OBSERVATIONS ON THE NESTING HABITS AND FLOWER RELATIONSHIPS OF SOME SPECIES OF MELANDRENA

(Hymenoptera: Andrenidae)

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Although the nesting habits of a number of European species of *Andrena* have been reported (Perkins, 1919; Malyshev, 1926; Bischoff, 1927; Ulrich, 1933; Nielsen, 1934; *et al*), fragmentary information is available for less than a dozen of the more than five hundred described North American species (Linsley, 1951). The available information is due largely to Packard (1868), Smith (1901), Rau (1922, 1935), Parker and Böving (1924), Hicks (1926, 1934), MacSwain (1945), Bohart (1952), and Sivik (1954). Pollen flowers have been reported for about ten per cent of the known North American species (Linsley, 1951) although details of pollen collecting behavior and diurnal activity cycles are essentially lacking for all. Except for *A. nigra*, species of the subgenus *Melandrena* are not commonly encountered in the field, apparently because they are most abundant very early in the season and collect pollen very early in the morning. Nothing has been recorded of the nesting habits of any North American species. For a key to the North American species see preceding paper by Linsley and MacSwain (1955).

When, in 1954, large populations of *Melandrena* were discovered in Short Canyon on the western edge of the Mojave Desert, an attempt was made to learn something of the habits of the group. Considerable biological data was gathered between April 11 and 18. Unfortunately much of this information was not very useful since it was later found that three superficially similar species of *Melandrena* (*A. mojavensis* Linsley and MacSwain, *A. oenotherae* Timberlake, and *A. deserticola* Timberlake) were involved and all were collecting pollen almost exclusively from one species of *Oenothera*. In 1955, the area was revisited, but inclement weather limited observations and interfered with bee activity. Since the opportunity for further studies in this area appears to be remote, our fragmentary biological observations are offered now. These

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are presented in the form of generalizations concerning the subgenus, brief comparative accounts of the species, followed by a discussion of some of the factors which may permit the coexistence of these three closely related species under conditions of what appears to be intense competition.

THE SHORT CANYON HABITAT

Short Canyon is located at the base of the east side of the Sierra Nevada mountains six miles west of Inyokern, Kern County, California. The canyon rises abruptly from its mouth to the upper section which is bounded on the north and south by sand covered hills and on the west by steep rocky slopes. The north slope has produced a broad alluvial fan which stretches down to the main wash in the center of the canyon. Three species of *Oenothera* bloom in the canyon in March and April (possibly also May and later). The large, white-flowered *Oenothera pallida* Lindl., grows in the fine sand of the wash but appears to be completely ignored by the species of *Melandrena*. *Oenothera clavaeformis* Torrey and Fremont, a small-flowered, whitish species grows on the steeper slopes at the base of rocky outcroppings and cliffs. *A. mojavensis* was found visiting this species under certain conditions. A small yellow-flowered species, *Oenothera dentata* var. *johnstonii* Munz, the main pollen source, was common on the floor and sandy slopes of the canyon. A large but scattered population of this plant occurs on the alluvial fan and a smaller but denser stand on a steep sandy area among the rocks on the sides of the canyon. These two areas are about one-quarter of a mile apart and are separated by the almost barren upper portion of the wash.

The weather in Short Canyon, like most of the Mojave Desert, is extremely variable in February, March and April and light to heavy winds blow from the mountains across the desert almost every day. The nearest weather station is at Inyokern, out on the desert approximately six miles east of the Canyon. Weather records have been kept since 1952 and, although not an accurate reflection of conditions in the canyon, they do give an indication of trends in the area. During this brief period, the months of February and April (March means were similar in the four years) were warmest in 1954, coolest in 1955. Thus in 1954 the mean of the daily maximums for these two months respectively were 21.5°C and 28°C, the minimums 4.0°C and 10.2°C. In 1955, the comparable figures were 15.7°C and 23.8°C, and −2.4°C and 3.8°C. In

the period February through April, 1954, there were only 12 days in which the minimum temperature fell to or below 0°C (none in April). During these months in 1955 there were 41 days at or below 0°C (7 of these in April). During the 1954 observation period (April 11-18) the average daily maximum was 31.0°C, the minimum 9.2°C. During the same period in 1955, the corresponding figures were 24.3°C and 6.0°C. These variations in temperatures appear to have had a pronounced effect upon bee activity.

Rainfall indirectly affected conditions for bees in Short Canyon through its influence on the abundance of flowers. Cattlemen operating in Short Canyon reported the 1955 spring the coldest in their experience in the area and forage for cattle the poorest. Total rainfall for the months of February, March, and April, 1955 was .07 inches. In the corresponding period in 1954, the total was 1.54 inches (Inyokern readings). These differences were apparently reflected in the pronounced differences in the abundance of *Oenothera* in Short Canyon in the two seasons.

Wind records from Inyokern are not correlated directly with conditions in Short Canyon. In general there was a down-canyon draft in the morning an up-canyon draft in the afternoon. When these were strong and gusty during periods of bee activity, they clearly reduced and hampered the flight of the bees.

DISTRIBUTION AND FLOWER RELATIONSHIPS

The North American species now assigned to the subgenus *Melandrena* (Lanham, 1949) are limited to the area from the Rocky Mountains (Wyoming, Colorado and New Mexico) to the Pacific Coast (Oregon and California). Of the species listed by Linsley (1951), ten are restricted to California.

In so far as now known, all of the species exhibit a high degree of oligolecty (or monolecty) being restricted in pollen collecting to a single genus of plants. Thus *A. nigra* Provancher appears to take pollen only from *Phacelia* (Linsley, 1938) and *A. oenotherae* Timberlake only from *Oenothera* (Timberlake, 1937) The Coloradan *A. anograe* Cockerell (1901) was also captured on *Oenothera* which is presumably its pollen source (a specimen from Salida, Colorado has *Oenothera* pollen on the legs). However, numerous species of plants are visited by various species of *Melandrena* for nectar alone, and this fact accounts for the large number of museum flower records reported by Timberlake (1937)

and Linsley (1938). An examination of available specimens of *A. grundeli grundeli* Linsley, *A. g. bernardina* Linsley, *A. vanduzeei* Linsley, *A. rubrotincta* Linsley, *A. flandersi* Timberlake, *A. blaisdelli* Cockerell, *A. rozeni* Linsley and MacSwain, and *A. linsleyi* Timberlake, revealed that the only kind of pollen being carried was that of *Oenothera*. This last species was also found collecting pollen from *Oenothera trichocalyx* Nutt. by P. D. Hurd and others at Hopkins Well, Riverside County, California, and *A. deserticola* Timberlake and *A. mojavensis* Linsley and MacSwain were shown to be *Oenothera* monoleges in the course of the present study. Thus, excluding *A. omninigra* Viereck which has not been recognized definitely in our material, all of the species and subspecies known to occur in California except *nigra* (Hydrophyllaceae: *Phacelia*), appear to be restricted in pollen source to *Oenothera* (Onagraceae). Further, near Needles, San Bernardino County, and at La Quinta, Riverside County, three species *(rubrotincta, linsleyi,* and *rozeni)* were captured together, as were *linsleyi* and *rozeni* at Hopkins Well, Thousand Palms, Palm Canyon and Salton Sea, Riverside County, and *rozeni* and *rubrotincta* 4 miles west of Desert Center, Riverside County. Since three species were also found in competition for the same pollen source in Short Canyon *(mojavensis, deserticola,* and *oenotherae)* and a fourth *(flandersi)* was found in small numbers, a number of evolutionary and ecological implications are involved.

Most of the species of *Oenothera* occuring in California grow in sandy areas, principally in desert regions. Such sites also appear to meet the nesting requirements of the associated species of *Melandrena,* at least to the extent indicated by the present study.

During mid-April, 1954, the time of day utilized for pollen collecting by *A. mojavensis, deserticola,* and *oenotherae* was largely limited to a period from about 40 minutes before sunrise to 30 or 35 minutes after the first direct sunlight reached the flowers. All three species were active during this period, and although specific differences in behavior are indicated these were not determined quantitatively. On April 14, 1954 (minimum temperature of previous night 5°C) the first bees were gathering pollen at 5:15 A.M., the sun reached the flowers at 5:54 A.M., and no bees were seen on the flowers after 6:30 A.M. On April 15, 1954 (minimum temperature of previous night 10°C), pollen collecting was first observed at 5:07 A.M., direct sunlight was on the flowers at 5:50

A.M., and no bees were seen after 6:23 A.M. By contrast, during cold spells (April 10, 17, and 18, 1955), the earliest and latest pollen collectors were, respectively 6:03–7:03 A.M., 5:41–6:22 A.M., and 7:10–7:29 A.M., indicating the modifying effect of cold temperatures (10-15°C lower at time of flight). In both years occasional individuals were seen visiting flowers (but not collecting pollen) in the later part of the afternoon and on overcast days, at other times.

When the bees emerged from their burrows for the first pollen trips of the morning, they had a tendency to visit flowers close to the nest. In two cases, the first load of pollen was gathered within two feet of the entrance. For the first trips, six or seven flowers were sufficient to provide a pollen load, although these loads frequently appear to be lighter than those gathered later. On April 14, 1954, the first five bees timed visited an average of 7.2 flowers per pollen load in an average period of 103 seconds. The next four bees collected from an average of 17.5 flowers per load over an average of 190 seconds but had to reject an average of 10 additional flowers from which the pollen had already been stripped. After the sun reached the flowers, the next four bees required only 178 seconds to complete a pollen load with an average of 16.3 yielding pollen and 16.5 lacking it. The same general behavior was evident on April 15, 1954.

While removing pollen from the flowers of *O. dentata*, the bees work slowly and ponderously. The pollen is carried loosely not only on the hairs of the tibiae, femora and trochanters but on much of the underside of the body. Many of the individuals are large and heavy in relation to the blossom, which usually bends downward from the bee's weight with the bee hanging underneath. Not infrequently bees will fall off of the flower to the ground and in cold weather they may remain for some time where they fall (they may be readily picked up by hand). Even under favorable conditions the bent over flower tends to obscure the bee and to make it difficult to estimate the number of individuals active at a given moment.

Unlike most other *Andrena*, the species of *Melandrena* are noisy fliers, suggesting the buzzing of certain anthophorids. This is evident when the bee is arriving at the flower site or leaving it but is not so obvious when it is moving from flower to flower. Sometimes, after a pollen load is completed, bees will fly to a low

shrub and "rest" before returning to their burrows. On other occasions, they fly directly to the burrow from the last flower visited.

ACTIVITIES AROUND BURROWS

In 1954 the activities of a number of bees around their burrows was observed on two consecutive days. On the third day eight of these were captured and were later identified as follows: one *A. mojavensis,* two *oenotherae* and five *deserticola.* Since most of their activity varied as much between individuals as between species a generalized account is reported here.

Most of the bees observed gathered pollen on both of the observation days and were captured when returning with additional pollen on the third day. Others, however, left their burrows on only two of these days and their burrows remained plugged with moist sand, either at or near the surface, during the other day. On pollen collecting days the burrows were usually opened long before the first flight, rarely only a few minutes before flight. After opening, the female remains just within the entrance until ready to leave. Flight away from the burrow is variable and some individuals fly a reconnoitering pattern over and around the burrow before the first and sometimes subsequent flights; others fly directly away. The first trip to the flowers and return is frequently as short as one minute, but in such cases the bee returns with a partial pollen load. The next several trips are completed in two to four minutes each and later trips in three to eight minutes. However this is the average condition and almost every individual varied on one or both days from this pattern.

When returning with a pollen load the females usually fly directly to the burrow and enter. More rarely they alight on bushes or the ground in the general nesting area and remain for several minutes before entering the burrow. The time individuals remained within the burrows varied from one to four minutes; but the time intervals for a given individual seldom varied by more than a minute.

The number of trips completed on a single morning correlates with the time of the first trip in relation to the starting time of other individuals. The bees which fly early usually makes six trips, those which start ten to fifteen minutes later seven or eight trips. In the latter cases the bees usually returned from their last trip in

a few minutes without completed pollen loads, or sometimes considerably later without any pollen.

The burrow is plugged with a core of sand five to fifteen minutes after the last trip of the morning. The plug is brought up from below and movements of the plugs indicate that three loads of moist sand are used. On warm days the burrows are unplugged at various times during the afternoon and usually plugged again before sundown.

Conspicious variations in these habits were observed in 1955 due to colder conditions. Under these circumstances many burrows remained closed all day and pollen collecting was sporadic.

Males were entirely absent from the nesting sites and flowers throughout the periods of observation in both 1954 and 1955. This suggests that mating takes place very early in the season before nesting activity has begun. A mating pair of the related *A. (M.) linsleyi* has been taken on February 26 and of *A. (M.) rozeni* on April 5 the male badly worn) (Linsley and MacSwain, 1955).

ANDRENA (MELANDRENA) MOJAVENSIS Linsley and MacSwain

This is the largest of the four species from *Oenothera* in Short Canyon. Female individuals range from 9.3 to 10.3 mm. in wing length[2] with a mode of 9.7 mm.

A large population of *A. mojavensis* nested in the steep sandy area among the rocks on the southern side of the canyon. A sample collection from this site on April 13, 1954, consisted of 70 *mojavensis* and 4 *oenotherae*; another on April 17, 1955, of 24 *mojavensis* alone. The species was also taken in numbers on the east facing slope of a hill at the northern edge of the canyon's mouth. A few individuals were found nesting on the alluvial fan at the northern side of the canyon in 1954 but only one in 1955.

Most observations of the flower habits of this species were made at the flowers of *Oenothera dentata* and it was only on the hills near the mouth of the canyon that it was found at *Oenothera clavaeformis* in the absence of the smaller plant species.

Burrows of *mojavensis* have a vertical entrance and, in the relatively coarse sand of the western slope, penetrate to an underlying layer of decomposing granite. Here the depth varied from 60 to 75 cm., and the diameter average almost 8 mm. A burrow in the finer sand of the alluvial fan had a similar diameter and a total depth of 60 cm.

[2] Measured from apex of costal sclerite to apex of forewing.

In 1955 the population of *mojavensis* on the upper slope was active on the flowers on April 17 and 18 although a cold wind was blowing down from the mountains and there was almost no activity among the bees nesting on the alluvial fan. However, this area is somewhat protected from the wind and receives sunlight earlier in the morning. Furthermore the slope receives the sun's rays more directly. On the warm morning of April 13, 1954 the first *mojavensis* were visiting the flowers on this slope at 5:10 A.M. and were numerous by 5:15 A.M. By contrast the first bees appeared on the alluvial fan at 5:20 A.M. and they were not abundant until 5:30 A.M. In this latter case it is suggested that the time difference is a reflection of the different species makeup in the two areas and the ability of *mojavensis* to fly slightly earlier than the other species.

In 1954 one female of *mojavensis* was nesting within a meter radius of a burrow of each of the other two species. On April 13 this female left her burrow at 5:21 A.M. and returned with a pollen load at 5:25 A.M. The female of *deserticola* left at 5:26 A.M. and returned with a load at 5:32 A.M. and the female of *oenotherae* left at 5:33 A.M. and returned with a load at 5:37 A.M. On this day the three females completed five pollen loads at 5:53 A.M., 6:06 A.M. and 6:03 A.M. respectively. Only the female of *mojavensis* made an additional trip from which she returned at 6:24 A.M. without pollen. On April 14 the female of *deserticola* did not leave her burrow but *mojavenis* made seven trips, the last a long one without gathering pollen and completed at 6:15 A.M., and the female of *oenotherae* eight trips. The female of *mojavensis* was not seen leaving on her first trip but returned with a full load at 5:16 A.M. (suggesting that she had left at about 5:10 A.M.) ; the other female *(oenotherae)* left at 5:28 A.M. returned at 5:29 A.M. with a poor load. Her second trip with her first full pollen load was completed at 5:35 A.M. and her last at 6:28 A.M. The times of first flight for four other females of *deserticola* and one other *oenotherae* on the same days were similar and are reported in the discussion of those species.

A conopid fly parasite of *mojavensis* was found in 1954. A female bee containing a large larval conopid was accidentally uncovered while digging a burrow of *Diandrena* on the alluvial fan. No adult conopids were observed in this area and it seems likely that the individual must have been attacked at an earlier period.

Although a number of burrows of *mojavensis* were observed on the upper slope no parasitic bees of the genus *Nomada* were seen to visit them. The same situation obtained with the burrow on the alluvial fan.

ANDRENA (MELANDRENA) OENOTHERAE Timberlake

A. oenotherae was described from thirty-four females most of which were from various localities in southern California, although two specimens were included from the San Francisco Bay region of California and one from the Chiricahua Mountains, Arizona. It is now the commonest species of the subgenus in collections and has been taken in association with several species of *Oenothera*. Females from Short Canyon range from 8.4 to 9.1 mm. in wing length with a mode of 8.9 mm. They are smaller than *A. mojavensis* and slightly larger than *A. deserticola*.

A few individuals of this species were collected on the southern slope of Short Canyon in 1954 but not in 1955. Burrows were not located on the slope but probably occured nearby. However, a somewhat larger number of individuals occurred on the alluvial fan. In 1954, two were found nesting and at least three others taken on the flowers of *Oenothera dentata*. In 1955 a total of 12 individuals were collected or found nesting in this same area.

The burrows of this species were located toward the upper portion of the alluvial fan either on or immediately adjacent to an unpaved road, where the sand was small-grained and hard-packed. The burrows were commonly in groups of two or three with burrows only a few centimeters apart. Less frequently they were found within a few centimeters of burrows of *deserticola*.

The observed burrows of *A. oenotherae* had slanting entrances which are readily separable from the vertical entrances of the other two species. The diameters and, to a lesser degree the depths, of the burrows vary with the size of the female so that the dimensions approach those of the smallest burrows of *mojavensis* or the largest of *deserticola*.

Data indicate that the seasonal activity of *oenotherae* in Short Canyon is slightly later than either *mojavensis* or *deserticola*. The clearest evidence of this is in the relative activities of females of *oenotherae* and *deserticola* on various dates in April, 1955. In early April when a majority of female *deserticola* were digging burrows the majority of female *oenotherae* were searching, presumably for suitable nesting sites. On April 10, numerous females

of the former species were gathering pollen but only one of the latter species was taken from the flowers. With other species of *Andrena* we have found that the species which appear first in the season also appear earliest in the day throughout the season. As stated above, *oenotherae* females were found to start their morning activity a few minutes to as much as twenty minutes later than females of either *mojavensis* or *deserticola*. Similarly on cold days when only one or two females were taken visiting flowers on the alluvial fan they were all *deserticola*. Of interest, was the capture of a female *oenotherae* and a female *deserticola*, on the same day in April, 1954, each of which was parasitized by a single female *Stylops*. Larvae were emerging from the *Stylops* female in the *deserticola* female but not from the other.

In addition to these parasites two unidentified species of nomadine bees were commonly seen entering the burrows of both of these *Melandrena* species and eggs and larvae of the parasites were found in several of the cells. Two meloid first instar larvae were also found in the cells, one a *Meloe* sp., the other *Lytta stygica* (LeConte). However, neither these beetles nor a bombyliid fly, which was seen to oviposit in the burrows, were shown to be parasites of these bees.

ANDRENA (MELANDRENA) DESERTICOLA Timberlake

A. deserticola was previously known from two females collected from the western part of the Mojave Desert. The series of females from Short Canyon range from 7.9 to 8.9 mm. in wing length with a mode of 8.4 mm. This is the smallest of the three species from *Oenothera* in Short Canyon.

This species was collected only on the alluvial fan where it was the most numerous of the three. In 1954 five were found nesting and nine taken on the flowers. In 1955 a total of 51 individuals was collected at the flowers or found nesting on this slope. Some females of all three species were collected at their burrows, identified and then released. The numbers of these latter individuals are not included in the figures given above.

Burrows of this species were most abundant adjacent to the road at the upper end of the alluvial fan. Their vertical entrances permit their separation from those of *oenotherae* and their narrow diameters from those of *mojavensis*. Upon excavation they were found to be the shallowest of the three species and several cells were only 45 cm. from the surface.

The diurnal activity and parasites of this species have been discussed under *A. oenotherae* above.

ANDRENA (MELANDRENA) FLANDERSI Timberlake

On April 12, 1954, two males and a female of this species were taken at flowers of *Cryptantha* during the middle of the day on the hillside where *A. mojavensis* was nesting. The female bore pollen grains of *Oenothera*. However, no other specimens were found and its ecological relationships with the three main species in Short Canyon remain unknown.

DISCUSSION

The factors which permit the survival of three competing species of *Melandrena* in Short Canyon were not obvious to us during the brief periods available for observations. Although the facts must await future investigations, perhaps a few speculations based upon other situations of which we have better knowledge, will be useful.

The various localities in which two or three species of *Melandrena* are known to compete successfully are desert localities in the Mojave and Colorado Deserts (Needles, Hopkins Well, Desert Center, Thousand Palms, La Quinta, Palm Canyon and Salton Sea). At Riverside and near Perris (Riverside County) two species *(oenotherae* and *blaisdelli)* fly at the same time but it is not known whether or not they collect pollen from the same species of *Oenothera*. Records from coastal and montane areas do not yet reveal more than one *Oenothera* monolege in a given locality. If these are indications of the true situation, it suggests that the desert habitat may be conducive to survival under competitive conditions.

In Short Canyon, a very favorable season, such as occurred in 1954, with an abundant pollen source extending over a long period of time and favorable flight conditions, is exceptional. Under such conditions, data available indicate that the three species share the available resources by differential nest site selection and slight differences in diurnal and seasonal activity. Thus *mojavensis* tends to nest on the steeper hillsides, *oenotherae* and *deserticola* in the flat, and *oenotherae* begins collecting pollen a little later in the morning and continues later in the season than do the other two species. There did not appear to be any competition for nesting sites, but competition for the daily supply of pollen was intense.

In cold seasons flight activity is greatly reduced and the survival of the species is close to the critical level. Although the available pollen is usually reduced, the bees are not able to utilize it

fully. Activity patterns are modified and the species which has the competitive advantage in the favorable season may not have it in the cold season. In dry seasons, the pollen source is greatly reduced, and the competitive pressure favors the species which is able to collect a pollen load rapidly in the early morning. The characteristic climatic variations in the desert regions may thus favor one species in one season and others in other seasons and in combination with differential nest site selection permit the survival of the three species in a single small area.

In the brief periods of observation during 1954 and 1955, parasites and predators were not observed to be significant limiting factors. There were some slight indications of different parasite complexes associated with various bee species. These could, in the favorable periods, contribute to the heterogeneity of the ecological situation and thus the survival of all three forms. If 1955 had been a favorable year for bee activity, it would have been an ideal time to make observations on this aspect.

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BOOK NOTICES

MORPHOLOGY AND BIOLOGY OF STURMIA HARRISINAE COQUILLETT (DIPTERA), A PARASITE OF THE WESTERN GRAPE LEAF SKELETONIZER. By Owen J. Smith, Paul H. Dunn, and John H. Rosenberger. Univ. Calif. Publ. in Ent., Vol. 10, No. 5, pp. 321-358, 25 text figs. University of California Press, Berkeley and Los Angeles; June 6, 1955. Price 50 cents.

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