Reports

Distinctive Type of Primitive Social Behavior among Bees

The purpose of this paper (*1*) is to describe a type of social behavior which we believe to be important in understanding the evolution of societies in higher bees. It is found in *Augochloropsis sparsilis* (Vachal) [Hymenoptera, Halictidae]. Our observations were made in the Bariguí roadside banks (*2*) near Curitiba, Paraná, Brazil, during the year July 1955–June 1956.

One of us has explained elsewhere (*3*) his conviction that social organization in the main groups of social bees (Halictinae and Apinae) did not arise, as it probably did in wasps and ants, through subsocial family groups in which a parent protects and feeds her larval offspring. This notion has been prevalent in the literature (*4*) due to evidence for care of larvae by adults of the bee genera *Allodape* and *Exoneura*. However, in all Halictinae and all but some specialized Apinae (such as *Apis*), the larval cells are closed; care of larvae during their growth is therefore impossible, and the subsocial family group becomes an unlikely antecedent to specialized social behavior with division of labor, caste differentiation, and so forth. Such specialized behavior occurs in certain groups of both Halictinae and Apinae, and steps in its establishment are said (*3*) to include the following: (i) nest aggregations; (ii) use of a common nest by several females, each of which constructs and provisions her own cells; (iii) initiation of division of labor and cooperation among such females; and (iv) differentiation of the females into queens and workers and establishment of a numerical preponderance of females over males.

Step i is well known (*2*). Step ii has been often reported and recently has received considerable attention (*5*). Step iv is of course well known in such groups as *Bombus,* the Meliponini, and *Apis,* and less well known in the social Halictinae (some species of *Lasioglossum, Halictus,* and so on). The importance of *Augochloropsis sparsilis* is that, unlike other bees for which details of the bionomics are known, it is a convincing example of stage iii, a status that may be called semisocial.

Each nest consists of a burrow extending into the bank and ending in one or several groups of adjacent cells. Each nest is ordinarily occupied by several female bees. The males leave the nests soon after emergence, and mating probably takes place elsewhere. The number of females per nest fluctuates with the season, as shown in Fig. 1 (bottom). The interrelations among these females are of primary interest in this study.

As the nests are used year after year, if they are not destroyed by erosion of the banks, it seems likely that the inhabitants of a nest are commonly sisters. However, it is apparent that this need not be the case, since we have found two and three females together in a simple burrow without cells; evidently when a female starts a burrow she may be joined by others which are not likely to be her sisters.

From observations of marked individuals we know that females of various ages go into the winter. The badly worn and tattered bees disappear in the fall, but some bees several months old, although still unworn or nearly so, overwinter with young unworn females. In the spring, all bees therefore start activity with relatively unworn mandibles and wings. Soon, however, some individuals become worn, and from that time on until late fall the population of females consists of a mixture of tattered and fresh individuals in various proportions (Fig. 1, top). In each nest there are usually, after early spring, individuals exhibiting considerable wear, as well as fresh and intermediate ones. This indicates diversity in activity among the females concerned. Mandibular wear must occur in the nest, while wing wear occurs in the field, probably around flowers. Bees that show one type of wear ordinarily show the other also; this indicates that bees that work ordinarily engage in both outside and inside activity.

Figure 1 (middle) shows that while all overwintering females have very slender ovaries (less than 0.25 mm wide) or slender ovaries (0.26 to 0.45 mm wide), great diversity in ovary size soon develops and persists throughout the egg-laying season. Ovaries which are much swollen (0.86 to 1.20 mm wide) almost invariably contain one or more oocytes 1.5 mm long or longer, and usually they contain one larger one, which approaches the size of a fully developed egg cell (about 3 mm long). No new bees reach maturity until January (the southern summer). Therefore, as Fig. 1 (middle) shows, an increasingly large percentage of the overwintering bees reach egg-laying condition during the spring and early summer. Although a few (2.4 percent of 85 dissected) females have much-swollen ovaries while their wings and mandibles are still unworn, in general such ovaries are associated with wear. Seemingly, most bees have done some work by the time they become egg layers. Among 241 females dissected during the year, 14.9 percent had much swollen ovaries and were therefore considered egg layers, but during November and the summer months when egg laying is at a maximum, 20 to 30 percent of the females had much swollen ovaries.

Another aspect of the diversity among females involves pollen collecting. Observations of nests which were later excavated revealed that often in a nest containing three or four bees, only one was making pollen-collecting trips. Or, especially in a larger nest, two or three were sometimes collecting pollen simultaneously. In such cases, when the nest was opened, there was never found more than one cell being provisioned. The pollen gatherers clearly cooperate in the provisioning of cells.

Pollen gatherers normally have slender to very-slender ovaries, and, although sometimes fresh, they usually show considerable and often maximum mandibular and wing wear. We judge from this that some females develop as pollen collectors and wear out and die without ever becoming egg layers. This surmise is supported by data from marked bees. Ninety-two females were marked (*6*) with colored paints during November and January. Bees for marking were obtained during warm days as they entered their nests after trips afield. About half of the bees marked were returning to their nests with pollen loads. After a series of such bees had been marked and allowed to re-enter their nests, it was usual to see the individuals marked as pollen collectors continuing in that activity for two or three weeks, but grad-

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ually they disappeared. Probably death of such bees is a major factor in the diminution of nest populations noted during October, November, and December (Fig. 1, bottom). The records are few and inconclusive, but we think that as pollen collectors die, they are replaced by other, previously relatively inactive bees. Reduction in egg production during November and December (Fig. 1, bottom) as well as other data suggest that egg layers probably also die during this period and are only partly replaced from among the previously inactive bees. After the second brood begins to appear, in January, nest populations and egg production rise.

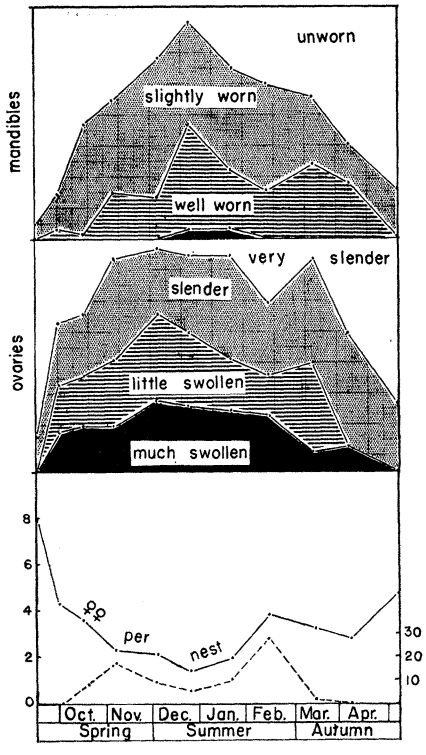

Fig. 1. Nest statistics and conditions of female occupants. (Top) The white and shaded zones vary in width according to the percentage of individuals having mandibles classified as unworn, slightly worn, well worn, and much worn. The four zones total 100 percent in vertical distance at any date. (Middle) White and shaded zones show fluctuations in percentages of females in four groups, classified according to size of ovaries. (For both these sets of percentages, the number of individuals examined was more than 20 for each date, with the exception of early October, when the number in the "middle" group was 11, and of April, when the numbers in the "top" and "middle" groups were 13 and 12, respectively.) (Bottom) Solid line shows average numbers of females per nest, plotted on the scale shown at the left (the number of nests examined, for each date, was 4 to 11, and trends were supported by data from many other nests for which we have only incomplete counts); broken line shows percentage of cells containing eggs, plotted on the scale shown at the right (the number of cells examined, for each date, was more than 49, except for April, when the number was 25).

Probably all females leave the nest from time to time to feed. Bees that become pollen collectors may do so more often, while those that become egg layers perhaps do so less often. As bees develop in one or the other of these directions, they show the results of wear, but a number of unworn bees with slender ovaries always remain in the nests. This number decreases steadily (Fig. 1, middle) until January, when new adults emerge. This indicates that bees leave this inactive state to become active either as foragers or as egg layers.

The division of labor described above occurs among bees which do not differ significantly in size, and all of which ordinarily are mated. Clearly, there is no morphological caste differentiation and, as might be expected, male progeny are little if any less numerous than female.

There are, however, a few unfertilized bees in the nests, as determined by examinations of spermathecae for spermatozoa (*6*). Among the overwintering bees dissected in spring and early summer, only one out of 86 was unmated. During January and February, between 15 and 20 percent of the females dissected were unmated; in some cases this was merely because they were young, but others showed wear and presumably would not mate. Over half of the pollen collectors studied during those months were unmated, and we think that most or all of the bees that remain unmated become pollen collectors. Like most other pollen collectors, they have slender ovaries, and usually worn wings and mandibles. Only rarely was more than one such bee found in a nest, and often there was none. Some unfertilized bees were found to be much more worn (with respect both to mandibles and wings) than any fertilized bees of the same age.

It is easy to see that the presence of such active, unfertilized bees might be an advantage to a colony, even though they are nonreproductive. We conjecture that the habit of extensive work on the part of unmated females served as a preadaptation that permitted selection for the regular occurrence of such individuals (workers) and thus provided for the establishment of a worker caste.

In summary, *Augochloropsis sparsilis* exhibits a type of social behavior in which several morphologically similar females, most or all of which mate, occupy a single nest. Division of labor is established, for some females become egg layers, others pollen collectors; cooperative activity includes joint provisioning of cells by two or three bees. A few of the females never mate; these work more than most mated bees, a fact which perhaps provides the basis on which selection can work toward establishment of a regular nonreproducive worker caste.

CHARLES D. MICHENER
Department of Entomology, University of Kansas, Lawrence
RUDOLF B. LANGE
Instituto de Historia Natural and *Faculdade Catolica de Filosofia, Curitiba, Paraná, Brazil*

References and Notes

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2. C. D. Michener *et al.*, *Ecology*, in press.
3. C. D. Michener, *Proc. Intern. Congr. Entomol. 10th Congr.*, in press.
4. See, for example, W. M. Wheeler, *Social Life among the Insects* (Harcourt, Brace, New York, 1923).
5. C. D. Michener and R. B. Lange, *Ann. Entomol. Soc. Am.*, in press; J. G. Rozen, Jr., and C. D. MacNeill, *ibid.* 50, 522 (1957).
6. For techniques of study, see C. D. Michener *et al.*, *Insectes Sociaux* 2, 237 (1955).

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Absorption of Cosmic Radio Noise during the Great Aurora of 11 February 1958

During the night of 10–11 February 1958 observers in clear portions of the United States witnessed one of the largest aurorae of the current sunspot cycle. Although heavy clouds blanketed Boulder, Colorado, two receivers normally used for measurements of the absorption of 18 Mcy/sec galactic radio noise operated throughout the night. One of these receivers recorded the total power from a vertically-beamed antenna approximately 50 by 90 deg wide between the half-power points. The other receiver measured power in a two-element, Ryle phase-switching interferometer with a baseline 16.8 wavelengths long, oriented at an azimuth 41 deg east of north. The elements of the interferometer were steerable corner reflectors with beams 40 deg wide and 60 deg high, at a fixed orientation elevated 35 deg toward the northeast. The output of the interferometer split into two channels, one recording the average power (called "total power") between the two halves of the Ryle switch axle, the other the power difference (called "phase power") between the two half-cycles.

Figure 1 shows the three records. Two principal events occurred, between 0545