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George E. Bohart
Utah State University

Earle A. Cross

TIME RELATIONSHIPS IN THE NEST CONSTRUCTION AND LIFE CYCLE OF THE ALKALI BEE[1]

GEORGE E. BOHART, U. S. D. A.; Agr. Res. Serv., Entomology Research Branch,[2] and
EARLE A. CROSS, Entomology Department, Kansas University

The alkali bee, *Nomia melanderi* Ckll., inhabits large nesting sites in inorganic sandy or clayey soils having abundant subsurface moisture. Alkaline flats or low mounds with scanty vegetation are usually chosen. There is one principal generation, which flies for about 6 weeks during July and August. Its progeny overwinter in their brood cells as naked prepupae.

A typical alkali bee nest consists of a vertical shaft from 6 to 8 inches deep leading from a spoil mound at the soil surface to a series of three or four branch burrows, which are 2 to 3 inches long and diverge from nearly a common level. The cells are oval chambers arranged in close series directly beneath the branch burrows and connected with them by entrance burrows from ½ to ¾ inch long. A well-developed nest often has one side burrow which is longer than the others and extends downward to a depth of 8 or 9 inches, where it branches to form another but smaller group of cells. The deeper series is contructed and provisioned after the main one. Otherwise there seems to be no relationship between location of cells and time of their construction. Cells may be built anywhere along a branch burrow, and several branches may be used in locating a consecutive series of cells.

A cell is first formed as a large wide-necked chamber at the bottom of the entrance burrow. It is then partially filled with fine soil particles to form a perfect oval closed in at the top to form a neck just wide enough to admit the bee. The walls are polished with a transparent, waxy material that is presumably applied with the glossa. The cell is then provided with a spheroid of pollen moistened with nectar. Finally, a large banana-shaped egg is attached at both ends to the top of the pollen ball, and a spiral ceiling is constructed over the cell. The finishing touch is a plug of earth in the entrance burrow.

In Cache Valley, Utah, during July 1952, we studied rates of nest construction and brood development by digging out a series of nests of known ages. This technique furnished data on the rates of cell preparation, food storage, oviposition, and larval development. It also helped us trace the development of several parasites.

Nests were marked with greenhouse stakes either in the late afternoon when they were started or early the next morning when the shape of the mound characterized a half-day-old nest (fig. 1). Marked nests were excavated for each day of age from 1 to 19. In addition, nests 12 and 36 hours and 22, 25, and 30 days old were excavated. Whenever possible, more than one nest of each age was examined. Some of the female adults captured during excavation were dissected to permit a count of the number of eggs remaining in the ovaries.

New females emerged in the mornings from 8 to 11. They left the site shortly and did not return until midafternoon. Males were abundant during both periods and made sure that no females were left unmated. After making brief visits to existing nests and several unsuccessful starts, most of the females were able to make a successful entry into the soil by about 4 p. m. on cool days and 6 p. m. on hot days.

FIG. 1. Nest mounds: long pencil points to ½-day-old nest (flat top); short pencil to older nest (conical).

The bees were able to dig themselves under the moist clay surface in 7 to 12 minutes. Progress was then more rapid, the first inch of penetration taking 20 minutes and the second, 15 minutes. No additional record of the digging activity within the first 12 hours was obtained. However, the exposure of two nests a little more than 12 hours old and the size of mounds at others showed that the main burrow, usually 6 to 8 inches deep, was normally completed during the first night. The time required for digging the first 2 inches indicates that the burrow could be finished in 1½ to 2 hours. However, the burrowing probably proceeds more slowly as it becomes necessary to carry the material farther, and more time may be spent in perfecting the walls as the burrow is deepened. Digging activity during

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the night could be determined by collecting and measuring the spoils material at regular intervals.

The bees spent most of the next day roughing in a series of brood cells and polishing one of them for the reception of food. Only rarely did we observe a bee bringing pollen to the nest during this first day of nesting activity. Generally the first cell was fully provisioned with a pollen ball on the second day; on the third day the first egg was laid, and the cell was walled off. This pattern of preparing a pollen ball on one day and laying an egg on it the next day was the rule for the next 20 to 22 days.

The irregularity of the total-cells line in figure 2 and its divergence from the theoretical line for a one-per-day rate reflect the bees' habit of roughing in several cells at once in advance of their needs. Our observations, which were made in the late afternoon, revealed many nests containing one polished cell empty of provisions. If all cell construction takes place at night, then two cells must commonly be made at a time, one being provisioned the next day. On the other hand, it is possible that, whenever a bee finishes provisioning a cell by early afternoon, it polishes a new one before evening. Only in the case of the 12-day-old nest was there more than one empty polished cell. This nest was examined after a 2-day rainy period and appears to represent an ability to take advantage of unusual circumstances.

TABLE I

CONTENTS OF CELLS OF 37 *Nomia melanderi* NESTS OF VARIOUS AGES, NEAR PETERSBORO, UTAH, JULY 1952

Age of Nest in Days	Number of Nests Examined	Number of Cells										Total Number of Cells
		Rough	Polished but Empty	Provisioned, No Egg	Pollen Ball + Egg	Larva 2–3 mm.	Larva 3–6 mm.	Larva 6–10 mm.	Full-Grown Larva	Prepupa	Parasitized or Diseased	
1	4	2	1	0	0	0	0	0	0	0	0	3.0
2	4	3.7	0.5	0.5	0	0	0	0	0	0	0	4.7
3	3	4	0	1	0.7	0	0	0	0	0	0	5.7
4	2	5.5	0.5	1	1.5	0	0	0	0	0	0	8.5
5	2	4.5	0.5	0.5	2	0.5	0	0	0	0	0	8
6	1	6	1	1	2	1	0	0	0	0	0	11
7	2	5	0.5	1	1.5	1	1	0.5	0	0	0	10.5
8	2	4.5	0.5	0.5	2	1	1	1	0	0	0	10.5
9	2	5.5	0.5	0.5	2	1.5	2	1.5	0	0	0	13.5
10	2	6	0	1	2	1	2	1.5	0	0	0.5*	14
11	1	3	0	1	2	2	2	1	1	0	1*	13
12	2	4.5	3	1	1	1	2	1.5	2	0	0.5*	16.5
13	1	4	0	1	1	1	1	2	3	0	0	13
14	1	5	1	1	2	1	1	1	3	1	2*	18
15	1	2	0	1	2	1	1	2	2	3	0	14
16	1	1	0	2	2	1	2	2	3	3	1†	17
17	1	0	0	1	1	1	2	1	4	6	1‡	17
18	1	2	0	1	2	1	2	0	4	6	1†	19
19	1	3	0	1	1	2	3	2	3	4	1†	20
22	1	1	1	1	1	1	2	2	2	8	1†	20
25	1	1	0	1	1	0	1	2	3	6	2†	17
30	1	1	0	0	0	0	0	0	1	12	4§	18
Total.....	37	74	10	19	29.7	18	25	21	31	49	15	291.9

*Larvae of sarcophagid flies.
†Puparia of sarcophagid flies.
‡Moldy *Nomia* larva (dead).
§Two cells with sarcophagid pupae and 2 with moldy *Nomia* larvae (dead).

The progress made in cell construction and brood development in 37 nests excavated at various ages up to 30 days is shown in table I. Figure 2, based on this table, illustrates how closely the bees adhered to a one-per-day rate in making their pollen balls and laying their eggs. The deceleration in these activities recorded for nests over 20 days old may have been caused by slower ovogenesis. Another probable contributing factor was parasitism of the adult bees by larvae of the conopid fly *Zodion obliquefasciatum* Macq. The developing maggots of this parasite progressively starve the ovaries and then crowd them out.

It is not known whether the oviposition rate is determined by the time required for provisioning cells or by the rate of ovogenesis. The latter is more logical, for one would expect more variation in the rate if external conditions, such as weather and availability of food, were the limiting factors. Furthermore, the drive to prepare cells at the usual rate even during inclement weather suggests a motivation from within.

During a typical day, then, a female alkali bee (1) lays an egg on a pollen ball and then seals the cell and plugs the entrance, (2) provisions the next cell with a pollen ball, and (3) polishes a new one. It is not known whether eggs are deposited in the evening after the day's activity or in the morning before the new flight period. Evidence based on accumulation of spoils material indicates that branch burrows and new cells are constructed at night.

with the usual size of a nest. Each ovary of the alkali bee is composed of 3 ovarioles. Four prenesting females that were dissected had 4 eggs in each ovariole (total 24), the anteriormost being quite small and translucent. A bee from a 12-day-old nest had 15 eggs, and additional eggs were not being produced. One from a 25-day-old nest had only 3 eggs remaining, one in each ovariole. All these dissections indicated a capacity of about 25 eggs. The largest nest

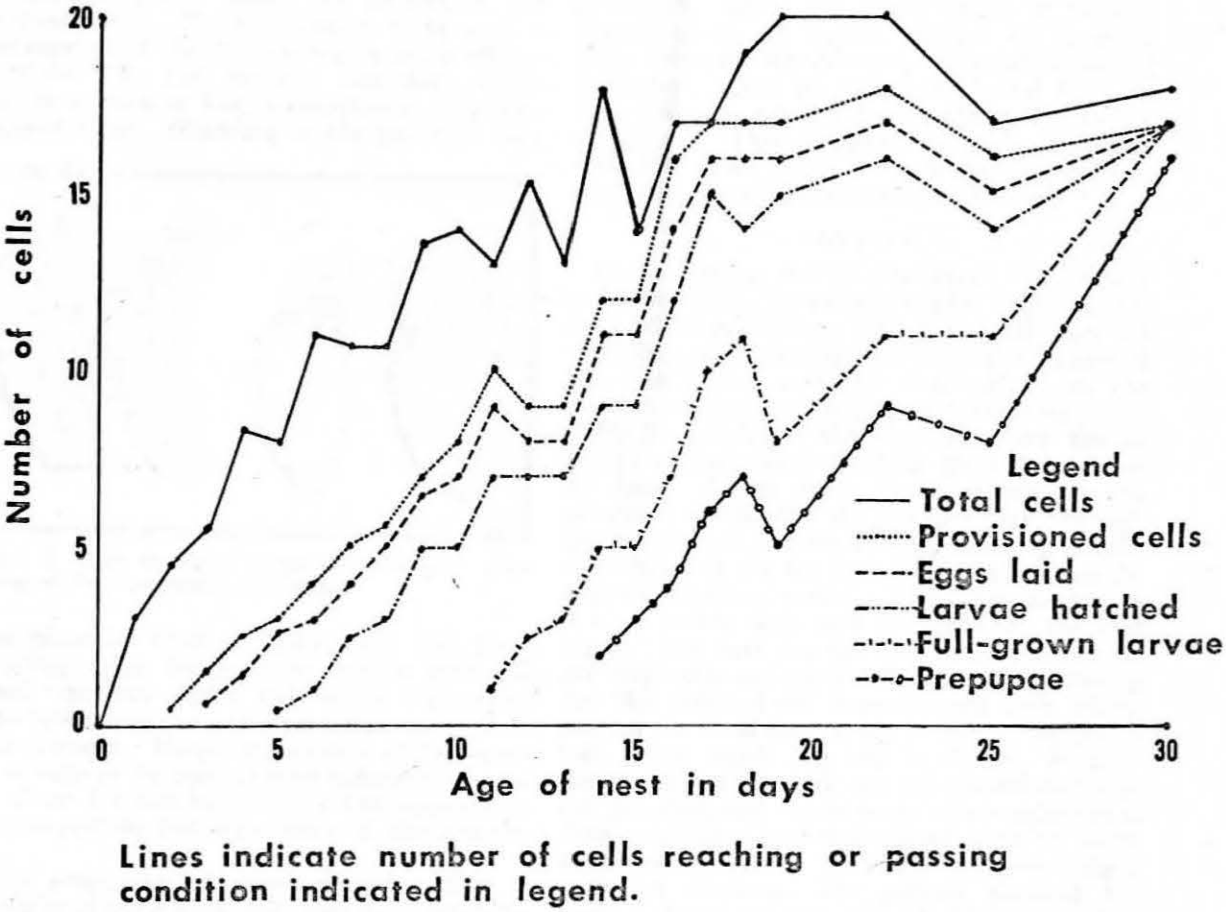

FIG. 2. Cell progress in 37 nests of *Nomia melanderi*. Petersboro, Utah, July, 1952.

According to our observations only one nest is prepared and provisioned by each female. A number of marked females were never seen again, but others, a few of which were observed for as long as 26 days, worked only in single nests. However, it is probable that a bee prevented from using a nest she had only begun to provision would start another. It would be of interest to know at what point in the progress of her nest building a bee would lose the instinct to start again.

Another line of evidence that the alkali bee does not ordinarily prepare more than one nest lies in a comparison of her egg-producing capacity

we found contained 24 cells with brood, and usually there were 15 to 20 cells with brood in a completed nest.

As indicated by the age of the nests in which eggs, developing larvae, full-grown larvae, and prepupae first appeared, the major developmental periods are as follows (table I): incubation, 2 days; larval growth, 6 days; transformation to prepupa, 3 days; total, 11 days. Most of these figures are corroborated by the numbers of each stage appearing in nests of various ages. For example, 2 full-grown larvae in 12-day-old nests, 3 in a 13-day-old nest, and 3 full-grown larvae plus 1 prepupa in a 14-day-old nest all point to a 6-day period of larval growth if one assumes a one-per-day egg-laying rate. The relatively constant rate of larval development is evidenced by the one-per-day routine of nest development still discernible in the case of developing larvae and prepupae. This feature is readily seen in figure 2, where correction is made for the sarcophagid parasites which replaced *Nomia* in many of the cells.

There is no development of the prepupae until the late-spring sun warms the ground at the brood-cell level. The first change to be seen is an elongation of the thoracic region and a softening of the body wall (fig. 3). This stage, which lasts for a week or less, is sometimes called the propupal stage. Shedding of the prepupal skin

FIG. 3. Left to right: prepupa; "propupa;" pupa forming within "propupal" skin; pupa.

takes place in Utah in both June and July, depending upon temperature factors governed by soil type, cell depth, and surface vegetation. In the laboratory the pupal period generally lasts about 3 weeks. However, evidence from inspection of cells in the nesting sites indicates a lag of only about 2 weeks between the first appearance of pupae and the first appearance of adults in the cells.

Peak emergence of males precedes that of females by about 1 week, but there is considerable overlapping. The total period of emergence may last for nearly a month because of differences in temperature within the cells. The teneral adults spend their first 3 or 4 days hardening within their cells. Even after emerging from the ground, the adults have rather soft and glistening wings and must crawl about and take short "hops" for several minutes before making sustained flights. During this period the females are readily mated, as many males are already flying over the site.

Evidently there is a partial second generation in at least some localities of Utah. At sites in both northern and central Utah large numbers of freshly emerged males have been seen to appear suddenly in August at a time when males from the previous emergence were already old and tattered or gone altogether. More definite evidence of a second generation was found in August near Flowell, Utah, where a nesting site was discovered in some new soil used to plug a break in an irrigation pond. Nesting activity was nearly over, but several fresh-looking males were flying over the site. Digging revealed a number of white and pigmenting pupae of both sexes. Although this site was destroyed soon afterwards, it can be assumed that these pupae would soon have become the adults of a second generation, since the pupal stage of bees is always short. A logical method for learning more about the significance of this partial second generation would be to remove brood from an area within a nesting site in the spring before emergence. Then, if pupae can be found in this area the same year, the presence of second-generation bees on the site is established.

SUMMARY

On a nesting site of the alkali bee, *Nomia melanderi* Ckll., in western Cache Valley, Utah, 37 marked nests from 12 hours to 30 days old were excavated to chart the nesting activities of the female bee and the development of the immature stages to the prepupal condition.

Findings indicate that typically each female builds a single nest of 15 to 20 cells in about 30 days. A bee starts her nest late in the afternoon of the day she emerges from the soil, having first left the site to feed. Mating usually takes place on the site both before and during the nest-construction period. The main burrow is 6 to 8 inches deep and is completed the first night. The next day the first two or three cells are roughed in and one is polished. The following day this polished cell is provisioned with pollen, and on the third day an egg is laid on the pollen ball, after which the cell is closed. A daily routine of one egg laid, one cell provisioned, one cell polished, and one or more cells roughed in is thus established and maintained until 15 to 20 eggs have been laid. Thereafter the rate of these activities declines. The periods required for various phases of nest building and brood development are: prenesting and mating flight, ½ day; preoviposition period during which nest building progresses to the first finished cell, 2 days; incubation period, 2 days; larval growth, 6 days; transformation to prepupa, 2 to 3 days; egg to prepupa, 10 to 11 days.

The prepupal period lasts through the fall, winter, and spring, and pupation, which usually begins in June, requires 2 weeks. The teneral adult remains in its cell for 3 or 4 days before taking flight. Emergence of adults at a nesting site may last nearly a month with the peak for males preceding that for the females by about 1 week. Usually there is a single generation of adults in the summer, but evidence of a partial second generation has been found in some localities.