JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
69(4) suppl., 1996, pp. 260–273

Nesting Biology and Foraging Patterns of The Solitary Bee *Melissodes rustica* (Hymenoptera: Apidae) in Northwest Arkansas

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ABSTRACT: Field observations of nesting behavior and foraging activity of the solitary bee *Melissodes rustica* (Say) were made at a nesting site in northwest Arkansas. The nesting phenology is unusually late in the year for bees, with females emerging in mid- to late September and provisioning burrows until the first hard frost in late October or early November. More than 200 females constructed and provisioned individual burrows at the aggregation. Daily activity patterns were closely correlated with surface soil temperature and wind speed. Females made six to seven foraging trips per day, all of which included pollen provisions except the last. Pollen was apparently gathered from the genera *Aster* and *Erigeron* in the family Asteraceae. Trip duration increased later in the day, as did the time spent in the burrow between trips. Hence, females spent more time collecting pollen and took longer to dispose of the pollen as the day wore on. On the last trip of the day, females returned without pollen. There was little variance among the continuously observed females for any of these patterns. Females continued to enter a single burrow for more than 10 days, and provisioned more than one cell per burrow. No communal nests were observed and no nest parasites (e.g., *Triepeolus*) were collected from the aggregation. We speculate on possible causes of the late nesting phenology of this bee.

The nesting biology for most of the more than 100 species of solitary bees in the genus *Melissodes* Latreille is little known or obscure. Only a handful of investigations have been made during this century, most notably those of LaBerge, who revised the genus in North and Central America and described the nesting biology and flower preferences for several species (LaBerge, 1956a, b, 1961). Several subsequent studies provided useful information on nesting phenology and nest architecture, including Thorp and Chemsak (1964) on *M. pallidisignata* Cockerell, Clement (1973) on a northwestern population of *M. rustica* (Say), Buchmann and Jones (1980) on *M. persimilis* Cockerell, and Triplett and Gittins (1988) on *M. tepida* Cresson. We refer the reader to these papers for information on the biology of *Melissodes* of the Western Hemisphere. They provide the foundation for our comparative investigation of nesting biology and foraging behavior of an Arkansas population of *Melissodes rustica* described herein.

LaBerge (1961) has reported *M. rustica* from a large variety of habitats across much of the central and eastern U.S., southern Canada, and central Mexico. Across that wide distribution this species has been recorded as active from April to November, and as visitors to a wide variety of composite flowers. The only previous account of the nesting biology of this species was that of Clement (1973), based upon an aggregation located in Yellowstone National Park, Wyoming at relatively high elevation (2394 m).

In the hills of the Ozark Plateau in northwest Arkansas, *Melissodes rustica* is

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one of the latest bees to appear in the fall, when only the latest blooming composites are still in flower and the threat of frost or even snow looms near. The *M. rustica* aggregation was first discovered in the fall of 1993 on the University of Arkansas, Fayetteville campus under a small, easterly-facing holly (ornamental *Ilex*) tree beside a campus walkway, at an elevation of 423 m. During that fall several features of their nesting and mating biology were observed and photographed, and specimens were collected for identification. Subsequently, a second nesting aggregation was found less than one km away.

Because solitary and primitively eusocial bees have been shown to exhibit geographic variation in behavior, (e.g., Sakagami and Maeta, 1984; Eickwort, 1986; Packer, 1986) and other bionomic features, our study of the nesting biology and foraging behavior of the *M. rustica* population discovered in northwest Arkansas provides an interesting contrast to the Wyoming population. The Arkansas population represents a southeasterly portion of the species' range (LaBerge, 1961).

We are pleased to dedicate this study to the memory of George Eickwort, who took great pleasure in observing bees such as these in the wild, and who so enthusiastically promoted the study of bee biology throughout the world.

Materials and Methods

STUDY SITES: Two aggregations of *M. rustica* were located in September 1993, on or near the University of Arkansas, Fayetteville campus (36°3′45″N, 94°9′26″W, Fig. 1). At that time initial observations established that both sites were synchronized in female emergence and mating activity, which occurred at the aggregations and resembled the behavior described in previous reports of *Melissodes* mating behavior (e.g., Thorp and Chemsak, 1964; Clement, 1973; Triplett and Gittins, 1988). The following year, when females were first seen to emerge on 16 September 1994, the on-campus site was selected for a study of nesting and foraging behavior. The total area of the aggregation was measured and specific burrows were mapped for later observation. The off-campus aggregation, located approximately one km from the aggregation on campus, was used primarily as a source of bees for determination of body size and quantity of pollen brought back to the nest by returning females, without having to collect females from the focal aggregation. A rough approximation of the total number of nests at each site was made by counting bees within a limited area and extrapolating across the entire area of the site. Bees were identified by comparison with determined collections housed in the University of Arkansas Arthropod Museum, and by W. E. LaBerge (Illinois Natural History Survey). Voucher specimens were deposited in the Arthropod Museum, University of Arkansas, Fayetteville.

LABELING BEES AND NESTS: To facilitate the identification and tracking of individual females during nest construction and foraging, females at the on-campus aggregation were captured with aerial nets on 21 September 1994 and given a unique set of color marks on the thoracic dorsum, abdomen, and/or wing using paint pens (Faber Castell™). Approximately 115 females were thus marked and allowed to fly off. Returning females could be positively identified at distances of 2 m or more. Thirty females were positively identified with particular burrows, which were then individually tagged with numbered, colored plastic flag pushpins

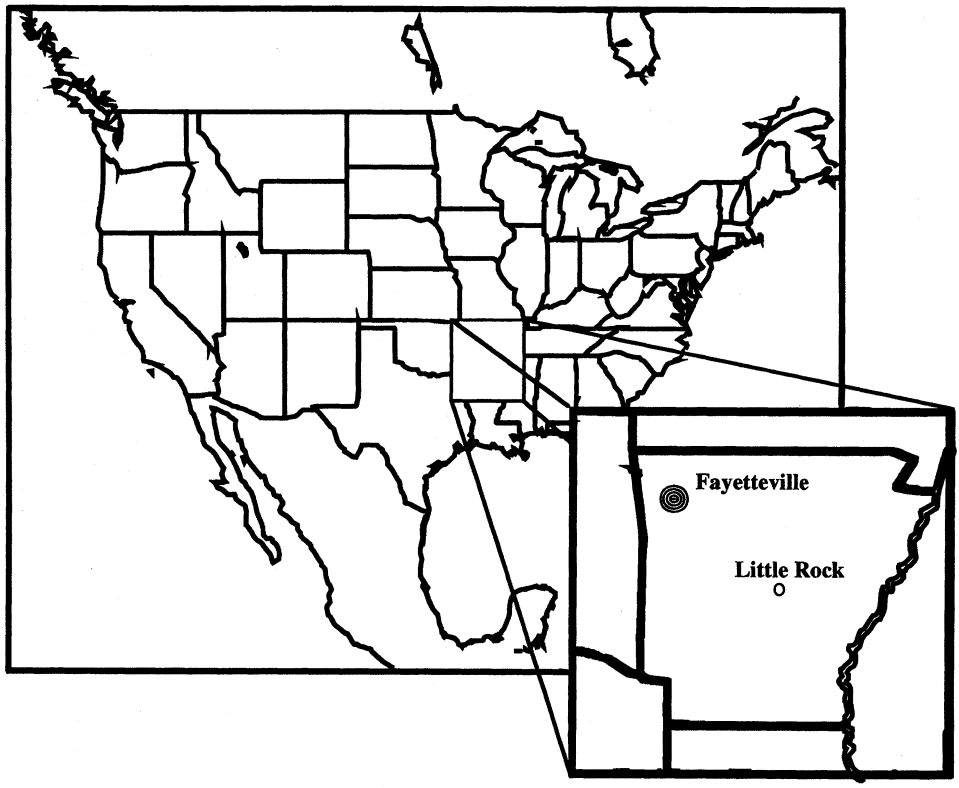

Fig. 1. Geographical location of the site of the studied aggregation in northwest Arkansas, on the University of Arkansas campus. Elevation and coordinates for this site are provided in the text.

(BC Office™) placed in the soil near each burrow entrance (the distribution of the labelled nests is provided in Fig. 2). Females were left undisturbed for the next several days, during which observations were recorded on burrow construction.

FIELD OBSERVATIONS: Continuous observations on diurnal foraging activity and nest provisioning by the tagged females began on 27 September, and continued for three days. Thereafter, daily periodic observations were made on each nest through 21 October 1994. Activity of approximately 25 females was recorded from the time of first emergence in the morning until the last foraging trip at the end of the day. Using synchronized wrist watches, each observer monitored between 4 to 6 females, recording the time of each departure and subsequent return to the nest, and the presence or absence and color of pollen on the metathoracic scopae. This provided us with the duration of each foraging trip and the time spent in the burrow after each foraging trip. Clear plastic cups (9 cm diameter, 9 oz (=532 ml) volume) were placed over individual burrows to temporarily slow the bees, enabling the accurate identification of each female and collection of exact arrival and departure times. The cups were removed as a female emerged from her burrow or approached the entrance after a foraging trip, allowing activity to continue undisturbed.

ENVIRONMENTAL MEASUREMENTS: On each full day of continuous observations,

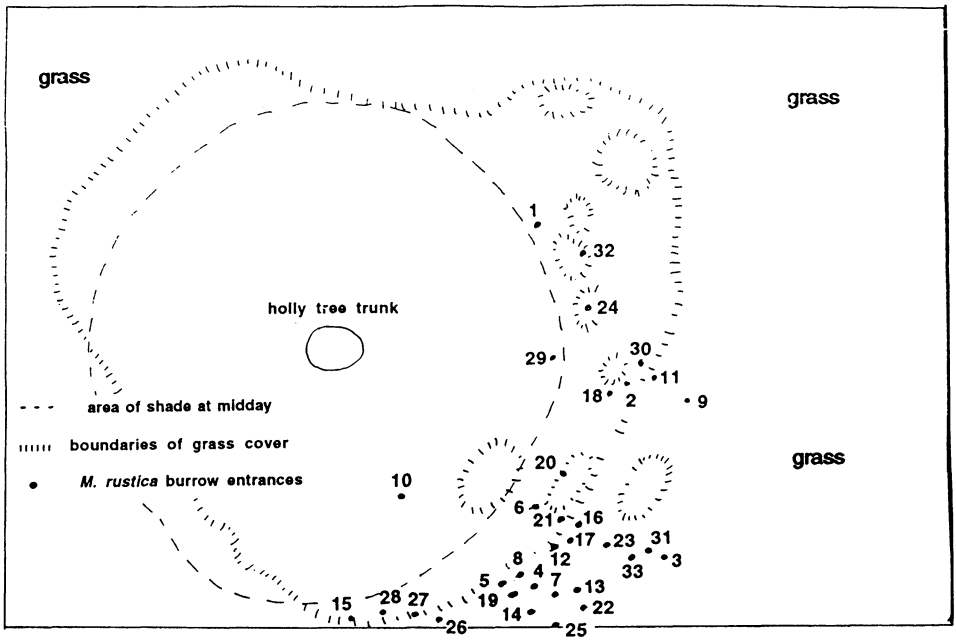

Fig. 2. Map of *M. rustica* aggregation with the burrows for which data were taken marked and numbered. The labelled nests represented approximately 15% of the total number of active burrows. The area covered by the map is approximately 3 × 4 m.

and on subsequent days of partial observations, several environmental variables were monitored hourly throughout the day. Soil temperature was monitored at a depth of 4 cm below the surface using a mercury immersion thermometer (Fisher Scientific™). Soil surface temperature was recorded from four areas within the aggregation using an Omegascope infrared pyrometer (Omega Engineering Group™). Ambient temperature and relative humidity were recorded in the shade at a height of 1 m, with a mercury immersion thermometer and sling psychrometer (Taylor Instrument™), respectively. Wind velocity was recorded at 1 m above ground using a hand-held wind meter (Dwyer Instruments™). Soil type was compared by eye (appearance, texture, moisture) to descriptions from other investigations (Thorp and Chemsak, 1964; Clement, 1973).

POLLEN MEASUREMENTS: Pollen loads were assessed from a sample of foraging females returning to nests at the off-campus site. Samples were taken by rapid sweeps of an aerial insect net over several portions of the nesting aggregation. Approximately 30 females were collected during two intervals of the study, placed in cyanide vials, and returned to the laboratory for removal and weighing of pollen masses. Three measurements were recorded for each female using an analytical balance (Denver Instrument™): total body mass (g) with pollen, mass (g) of left metathoracic leg with pollen, and left metathoracic leg without pollen. These data were used to calculate (1) weight of pollen collected by females during a foraging trip and (2) body weight of each adult female. All pollen loads were saved and frozen at −80°C for later analyses of type and size.

FLOWER SPECIFICITY: Flowers were surveyed to determine which species were being utilized for pollen and nectar by both males and females. To determine the degree of flower specificity exhibited by females, bees were collected from flowers in the vicinity of the study site and from other sites up to 20 km away. Plant determinations were made with reference to Hunter (1992) and Smith (1994). Pollen color was also recorded for all females returning to the nest during the period of continuous observations of diurnal activity.

NEST EXCAVATIONS: Two excavations were made at the on-campus aggregation using modifications of the methods of Triplett and Gittins (1988). None of our methods resulted in the exposure of an entire burrow, from surface entrance to distal cell(s). Because these bees plugged their burrows with loose soil (Clement, 1973) it was not possible for us to follow a burrow from entrance to nest cell by careful tunneling and teasing away of surrounding soil. However, by digging a trench we were able to collect several cells containing pollen provisions and young larvae. Each cell was carefully removed from the soil intact, placed in a covered petri dish, returned to the laboratory and kept at 4°C until examined for size and weight of the pollen mass. Soil depth was recorded for each excavated cell.

STATISTICAL ANALYSES: Effects of environmental variables on diurnal activity of females were determined using multiple regression analysis (SAS Institute, 1987). The diurnal activity of females in the aggregation was estimated by calculating the proportion of observed active (flying or digging) females to non-active females. A mean activity index for the aggregation was then derived for all bees at half hour intervals throughout the day. This activity index ranged from 0, with no females in the aggregation active, to 1, with all of the females active. To determine environmental effects on the activity of females, the measured environmental variables were included in a multiple regression analysis (SAS Institute, 1987) with the activity index as the dependent variable. To fulfill assumptions of normality, a square root, arcsine transformation was applied to the activity index, and all observations with an activity index value of 0 or 1 were removed (Sokal and Rohlf, 1995).

Simple linear regressions were performed to determine whether length of foraging trip and time spent in the burrow between trips was dependent on time of day (SAS Institute, 1987). To determine whether a temporal pattern existed in pollen collection, a contingency analysis was performed in which the proportions of trips made with and without pollen across all observed females were compared between the morning (09:00 to 13:30) and the afternoon (13:30 to 18:00). All analyses were performed using SAS, version 6.09.

Results

NESTING BIOLOGY: Females of *Melissodes (Eumelissodes) rustica* in northwest Arkansas emerge and begin nest construction from mid- to late September and can be found provisioning nests until late October (or the first hard frost). Males probably emerge first and mating most likely occurs at the nesting site, as we observed in 1993, and as reported by other studies of the subgenus *Eumelissodes* (Thorp and Chemsak, 1964; Clement, 1973). In 1994, however, no males were seen at the nesting sites and mating was not observed except for occasional attempts on flowers. Thus mating behavior appears to be variable from year to year.

Fig. 3. Female *M. rustica* moving soil at entrance to nesting burrow at the main aggregation, during the final stages of nest construction.

Females were seen excavating nests between 16 and 27 September 1994 (Fig. 3). Burrows were constructed in gently sloping areas of somewhat dense sandy soil, both in patches bare of vegetation and areas partially covered by grass. Methods of nest construction and soil type were substantially similar to those described by Clement (1973) for *M. rustica* in Wyoming and by Thorp and Chemsak (1964) for the closely related species *M. pallidisignata.* Also as reported by these authors, the distance between burrows was often no more than 2–3 cm., and no communal nests were observed; only a single female was observed to enter each burrow. Nests in our aggregation were similar to those in these other reports in that burrows were partially filled in with loose soil (sometimes obscuring the entrance hole) and extended to a depth approximately 15–18 cm below the surface. Nest cells were oval (Fig. 4A), approximately 11–14 mm long, 6–7 mm wide and lined with a shiny, waxy material. Cells were provisioned with a pollen mass that filled about half of the cell (approximately 4–5 mm long, 6 mm wide) and possessed a liquid surface (Fig. 4B). However, unlike the single-celled nests reported by the above authors, the Arkansas population probably constructed and provisioned nests that contained multiple cells. Females collected sufficient pollen in a day (0.01 g/trip × a mean of 6 trips per day = 0.06 g/day) to provision a single cell. It was thus possible for a female to have provisioned ten or more cells during the period of our study, depending on the vagaries of the weather (described below). Throughout the period of observations females always entered the same burrow and were never seen to construct more than a single burrow. Parasites (typically *Triepeolus* spp. for *M. rustica* in the eastern U.S.—Mitchell,

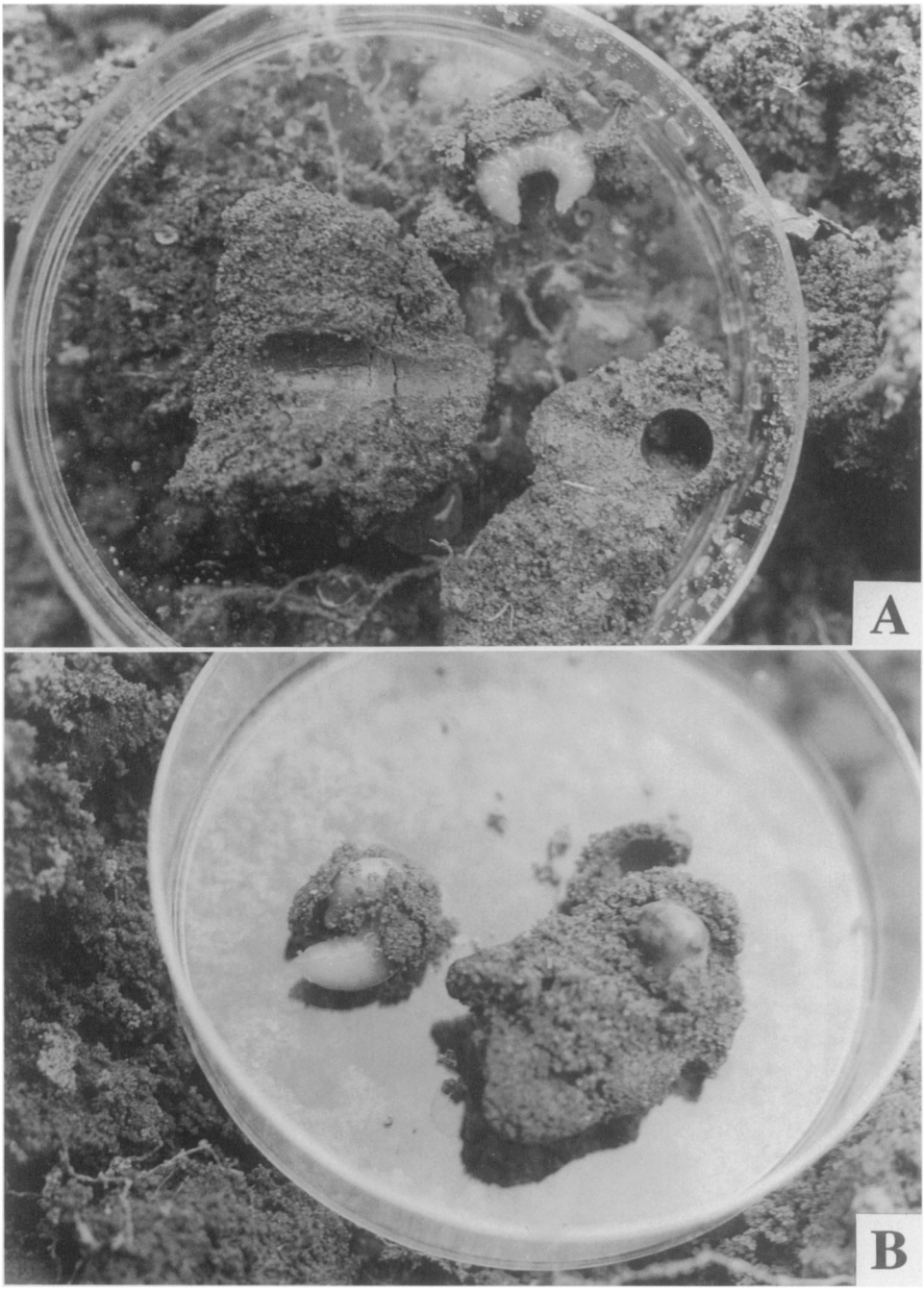

Fig. 4. Materials from excavated nests of *M. rustica* showing (a) nearly mature larva and oval brood cell with shiny lining and (b) half mature larva and remains of food provisions. Note the partially liquefied state of the pollen mass.

Table 1. Values and contributions of several environmental variables associated with the variance in mean activity level at the *M. rustica* aggregation. * Asterisk indicates that value for this category is not meaningful to report.

Environmental variable	Mean	Standard error	Significantly associated with activity
Time of day	*	*	No
Subsurface temperature	24.30°C	0.80	No
Relative humidity	47.85%	2.68	No
Ambient temperature	27.29°C	0.81	No
Soil surface temperature	31.70°C	1.36	Yes
Wind speed	2.28 mph	0.07	Yes

1962) were never observed at either aggregation during the entire phase of the nesting cycle.

DIURNAL ACTIVITY PATTERNS: Of the environmental variables measured (Table 1), only two, surface soil temperature and wind speed, were significantly associated with the overall activity of females in the aggregation (Table 2). Females primarily left their burrows for the first time between 08:30 and 10:30, and returned to their burrows for the last time between 16:30 and 18:30. Females appeared to spend longer in their burrows later in the day (Fig. 5; $P = .0001$). A marginally significant relationship ($P = .037$) was found between amount of time females spent on a trip, and the time of the day (Fig. 6).

Females made approximately 6 trips per day with pollen, and one trip without pollen (Table 3). The proportion of trips made with pollen as compared to without pollen changed throughout the day (Fig. 7), with a higher proportion of females returning to the nest on their last trip of the day without pollen. The color of the pollen masses did not seem to vary within a day, between days, or between females, and was always a bright yellow color. The average pollen mass brought back by females was .01 gms (Table 3), and there was not a significant relationship between the mass of the female and the mass of the pollen load which she was carrying ($F_{1,26} = 2.3192$; $P = 0.1399$).

FLOWER SPECIFICITY: Table 4 provides a summary of the flower species surveyed, and those at which *M. rustica* were found foraging in the Fayetteville area. It should be emphasized that this bee emerges late enough in the fall that only a

Table 2. Analysis of variance for the multiple regression of the activities in Table 1.

Source	d.f.	Sum of squares	Mean square	*F* value	Prob > *F*
Model	2	1.84341	0.92171	22.271	0.0001
Error	21	0.86909	0.04139		
Total	23	2.71251			

Estimates of the model parameters

Variable	Parameter estimate	SE of estimate	T Value for H_0: that the parameter = 0	Prob > |T|
Surface temperature	0.028071	0.005465	5.137	0.0001
Windspeed	0.197398	0.076906	2.567	0.0180

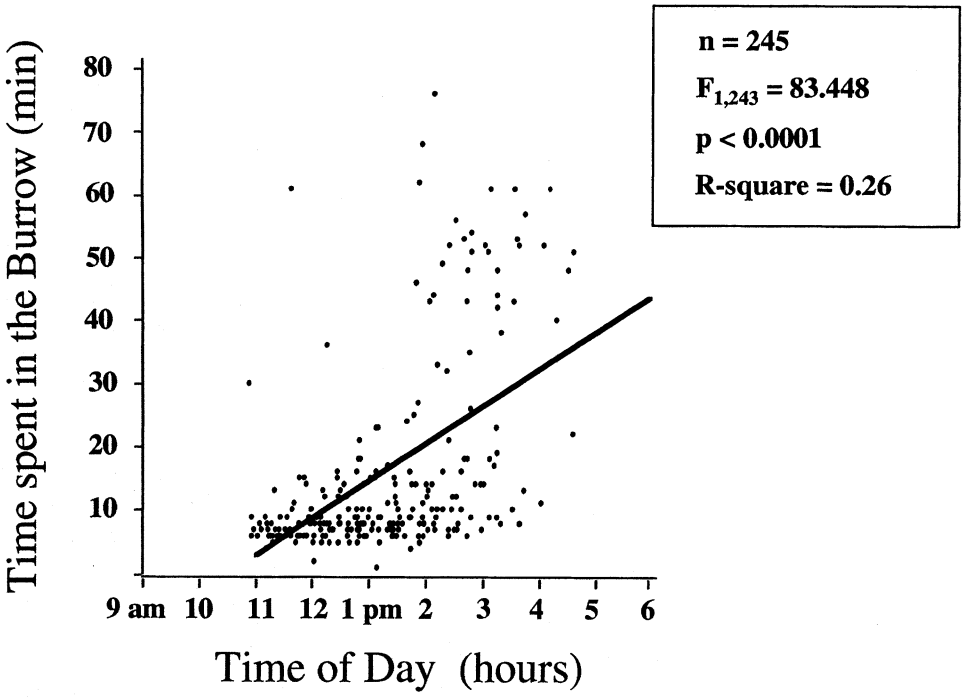

Fig. 5. Linear regression of time of day (in hours) versus time spent in the burrow at each return to the nesting site (in minutes).

limited range of plant species are still in flower. Furthermore, a minimum flight distance of one-half km was required of the bees on the University of Arkansas campus to reach any significantly-sized populations of favored plants. All flowers visited by *M. rustica* were in the family Asteraceae. However, there were significant differences in the range of species visited by males and by females. Females were found only on a few species of *Aster* and one *Erigeron* sp. Males, on the other hand, visited a broader, although limited, range of composites in the area (Table 4). Pollen loads from returning females at the aggregations appeared extremely uniform in color and texture, further suggesting some specificity in flower choice, although pollen loads were not analyzed taxonomically. No individuals were seen visiting *Solidago,* despite the abundant inflorescences of several species in the area during the activity period of *M. rustica.* This contrasts with LaBerge's report (1961) that *Solidago* was the plant genus most commonly associated with *M. rustica* throughout its range (followed by *Aster*). At one site near the off-campus aggregation, males repeatedly attempted to mate with females on flowers of *Aster.*

Discussion

A GENERALIZED LIFE CYCLE OF MELISSODES: Our investigation of the nesting and foraging biology of *Melissodes rustica,* coupled with previous findings from studies of this and other closely related species in the genus, produce a consistent picture of a generalized *Melissodes* life history. Typically, the species appear to

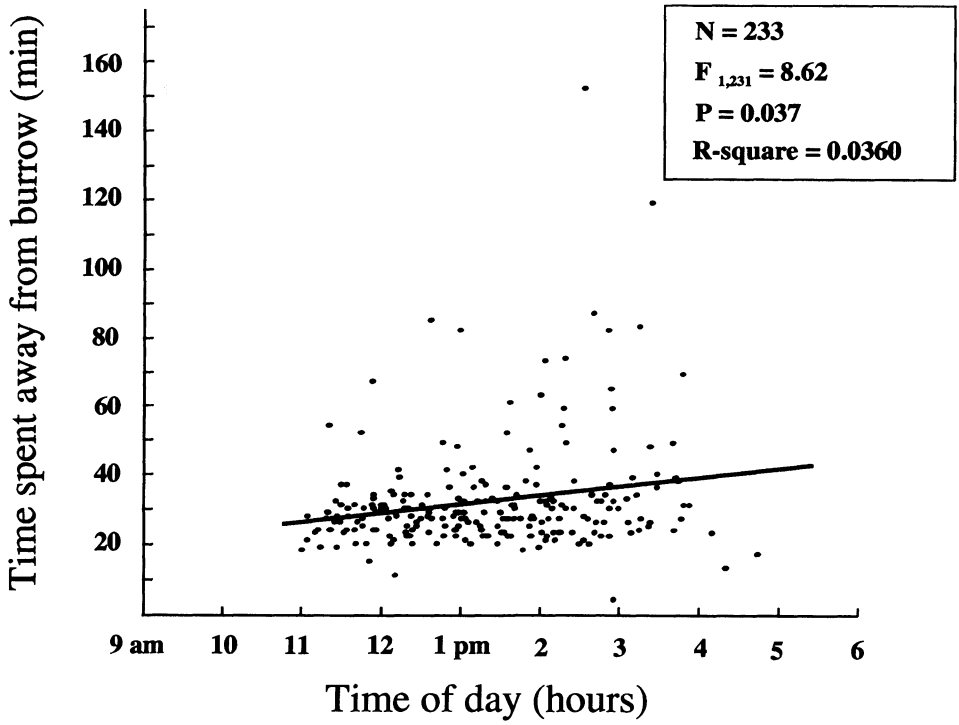

Fig. 6. Linear regression of time of day (in hours) versus time spent away from burrow on each foraging trip (in minutes).

be univoltine, with adults active for a month or less. Nests occur in aggregations and are constructed in at least partly sandy soil to a depth of 10–20 cm below the surface by a solitary female. The burrows are partially plugged or filled with loose excavated soil. Brood cells are relatively uniform in size (6–8 mm wide by 10–15 mm long), oval in shape, and lined with a thin, shiny layer of wax, probably laid down as a protective lining by the Dufour's gland (Batra and Hefetz, 1979). In the cases for which detailed information is available (as above), males

Table 3. Means, standard errors, and sample sizes for several aspects of the activity and size of female *M. rustica* and their nest provisioning. Provisioning females were observed for approximately 15 days total (ended by frost).

	Mean	Standard error	*N*
Trips per day	6.79	0.26	43
Trips with pollen	5.98	0.31	43
Trips without pollen	0.78	0.09	43
Time in burrow (min)	14.75	1.00	253
Time on pollen-collecting trip	28.92	0.87	257
Time on non-pollen-collecting trip	40.06	5.26	34
Body mass (g)	0.06	0.003	28
Pollen load (g)	0.01	0.0003	57
Days female is active	9.30	0.51	19

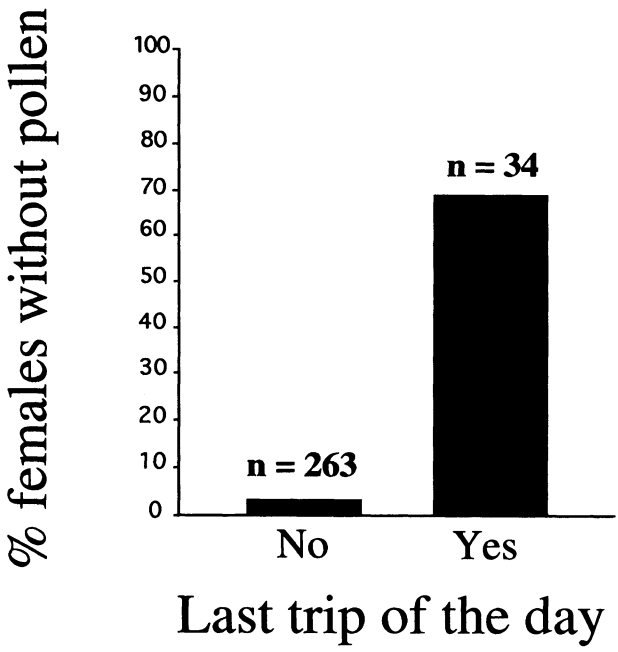

Fig. 7. The percentage of females returning to the nest site without pollen, according to whether or not it was their last trip of the day.

emerge first, establish territories around the nesting aggregation, and mate at or near the nesting site (although some matings and attempted copulations may also occur at nearby flowers). Our observations of two aggregations of *M. rustica* in northwest Arkansas suggest that the mating dynamics might vary from year to year, possibly depending on weather and patterns of emergence.

Table 4. Species of composite flowers which male and female *M. rustica* were observed to visit near the aggregation studied in northwest Arkansas.

Flowers (all Compositae)	*Melissodes rustica*	
	Males	Females
Aster anomalus	present	present
Aster pilosus	present	present
Aster (ornamental)	present	present
Bidens aristosa	present	absent
Echinacea purpurea	absent	absent
Erigeron annuus	present	present
Eupatorium altissimum	absent	absent
Eupatorium coelestinum	absent	absent
Eupatorium rugosum	absent	absent
Grindelia squarrosa	present	absent
Helenium tenuifolium	present	absent
Rudbeckia hirta	present	absent
Solidago caesia	absent	absent
Solidago canadensis	absent	absent
Tagetes erecta	present	absent

Flower visitation records for *Melissodes* are often diverse for individual species but the general pattern indicates that females visit a limited spectrum of flowers for pollen, often from a single genus (sometimes two genera). Males probably use a much wider array of plants as nectar sources, as may females. In the subgenus to which *M. rustica* belongs (*Eumelissodes*), the plants utilized are typically composites (Asteraceae). Our observations confirm these prior reports.

The foraging effort required to produce an offspring appears to be remarkably consistent in our and prior studies. Females are most active during mid-day, once soil-surface temperatures reach a critical level, and make 6–7 foraging trips during the day. The last foraging trip occurs in late afternoon and may entail only the collection of nectar. A single cell is stocked with the provisions supplied by these 6–7 trips; the female spends the remainder of the day completing the cell and laying an egg (possibly also making a new cell for the next day). The distances the bees must fly to obtain full loads of nectar and pollen must be quite variable, depending on the habitat. Our survey of plants in the vicinity of our *M. rustica* populations indicates that these distances can be considerable (>0.5 km). The weight of the pollen mass stocked into a single cell for an individual offspring has rarely been accurately measured, but is probably on the order of 1.3–2.9× the mass of an adult emerging bee, on the basis of comparable data from andrenids (Miliczky and Osgood 1995) and megachilids (Klostermeyer et al., 1973). The report of pollen masses in cells of *M. tepida* weighing 4.5 g (Triplett and Gittins, 1988) is probably in error, as this would be many times greater than that required for the development of a single bee.

NUMBER OF CELLS PER BURROW: A VARIABLE TRAIT IN MELISSODES?: Previous reports of several species of *Melissodes* vary with respect to whether nests contain single or multiple brood cells. Most accounts, including the previous study of *M. rustica,* state that only a single cell is constructed per nest. Our experience with the difficulties of excavating nests of *M. rustica,* due to the efficient back-filling (plugging) of burrows by the bees, suggests that direct observation of cell numbers by excavating a burrow may be misleading. In our study, we were unable to successfully excavate complete nests to obtain direct cell counts. Nonetheless, several lines of evidence suggest that a burrow must contain multiple cells.

First, our observations of the diurnal foraging patterns of females (6–7 trips per day, the last for nectar only) suggests that sufficient provisions can be collected in a single day to fully stock one cell. The same individuals continued to carry provisions into their respective burrows, through the same entrance, for a minimum of 7–10 days. Furthermore, our observations on the quantity of pollen collected by females during a single day's foraging roughly approximates the size of the pollen masses collected from the excavated nest cells. During the 7–10 day period we observed individuals foraging, each female made a total of 40–70 trips. The total amount of pollen represented by this number of trips may be sufficient to stock many more than one cell.

Second, many of the bees were observed to stock the same burrow during most of their known adult lifetimes (close to 2 weeks). If this effort resulted in the provisioning of only a single brood cell, the females would not, even under ideal conditions, be able to replace the parental generation and the population would gradually go extinct.

It is likely that under some conditions *Melissodes* does produce only a single

cell per nest, perhaps in situations where new burrows are easy to dig, or where suitable soil space or time does not allow multiple cells. Furthermore, there might be advantages to this habit in the avoidance of parasitism. However, to maintain a stable population, females would have to excavate and stock several single-cell burrows during their lifetimes, contrary to the report by Clement (1973). We view with some skepticism reports that *Melissodes* species stock the same cell in a single burrow for days on end (unless the nesting season is found to be longer than we observed and conditions are unsuitable for multiple foraging trips per day).

WHY DOES *M. RUSTICA* NEST SO LATE IN THE YEAR?: One of the most striking features of *M. rustica* in northwest Arkansas is that it emerges late in the year, when few other bees are still around. This has its risks, as in 1993 when their nesting activity was cut short by a hard frost, which was followed soon after by the first snowfall of the year. A simple explanation for this late-season nesting might be that in this portion of its range *M. rustica* has specialized on flowers with morphologies allowing relatively easy access to pollen and nectar (especially *Aster* spp.) that bloom through the late fall. By emerging late in the year, *M. rustica* can avoid competition with other generalist bees that could compete for pollen and nectar on these relatively accessible flowers.

Alternatively, by emerging late these populations of *M. rustica* could also be avoiding parasitism. Although one species of nest parasite, *Triepeolus pectoralis* (Robertson), has been collected at nesting sites of *M. rustica* in some regions of the eastern U.S. (Mitchell, 1962), no *Triepeolus* spp. have ever been recorded in Arkansas later than early August, although *Triepeolus* have been collected locally earlier in the season. No nest parasites were observed at either of the two aggregations monitored in 1993 and 1994.

FUTURE WORK: Several interesting questions still remain concerning our local populations of *M. rustica.* For instance, are they able to escape parasitism every year? To what degree does variation in the late fall weather affect population dynamics? What is the normal pattern of male activity, especially mating behavior? How much gene flow occurs between local aggregations? With only a month or so of potential observation time each year, persistent and predictable aggregations of bees such as these local *M. rustica* can repay study for many years.

Acknowledgments

We would especially like to thank Wally LaBerge for his expert confirmation of our identification of *M. rustica,* and for helpful comments on the biology of *Melissodes* in general. Jim Cane and Robbin Thorp gave us useful information on nest excavations and assessment of pollen provisions. Jim Cane helped excavate burrows during a visit to our campus in October 1994, and Kristine Sillett provided help with foraging observations. We are indebted to Chris Carlton and Laurin Wheeler for initially alerting us to the nesting sites and Laurin Wheeler for his generous loan of the Omegascope for measuring soil surface temperatures. Byron Alexander and two anonymous reviewers provided useful comments on the manuscript. Finally, we would like to thank the University of Arkansas grounds crews for leaving the campus aggregation undisturbed during the project; our tiny obstacle courses of numbered flags (and sometimes cups) were graciously

respected. This work was supported by a grant from the National Science Foundation to SAC (GER-9450117).

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