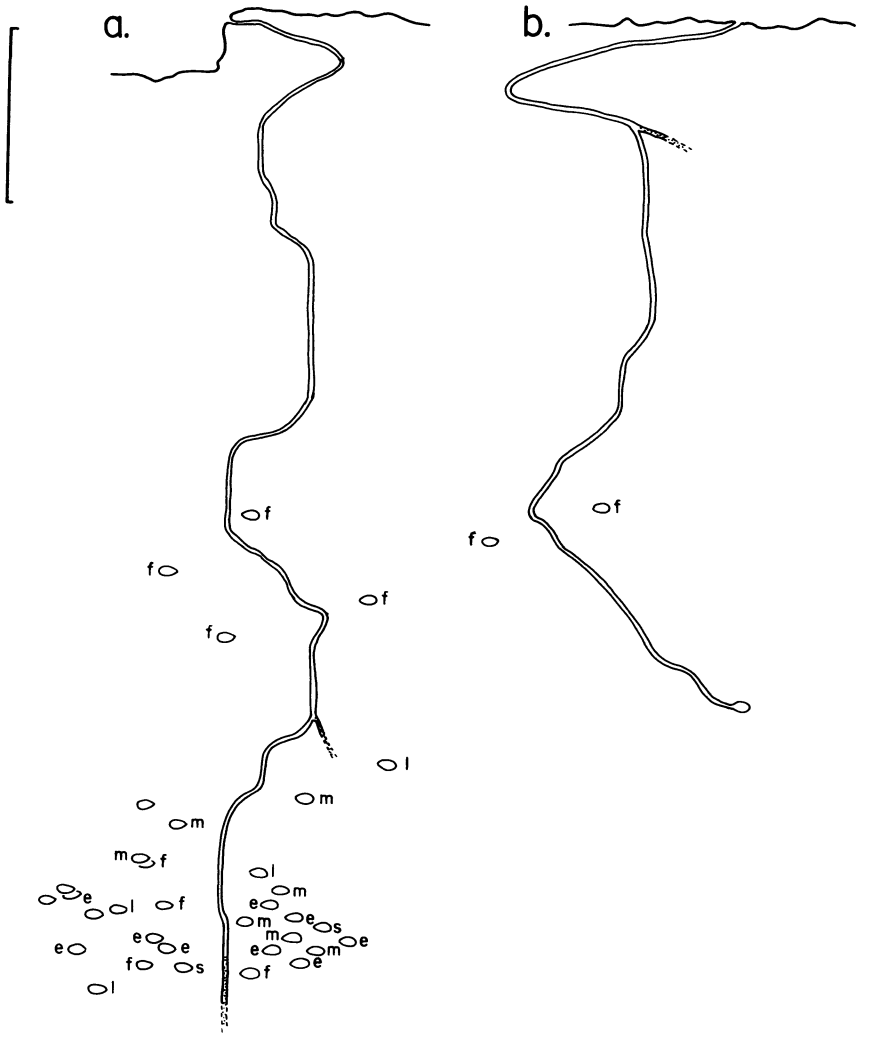

Fig. 10. Nests of *P. albipennis*. Symbols are the same as those used in Fig. 2. A cell (unlabelled) was currently being provisioned when the bee in nest 'b' was collected.

provision few cells per nest (one in the case of *P. maculigera,* Michener and Ordway, 1963), occupy up to several nests per lifetime and make unlined cells and spherical pollen balls coated with a shiny hydrophobic material.

P. difficilis and *P. luciae,* though similar morphologically, differ in a number of behavioral traits: (1) female *P. difficilis* forage during two distinct periods of the day, near dawn and dusk (Fig. 3), while *P. luciae* forage during late morning and mid-day; (2) *P. luciae* build shallower nests, with cells located between 7 and 17 cm below the surface, while *P. difficilis* cells were found from 10–30 cm deep; (3) *P. luciae* build, on average, 12 cells/nest while *P. difficilis* build an average of 5 cells/nest; and (4) *P. luciae* build shorter laterals than *P. difficilis.*

P. difficilis and *P. coreopsidis* are unusual among solitary bees in provisioning

two cells per day. Most solitary bees provision one or fewer cells per day. Exceptions to this rule are the nocturnal halictid, *Lasioglossum* (*Sphecodogatra*) *galpinsiae,* which provisions up to four cells per 24 hr period (Bohart and Youssef, 1976) and *Diadasia opuntiae,* which provisions up to three cells per day (Ordway, 1984).

Only one other species belonging to the subgenus *Cockerellia* has been studied previously. Michener (1963) excavated three nests of *P. lingualis* Cockerell in the banks of the Kansas River (Lawrence, Kansas) and found this species to be both bivoltine and communal (7–10 females/nest; $n = 3$). All three species of *Cockerellia* are similar in making very deep nests (0.5–1.0 m), in the overall pattern of nest architecture and in having apparently unlined cells with spherical, coated pollen balls. Although *P. albipennis* and *P. lingualis* are apparently quite closely related, they differ conspicuously in behavior, the former being apparently solitary and univoltine, the latter communal and bivoltine. *P. coreopsidis* differs behaviorally from *P. albipennis* in a number of ways: the former is multivoltine, facultatively communal, makes six to eight pollen trips per cell, forages all day long (Fig. 3) and consequently can provision up to two cells per day, while *P. albipennis* appears to be univoltine, solitary, makes five to six pollen trips per cell and forages only during the morning (Fig. 3), making the completion of two cells per day impossible. Feeding trips of the kind observed in *P. coreopsidis* have been reported for other species of bee (e.g., *Dasypoda plumipes,* Lind, 1968).

In general, the nesting behavior of members of the subgenus *Perdita* differs from those in the subgenus *Cockerellia* in the following ways: (1) *Cockerellia* require more pollen trips per cell, (2) while communality appears to be quite common in *Cockerellia,* no species of *Perdita* sensu strictu have been found to be communal, (3) *Cockerellia* build deeper nests with longer laterals, (4) nests of *Cockerellia* lack tumuli in contrast to nests of *Perdita* sensu strictu and (5) while females of *Perdita* sensu strictu appear to construct and occupy more than one nest in their lifetimes, those of *Cockerellia* seem rarely to switch nests, most likely because they remain in their natal nests. As a result, nests are occupied for a prolonged period of time, usually greater than the life of an individual bee.

The fact that solitary and communal nesting occurs within the same species (*P. coreopsidis*) leads one to wonder why females of this species, or any other facultatively communal species, choose one option over the other. Because (1) marked females were never observed to switch nests, (2) no females were ever observed digging new nests and (3) nests contained cells from previous generations, the communal associations observed in this study probably arise because females remain in their natal nests. If this is true, the number of females in a nest is determined simply by the number of female offspring of the previous generation who successfully emerge as adults, and therefore, communal nest-mates may be close relatives. The cost in time and energy of new nest excavation may make it undesirable for a female to try starting her own nest. This cost could be especially high at the *P. coreopsidis* locality because of a very hard, dry layer of soil beneath the surface.

If females commonly remain in their natal nests, why do nest populations not grow beyond the observed maximum of 14 females/nest? Either dispersal and solitary nest initiation by some females, or high mortality, or both, could limit nest population size. If new nest initiation at the study site was common, however,

Table 1. Summary of nesting and foraging behavior for *Perdita* species studied to date. "Prolonged" nest occupancy refers to species in which nests are occupied for more than the life of an individual bee.

Subgenus Species group Species	Median no. pollen trips per cell (range)	Number cells completed per day	Foraging period	Mean ± SEM number of females per nest (range; *n*)	Median duration nest occupancy in days (range)	Estimated number generations per year	Presence/ absence tumulus	Number cells per nest (*n*)	Range of cell depth in cm	Range of lateral length in cm (*n*)	References
Cockerellula											
P. opuntiae			9:30–13:00	8.9 ± 1.5 (1–38; 30)	prolonged		–	215 (1)	7–10		Custer, 1928; Bennet and Breed, 1985
Cockerellia											
P. albipennis	5.5 (5–6)	1	8:30–12:00	1		1	–	3–37 (4)	30–76		This paper
P. coreopsidis	6.5 (6–8)	1–2	7:30–18:00	3.2 ± 0.6 (1–14; 33)	prolonged	>2	–	1–34 (14)	18–65		This paper
P. lingualis				8.0 ± 1.0 (7–10; 3)	prolonged	2	–	68 (1)	15–85	0.2–6.0	Michener, 1963
Perdita											
Halictoides											
P. halictoides				1		>1	+	1–3	17–30	0.8–1.7 (3)	Eickwort, 1977
P. sexmaculata				1					4.8–8.3		Rozen, 1967
Octomaculata											
P. maculigera	2	2		1	1	1	+	1	5.5–30		Michener and Ordway, 1963
P. nuda	4.5 (4–5)		9:30–16:30	1		1	+	1–8	15–78	1.1–7.0	Torchio, 1975
P. octomaculata	4		9:10–2:00	1	1 (1–9)	1	–	1–5	21–88	0.8–9.0 (7)	Eickwort, 1977

Table 1. Continued.

Subgenus Species group Species	Median no. pollen trips per cell (range)	Number cells completed per day	Foraging period	Mean ± SEM number of females per nest (range; *n*)	Median duration nest occupancy in days (range)	Estimated number generations per year	Presence/ absence tumulus	Number cells per nest (*n*)	Range of cell depth in cm	Range of lateral length in cm (*n*)	References
Sphaeralceae											
P. confusa									16		Rozen, 1967
P. difficilis	2.5 (2–3)	1	7:00–9:00 and 17:00–19:00	1	1 (1–5)	1	+	1–20 (12)	10–30	1.5–6.0 (12)	This paper
P. luciae	2.5 (2–3)		9:00–13:00	1		1	+	2–21 (13)	7–17	0.25–2.5 (15)	This paper
P. zebrata				1			+	5–8	18		Custer, 1929; Rozen, 1967

I would have seen tumuli, but none were observed. Perhaps those females that initiate new nests do so after dispersing away from the parental nest site.

Irrespective of how the number of females sharing a nest is determined, one can ask how life in a solitary nest differs from life in a communal nest. In terms of foraging behavior, there do not appear to be any differences: the duration of foraging trips, time spent in the nest between trips, the time of day spent foraging, the number of trips required to provision a cell and the number of cells completed per day are not significantly different in solitary and communal nests. It has been suggested (Lin and Michener, 1972; Michener, 1974; Abrams and Eickwort, 1981) that one consequence of communal nesting could be improved defense against parasites. Abrams and Eickwort (1981) found that the rate of parasitism by *Nomada articulata* decreased as the number of females per nest increased in the communal halictid *Agapostemon virescens.* They attribute this to nest guarding behavior, a common feature of many bee societies. In *P. coreopsidis* no guarding behavior was ever observed and therefore communality in this species may not necessarily result in reduced parasitism. Unfortunately, parasitism was too infrequent during the *P. coreopsidis* study to draw any quantitative conclusions. However, anecdotally, the nest with the highest rate of parasitism was one of the most populous nests, with 10 females. Perhaps parasites are attracted to the frequent departures and returns of bees in more populous nests. In summary, there were no obvious differences observed between communal and solitary nesting.

One potential outcome of communal nesting could be intraspecific cleptoparasitism, a behavior widespread among the bees (Eickwort, 1975; Wcislo, 1987). Although no evidence for cleptoparasitic behavior was obtained in this study, the situation appears ideal for such behavior to evolve because (1) cells currently being provisioned are often clustered in the same area of the nest (see above), (2) nest-mates would have access to each other's cells during provisioning bouts, (3) most residents of a communal nest have a fully mature oocyte while cell provisioning is taking place and (4) egg production is rapid, with some females capable of laying two eggs per day. Intraspecific cleptoparasitism, viewed in a different light, is reproductive division of labor. If nest-mates of *P. coreopsidis* are truly related, as suggested above, kin-selection would be expected to favor altruistic (or conversely, parasitic) behavior in this species. It is unclear what factors, if any, are counteracting the apparent impetus toward reproductive division of labor in *P. coreopsidis.*

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Beltsville, Maryland) identified the phorid fly. Penelope Kukuk and Bill Wcislo commented on earlier drafts of this paper. I am also grateful to the two reviewers for their significant improvements. This research was supported, in part, by a Theodore Roosevelt Memorial Grant from the American Museum of Natural History. Contribution No. 2067 from the Snow Entomological Museum, University of Kansas, Lawrence.

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