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The Nesting and Foraging Behavior of *Perdita texana* (Cresson) (Hymenoptera: Andrenidae)

JOHN L. NEFF¹ AND BRYAN N. DANFORTH^{2,3}

ABSTRACT: *Perdita (Macrotera) texana* is a ground nesting, univoltine, facultatively communal bee species found in western Texas and southern Oklahoma. As many as 28 females may share a single nest, but most nests have no more than five females and approximately 25% of the nests are occupied by a single female. Most nests are constructed *de novo* each year but some females reuse their natal nests. There is no apparent reproductive division of labor among nestmates, as all residents of communal nests forage and have developed ovaries. Nests consist of a single main tunnel and several laterals leading to brood cells. Females provision a single cell per day with pollen and nectar collected exclusively from *Opuntia (Platyopuntia)* spp. All evidence indicates that *P. texana* is a successful pollinator of *Opuntia*. Cell provisioning requires an average of 8 pollen trips and occasionally an additional nectar-only trip. Pollen trips average 6 min, while nectar trips average 17 min. The entire cell-provisioning process requires 72 min on average. *P. texana* is unusual among bees in that males are regular occupants within nests. Males enter nests throughout the afternoon and reside there until the following morning, leaving just prior to the beginning of cell provisioning by females. The biology of *P. texana* is compared to that of other *Perdita* species, and the evolutionary implications of communal nesting are discussed.

The genus *Perdita* contains over 600 species of solitary or communal bees which are most common in the arid southwestern U.S. and northern Mexico. The biology of only a fraction of the species has been studied (review by Rozen, 1967; Torchio, 1975; Eickwort, 1977; Bennett and Breed, 1985; Danforth, 1989). The purpose of this paper is to describe the foraging and nesting behavior of a relatively basal member of the genus, *P. (Macrotera) texana*.

P. texana is an interesting species for a number of reasons. First, communal nesting, the sharing of a nest by two or more conspecific females who build and oviposit in their own cells (Eickwort, 1981), raises some interesting evolutionary questions. For example, what are the origins of communal nesting, and what are the implications of communal nesting for the evolution of more elaborate levels of social behavior (Lin and Michener, 1972)? Second, *P. texana* is unusual among solitary bees because some males spend extended periods of time in the nests of females, where mating may take place. Males enter nests in the afternoon (1130–1500 hr), and remain until the following morning, when they leave approximately one hour before the peak of female foraging (peak of male departure: 1000–1100 hr; peak female foraging: 1200–1330 hr). The existence of morphological and behavioral polymorphism in males of *P. texana* may shed light on theories concerning the origin and maintenance of alternative reproductive behaviors (Austad, 1984) and evolutionarily stable strategies (Dawkins, 1980). Studies of male be-

¹ Central Texas Melittological Institute, 7307 Running Rope, Austin, Texas 78731.

² Snow Entomological Museum, Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

³ Current address: Department of Entomology, Smithsonian Institution, National Museum of Natural History, Washington, DC 20560.

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havior, conducted along with the observations presented here, will be reported elsewhere (Neff and Danforth, in press).

Materials and Methods

This study was conducted at three localities in Texas over the course of ten years (1981–1990), although nest-related activities were studied in detail only from 1987–1989. Studies were restricted to mating and foraging behavior at Brackenridge Field Laboratory (BFL) of the University of Texas, Austin, Travis Co., since no nests were discovered there. BFL contains a mixture of mountain cedar (*Juniperus ashei*) and live oak (*Quercus fusiformis*) with small areas of grassland. *Opuntia macrorhiza*, the most abundant cactus, occurs at low density throughout the grassland and sparsely wooded areas. The *P. texana* population at BFL was always quite small and apparently became extinct sometime between 1986 and 1987. Studies of nesting biology were conducted at Pedernales Falls State Park (PF), Blanco Co., and a series of sites 11–14 miles north of Coleman along Highway 283, Coleman Co. (CC). PF consists mostly of open mountain cedar and live oak woodland interspersed with areas of grassland habitat. *Opuntia engelmannii*, *O. macrorhiza* and *O. leptocaulis* are locally abundant at PF. Soil types at PF are quite hard and shallow with underlying limestone, typical of the Edwards Plateau, although there are also scattered areas of deeper, sandy soils. The CC sites are in heavily grazed upland grasslands with heavy, stony clay soils and many rocky outcrops. *Opuntia engelmannii* is common in this area, particularly on slopes and rocky outcrops but also scattered throughout the grasslands.

Female *P. texana* were individually marked on the mesoscutum with one or two spots of enamel paint. Provisioning rates of females were determined both by timing unimpeded activity at nests or, when nests were more widely scattered, by covering entrances with plastic cups and quickly removing and replacing them to allow entrance or departure. The presence of pollen loads on entering females was also noted. Nests were excavated by blowing a fine mist of talcum powder down the tunnel to mark its path before soil was carefully dug away. Nests were usually excavated late in the day (after 1600 hr) to insure that all residents were present. Pollen-load weights and fresh-dry weight relations are based on samples of females collected returning to nests at PF and CC in May, 1989. Pollen balls used for dry weight measurements were collected at CC in May, 1988. Adults and pollen balls were dried at 50°C for 1–2 days.

Cactus nomenclature is modified from Benson (1982). We use *O. engelmannii* as the name of the common large prickly pear of central Texas, commonly referred to as *O. lindheimeri* (Parfitt and Pinkava, 1988), and *O. macrorhiza* for the small prickly pear with tuberous roots. The latter may intergrade with *O. compressa* in this area. Plant vouchers are deposited at the University of Texas Herbarium (Plant Resources Center).

Timberlake (1958) recognized two subspecies of *P. texana* (*P. t. texana* and *P. t. abluca*), but we find that bees from Bastrop (the presumed type locale of *P. texana*) intergrade with individuals from more westerly populations and thus we recognize only a single taxon, *P. texana*. Insect voucher specimens are deposited in the Snow Entomological Museum, University of Kansas, Lawrence, and the Central Texas Melittological Institute, Austin.

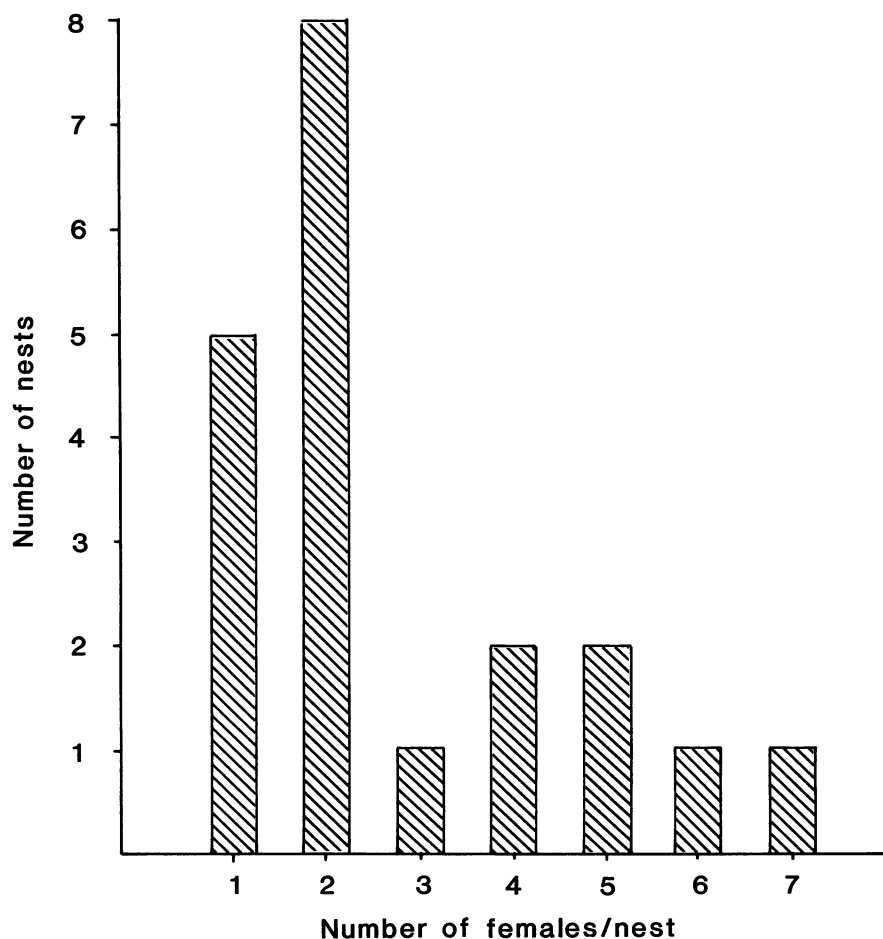


Fig. 1. Histogram of the number of females per nest in 20 nests excavated at CC.

Results

NEST OCCUPANCY AND STRUCTURE: *P. texana* commonly nests gregariously (*contra* Thornhill and Alcock, 1983). Aggregation size varied from single, isolated nests at PF and small, scattered aggregations of 4 to 10 nests found at several sites at PF as well as near Sayersville, Bastrop Co., Texas, and Langtry, Val Verde Co., Texas, to very large aggregations at CC involving hundreds of nests, with up to 12 nests/m². Nests at all localities were restricted to flat or gently sloping surfaces with little or no vegetative cover. All nests at PF were found in areas of bare soil or very sparse herbaceous vegetation, primarily on dirt roads and fire trails, while nests at CC were scattered amid low, sparse vegetation as well as on an abandoned dirt road. Soils at all nest sites are reasonably soft and easily excavated after spring rains but bake to a brick-like composition by mid-June. Soils ranged from evenly textured red soils with a high coarse sand component (two sites at PF and Sayersville) to very stony dark soils with a high clay content (CC and one site at PF).

Female *Perdita texana* are facultatively communal with at least some communal

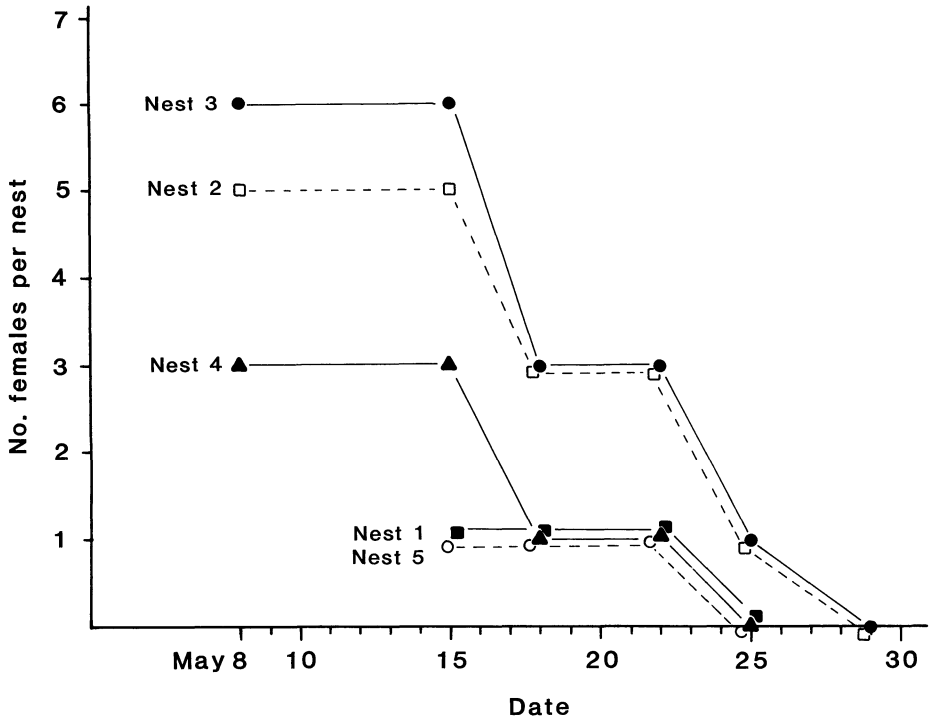


Fig. 2. Relationship between the number of females per nest and date, for five nests studied at PF in 1989.

nests occurring at all sites we studied. The number of females per nest in 20 occupied nests excavated late in the day at CC ranged from 1–7 ($\bar{x} = 2.8 \pm 0.4$) but 65% of the nests had only 1–2 females per nest (Fig. 1). These figures probably underestimate the maximum number of females per nest since nests were excavated towards the end of the flight season. Study of the number of foraging females at five nests in a 0.5 m² area at PF indicated the number of females per nest declines through the season (Fig. 2). It is also clear that some nests never have more than one female. The greatest numbers of nest residents were seen at two unusual nests at PF, with 28 and 25 females per nest (based on counts of foraging females). These nests were occupied the previous year and had 12 and 10 females per nest.

Forty-seven of the 51 females dissected from 12 communal nests at CC had fully mature ovaries. Three of the four bees with undeveloped ovaries appeared to be teneral as judged by pale coloration and/or extensive fat body. Therefore, there is no evidence of reproductive division of labor among females sharing a nest. That *P. texana* is communal rather than quasisocial is supported by two observations: (1) the number of females in nests usually equalled the number of open or recently completed cells (Fig. 3a–d); and (2) individually marked bees varied little in the number of foraging trips taken on a given day (between 7 and 9; see below).

Ten bees collected during nest excavations were in the process of forming pollen balls but had not yet laid their eggs. The mean length of the largest oocyte in these

females was 1.89 ± 0.06 mm, and the mean width of the largest oocyte at its midpoint was 0.39 ± 0.02 mm ($n = 10$). Freshly laid eggs measured 2.20 ± 0.04 mm by 0.49 ± 0.03 mm ($n = 8$).

P. texana is typically active throughout May in central Texas, a period which roughly coincides with the peak bloom of *Opuntia* (*Platyopuntia*) species. Nest areas are commonly re-occupied (at least 5 consecutive years at PF), and at least some individual nests are re-utilized as well. However, nest re-use is apparently uncommon, as most nests appear to be freshly initiated each spring. Individual nests may be active for up to 28 days, although no marked individuals were active for more than 3 weeks (males: 15 days; females: 18 days). Nest switching appears to be a rare event. One female at PF was observed to abandon the solitary nest in which she had spent the previous night and enter a nearby communal nest, where she commenced provisioning. Furthermore, at both PF and CC females without external pollen loads were commonly observed in search behavior at nest sites. It is not clear if these were simply "lost" females, females initiating new nests, or females in the process of switching to new nests. *P. texana* is almost certainly univoltine, but emergence is not highly synchronous, a fact which may explain the presence of teneral females in the latter half of the flight season (see above).

New nests have a conspicuous, low conical tumulus, 4.0–7.5 cm in diameter, with the entrance in the center, or on the upslope if on a slanting surface. Tumuli of older nests (> 10 days) are usually not added to or replaced if removed by wind or rain. Nests are shallow, with most cells from 4–13 cm deep, rarely to 20 cm. Nest architecture is simple, consisting of a vertical main tunnel which descends 3.5 to 4.5 cm and then abruptly turns, giving rise to descending subhorizontal laterals leading to the cells being provisioned (Fig. 3). The main tunnel and laterals are unlined and vary in diameter from 4.25 to 4.7 mm. Nests with many females had extensive series of branching laterals (Fig. 3b). During cell provisioning the main tunnel and laterals remain clear of soil, but in nests excavated late in the day, after all females had returned to their nests, the main and lateral tunnels were often filled with loose soil.

Excavated nests had from 1 to 21 cells ($n = 20$). Cells contained either provision masses with eggs, feeding larvae, moldy provision masses or defecated prepupae, but no pupae or pharate adults were ever found. Cells were arranged singly, each at the end of a short lateral (1.5–2.0 cm long), and are ovoid, averaging 10.2 ± 0.4 mm ($n = 6$) long and 5.8 ± 0.1 mm ($n = 8$) in maximal cross-sectional width, with the long axis more or less horizontal. All cells had a thin, translucent, hydrophobic lining which could be peeled away from the wall. This lining did not extend onto the cell cap or along the tunnel walls. The cell cap was weakly concave and distinctly spiraled on the inner surface. Laterals were backfilled from the cell closure to the point of branching. The cap typically intergrades with soil filling the lateral and usually cannot be separated as a distinct structure. Completed nests were left open; thus it is likely that females simply keep working until they die.

Provision masses are spherical, evenly moist balls of cactus pollen averaging 3.9 ± 0.1 mm ($n = 4$) in diameter. Unlike the provision masses of some other *Perdita* (Rozen, 1967; Danforth, 1989) those of *P. texana* lack an obvious hydrophobic coating. Eggs are deposited on top of the pollen ball with both ends of the curved egg contacting the provision mass.

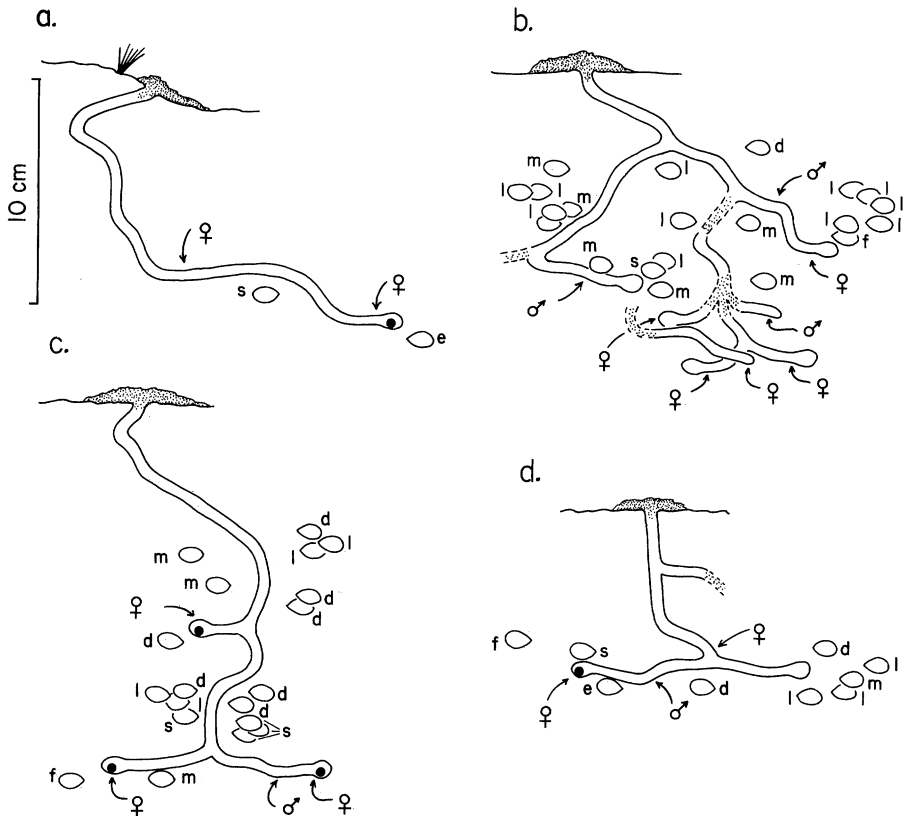


Fig. 3. Typical nests of *P. texana* showing locations of male and female residents when nests were excavated. All nests were excavated after 1500 hr and most likely contained all resident males and females. Letters indicate cell contents: e = egg, s = small larva, m = medium larva, l = large feeding larva, d = defecated larva (prepupa), f = fungal-infected cell. Partially completed pollen balls are shown as black circles.

Larval development was not studied in detail but appears to be quite rapid, judging from the presence of prepupae in nests less than 10 days old. Mid- and late-instar larvae feed lying on their dorsal tubercles, with the pollen ball resting on their venters. Like all known panurgines, *P. texana* does not spin a cocoon. Individuals overwinter as defecated prepupae. The resting prepupae are rather tough and rest on their dorsal tubercles while in a C-shaped posture on the floor of the cell. The fecal mass consists of a group of subspherical pellets containing *Opuntia* exines, adhering to the wall at the distal end of the cell.

INTRA-FLORAL BEHAVIOR: *Perdita texana* is oligolectic, normally restricting all foraging to flowers of *Opuntia* (*Platyopuntia*) spp. (Barrows et al., 1976 and pers. obs.), although females may occasionally take nectar from other taxa or collect pollen from other cacti such as *Echinocereus reichenbachii*, when *Opuntia* is absent (pers. obs.). Females of *P. texana* can, and normally do, complete a pollen load in one visit to an *Opuntia* flower (Barrows et al., 1976). One marked female at BFL completed 7 consecutive pollen loads from the same flower of *O. macrorhiza*, although other marked females were found collecting pollen in up to four different flowers during a provisioning series. Single visits to flowers of *O. macrorhiza* at

BFL, resulting in completion of a pollen load, averaged 6.87 ± 0.58 min ($n = 63$). Late visits to *O. macrorhiza* flowers, sometimes involving collection of small or partial pollen loads but always entailing long periods of nectar collection, averaged 15.45 ± 1.15 min ($n = 12$). Bees at PF, an area of much higher *Opuntia* density, foraged more quickly, averaging only 4.69 ± 0.45 min ($n = 27$) per flower for a pollen load. As at BFL, floral visits involving only nectar-collecting were considerably longer, averaging 16.56 ± 4.26 min ($n = 6$).

Opuntia anthers dehisce at or just before the initiation of anthesis. Pollen is easily dislodged from the anther sacs so much of pollen foraging entails harvesting loose pollen amidst the filaments rather than directly from the anthers. Females of *P. texana* harvest pollen in a biphasic manner. Initially, they move through or over the anther column while actively gathering pollen with the forelegs and transferring it to erect, finely tapering hairs (0.6–0.7 mm long) of the forecoxae and ventral surface of the mesepisterna (pollen collection phase). The bee then moves to the petals or the sides of the anther column and uses its fore and middle legs to transfer the accumulated pollen from the thoracic venter to the simple scopal hairs of the hind tibia (pollen transfer phase) before returning to the anther column for another bout of pollen collection. Small amounts of nectar may be added to the pollen load at this time, but completed pollen loads are relatively dry. Collection of a pollen load within a single flower commonly involves 7–8 series of these alternating behaviors. The grand mean for duration of pollen collection ($\bar{x} = 12.3 \pm 2.6$ sec, $n = 11$) is virtually the same as the grand mean for duration of pollen transfer ($\bar{x} = 11.6 \pm 0.9$, $n = 11$), although the duration of pollen collection is much more variable than pollen transfer (coefficient of variation of 71.1 vs. 26.7, respectively). Mean durations of pollen collection and grooming are not correlated ($r = 0.055$, $P > 0.05$) within a pollen collecting series. Females regularly engage in all aspects of pollen collection and transfer while *in copula*.

Nectar in the *Opuntia* species studied, as in other *Opuntia* species (Daumann, 1930), first accumulates in grooves in the walls, and later as a pool, in the nectary chamber located beneath the insertion of anthers in the hypanthial tube. Access to the nectary chamber is restricted both by a basal expansion of the style and the densely packed stamen filaments at the base of the funnel-shaped floral tube. Preliminary data indicate that nectar production in *O. engelmannii* may be copious but highly variable both in quantity and timing. Nectar volume in bagged flowers averaged 10.40 ± 3.76 μ l ($n = 11$), while sugar production averaged 4.29 ± 1.93 mg ($n = 11$). In a sample of 6 flowers at CC, nectar production peaked before 0920 hr in 2 flowers, between 0920 and 1130 hr in one flower and after 1130 hr in two flowers. Similar patterns of nectar production were observed in *O. macrorhiza*.

Nectar-collecting behavior in *P. texana* involves either first landing directly on the stigma (mainly by males) or more commonly, moving over the anther column to the style and then crawling down along the style through the anthers toward the hidden nectar chamber. Anther filaments in *Opuntia* are motile and become closely appressed to the style when triggered, further reinforcing the necessity of movement along the style, although activities of individual *P. texana* do not always trigger anther movement. The elongate mouthparts of *P. texana* (prementum + glossa = 4.9 ± 0.1 mm [$n = 8$] for females; 4.6 ± 0.1 mm [$n = 12$] for

males) presumably facilitate access to the hidden nectary. Bouts of nectar collecting averaged 40.7 ± 4.7 sec ($n = 14$), but individuals spent 20 or more min in single continuous bouts towards the end of the foraging period.

While pollen-laden females rarely move between flowers, (Barrows et al., 1976 and pers. obs.), they do often move between flowers and plants before collecting significant pollen on a given foraging flight. These movements may represent search for nectariferous flowers or newly opened, pollen-rich flowers, because, under conditions of high bee densities, pollen is rapidly depleted in individual flowers, primarily as a result of *P. texana* foraging.

With one exception (described in Danforth and Neff, in press) mating was observed only at cactus flowers and occurred throughout the period of female activity. The timing of first mating of individual females relative to emergence is not known (*contra* Ridley, 1989). Mating is initiated by males, who pounce on females arriving at flowers. We saw no indication of obvious courtship by males at *Opuntia* flowers. Males approach females from behind, initially attempting to grasp the female about the thorax with their mandibles, pinioning the wings, then sliding backwards to grasp the females about the first or second tergite and immediately inserting their genitalia. Males remain in this position, attached to females with their mandibles and genitalia, until the end of copulation. Foraging females continue their pollen or nectar collecting activities while *in copula*. Observations at PF indicate females *in copula* take more time to collect a pollen load than non-copulating females active at the same time. Females *in copula* took 5.37 ± 0.52 min ($n = 20$) to complete a pollen load vs. 2.57 ± 0.39 min ($n = 8$) for non-copulating females (unpaired *t*-test, $t = 3.229$, $P = 0.003$, d.f. = 26). Observations of marked females indicated they commonly mate several times a day, sometimes more than once per foraging trip, throughout their flight season.

PERDITA TEXANA AS A POLLINATOR: Previous studies have suggested that *P. texana* is simply a pollen thief, contributing little to the pollination of *Opuntia* (Barrows et al., 1976; Grant et al., 1979). While *P. texana* is probably less effective as a pollinator than some of the larger *Opuntia* visitors (e.g., *Diadasia rinconis* and *Lithurge apicalis*), we believe the role of *P. texana* as a pollinator has been underestimated. First, males and females regularly contact stigmas of *Opuntia* flowers. Individuals contacted the stigma in 30.6% of visits (19/62), 57.9% of these (11/19) upon first entering the flower. Second, at CC *P. texana* was by far the most abundant *Opuntia* visitor. Stigmas of those *Opuntia* flowers visited only by *P. texana* were densely covered with pollen within the first hour of the bee's activity. Seed production in open, visited flowers from two plants of *O. engelmannii* at this site averaged 271.0 ± 44.0 seeds per flower ($n = 8$) but only 21.1 ± 8.2 ($n = 8$) for flowers in fine mesh bags which prohibited all visitation. Activity of *P. texana* can lead to high levels of seed set although the relative levels of outcrossing due to its visitation remain unestablished due to self-compatibility of *O. engelmannii*.

FEMALE FORAGING AND PROVISIONING BEHAVIOR: All evidence indicates females provision a maximum of one cell per day. A provisioning series entails 7–9 pollen trips ($\bar{x} = 7.9 \pm 0.2$, $n = 13$), and occasionally a final nectar-only trip. The complete provisioning of a cell required, on average, 72.15 ± 5.3 min ($n = 13$). Marked bees initiated foraging from 0914 to 1326 hr, but no correlation was found between the duration of the provisioning period and the time of initiation of foraging (r

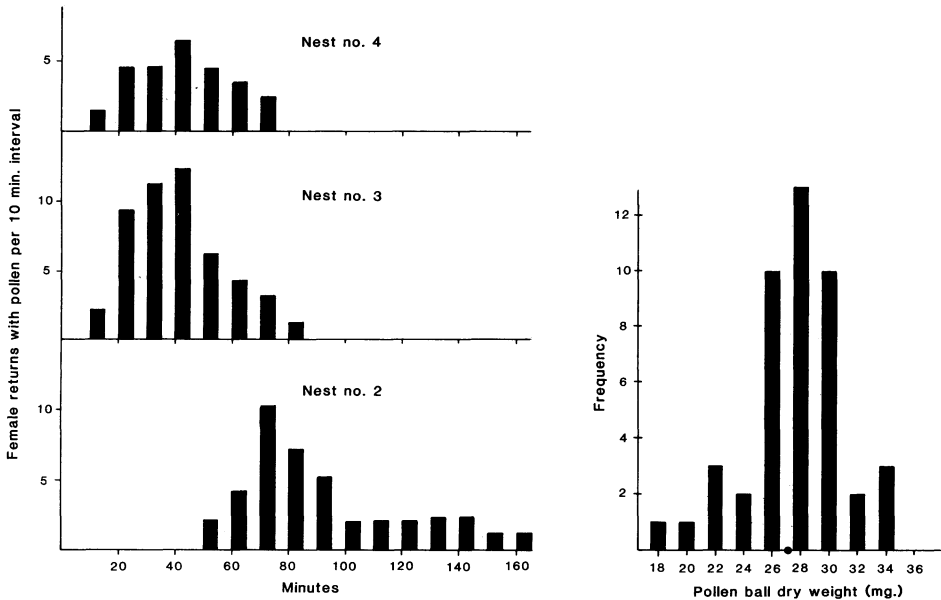


Fig. 4. Inter- and intra-nest synchrony in foraging behavior. Bars show the number of females returning to nests per 10 minute intervals throughout the observation period. Data based on nests at PF on 8 May 1989.

Fig. 5. Histogram of pollen ball dry weights collected at CC in 1988. The mean is indicated by the closed circle along the x-axis.

= 0.26, $P > 0.05$, $n = 13$). Individual pollen trips averaged 7.38 ± 0.68 min ($n = 98$). This value is somewhat misleading however, since the last trip of the provisioning series is always the longest, even though there is no correlation between trip duration and trip order for other pollen flights in a provisioning series. Based on observations at flowers, much of the last trip is spent collecting nectar. The last trip averaged 17.28 ± 1.76 min ($n = 13$), while the preceding trips averaged only 5.86 ± 0.59 min ($n = 85$). Time in the nest between trips averaged 1.78 ± 0.08 min ($n = 86$), excluding one very long period (32.09 min) spent by one bee who initiated foraging before full anthesis of *Opuntia* on that day.

Most foraging appears to be near the nest, typically within 20 m, although marked females were found over 40 m from their nests at PF. The diameter of the foraging area for females at BFL, an area with very low *Opuntia* density, was at least 190 m. Toward the end of the season, some females may not provision a cell on a given day but make only a single long nectar flight. While foraging activities of females within the same nest tends to be reasonably synchronous, there may be significant differences between peak activities at different nests (Fig. 4). Nest entrances are left open during the provisioning period but are usually closed with a loose soil plug following the completion of daily provisioning. In communal nests however, it was not unusual for the nests to be plugged before the last female had completed foraging, so that she had to dig her way into the nest.

Weights of pollen loads from a sample of females returning to their nests

averaged 2.64 ± 0.17 mg ($n = 35$) at CC and 2.6 ± 0.2 mg ($n = 10$) at PF. Pollen load weight averaged 14.3 ± 1.2 % ($n = 10$) of female fresh weight (PF only) and 38.1 ± 3.9 % ($n = 45$) of female dry body weight (combined data). No correlation was evident between pollen load weight and female fresh or dry body weight at either locality or for the combined data ($r = 0.008$, $P > 0.5$, $n = 45$). The nearly dry pollen loads are deposited in a cell after each trip, and nectar is added to the pollen mass after the final foraging trip.

The time required for pollen ball preparation and oviposition was not determined but apparently is prolonged. Excavated females at CC were still working on pollen balls from 1530 to 1800 hr even though foraging activity had peaked at 1130 and virtually all foraging was finished by 1500 hr. In several instances, cells with loose pollen loads were found during evening excavations. It is not clear whether these represented abandoned cells or partial cell provisions that would have been completed the following day.

The uncoated pollen balls quickly showed signs of drying when removed from cells, even when kept in closed containers. Pollen balls weighed within 2 hours of excavation averaged 49.9 mg ($n = 2$). Dry weights of pollen balls collected at CC in 1988 ranged from 18.0 to 34.5 mg ($\bar{x} = 27.6 \pm 3.5$ mg, $n = 45$; Fig. 5). Comparison of fresh and dry pollen ball weights indicates that approximately 45% of the weight of a fresh pollen ball is nectar. An estimate of the efficiency of energetic conversion during bee development is the ratio of the average dry weight of adult body to the average dry weight of pollen balls. The conversion ratio based on this estimate is 26% (7.091 mg/27.6 mg; average dry weight of adults based on 20 males and 20 females).

PARASITES AND PREDATORS: Despite the fact that *P. texana* may form very large nest aggregations, nest parasites were conspicuously absent. Several females of *Sphecodes mannii* (Halictidae) were observed briefly entering nests of *P. texana* at one aggregation at PF but no *Sphecodes* were found during excavations. It is likely that this bee was actually associated with *P. (Cockerellia)* spp. nesting in the area. No adult parasites were observed at CC, although meloid beetle larvae were found feeding on provisions in three cells of *P. texana* (parasitism rate of 3/177 cells excavated, or 1.7% in 1989).

Predation of both males and females of *P. texana* at *Opuntia* flowers by the generalist ambush predator, *Apiomerus spissipes* (Reduviidae), was commonly observed at PF.

Discussion

The level of social interaction observed among nestmates in *P. texana* is similar to that observed in other communal *Perdita* species (e.g., *P. lingualis*, Michener, 1963; *P. opuntiae*, Bennett and Breed, 1985; and *P. coreopsidis*, Danforth, 1989). There is no evidence of reproductive division of labor, and all females appear to forage. In contrast to *P. opuntiae*, which has as many as 38 females per nest ($\bar{x} = 8.9 \pm 1.5$ females per nest $n = 30$) (Bennett and Breed, 1985), *P. texana* typically has fewer females per nest ($\bar{x} = 2.8 \pm 0.4$, $n = 20$), although much larger nests (up to 28 females) may occasionally arise in cases of nest reuse. Communal associations of females in *P. coreopsidis*, *P. opuntiae* and *P. portalis* (Danforth, in press) are believed to arise by re-use of natal nests. The large number of females per nest in *P. opuntiae* is presumably related to the unusual nest site preferences

of this species (the Laramie sandstone formation called White Rocks near Boulder, Colorado), which may severely limit new nest founding.

The origin of communal nesting is often attributed to the benefits of shared nest defense (Michener, 1974; Eickwort, 1981; Abrams and Eickwort, 1981). We found no evidence of nest defense in *P. texana* and nest parasites were not conspicuous at our study sites. Furthermore, 25% of the nests excavated at CC had only one female. The advantages of communal nesting, if any, probably result from savings in the time and energy involved in new nest construction. Although nests were shallow, the soil in many places, especially under dry conditions, was very hard and difficult to dig, and large rocks often presented obstacles to nest excavation. In contrast to a communal halictid bee, *Agapostemon virescens*, in which over half of the marked females switched nests (Abrams and Eickwort, 1981), nest switching appeared rare in *P. texana*.

In intra-floral behavior, *P. texana* shows a number of similarities to *P. opuntiae*, a closely related species also oligolectic on *Opuntia* (*Platyopuntia*) spp. Both species regularly contact *Opuntia* stigmas and may serve as *Opuntia* pollinators. As in *P. texana*, and all other *Perdita* species we have observed, *P. opuntiae* utilizes a biphasic mode of pollen collection (Bennett and Breed, 1985). Similarly, females of both species may collect full pollen loads from a single flower and in both species foraging trips are brief ($\bar{x} = 5.86 \pm 0.59$ min, $n = 85$ for *P. texana*; $\bar{x} = 4.2 \pm 0.35$ min, $n = 8$ for *P. opuntiae*) in comparison to those of other species of *Perdita*, in which foraging trips commonly last 15–30 min (Danforth, 1989). The two species do differ in that *P. texana* normally completes a pollen load from a single flower while *P. opuntiae* commonly visits several flowers for a pollen load regardless of pollen availability. Presumably the copious pollen production of *Opuntia* flowers (*O. engelmannii* flowers at PF have 345–405 anthers per flower, $n = 4$) permits rapid pollen collection and results in the short duration of pollen-collecting trips. It is unclear why females provision only one cell a day since females of another, larger cactus specialist, *Diadasia rinconis*, active at the same time as *P. texana* at PF, regularly provision two to three cells per day (pers. obs.).

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