tained when salivary glands, denervated by removal of ipsilateral superior cervical ganglia, were compared with their contralateral controls. On chromotography, octopamine was present only in the innervated glands.

Kopin and his collaborators have shown that H^3-octopamine is formed after the administration of H^3-tyramine (*5*). The H^3-octopamine is retained by the same granules which store norepinephrine (*6*), and it can be released from the isolated perfused cat spleen by nerve stimulation (*7*). These observations and our demonstration that octopamine is a normal constituent of sympathetically innervated organs suggest that it is normally released, along with norepinephrine, from sympathetic nerves.

The physiological significance of octopamine is unclear. It has weak sympathomimetic activity, about 1 percent that of norepinephrine, and its concentration in the heart, for example, is only about 5 percent that of norepinephrine. However, the urinary excretion of its major metabolites is quantitatively comparable to those of norepinephrine (*2*, *8*), suggesting that octopamine turns over rapidly.

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References and Notes

1. V. Erspamer and G. Boretti, *Arch. Int. Pharmacodyn. Ther.* **88**, 296 (1951).
2. Y. Kakimoto and M. D. Armstrong, *J. Biol. Chem.* **237**, 422 (1962).
3. J. Axelrod, *ibid.* **237**, 1657 (1962).
4. J. P. Tranzer and H. Thoenen, *Experientia* **24**, 155 (1968); H. Thoenen and J. P. Tranzer, *Naunyn-Schmiedeberg Arch. Pharmakol. Exp. Pathol.* **261**, 271 (1968).
5. I. J. Kopin, J. E. Fischer, J. Musacchio, W. D. Horst, *Proc. Nat. Acad. Sci. U.S.* **52**, 716 (1964).
6. J. M. Musacchio, I. J. Kopin, V. K. Weise, *J. Pharmacol. Exp. Therap.* **148**, 22 (1965).
7. I. J. Kopin, J. E. Fischer, J. Musacchio, W. D. Horst, V. K. Weise, *ibid.* **147**, 186 (1965); J. E. Fischer, W. D. Horst, I. J. Kopin, *Brit. J. Pharmacol.* **24**, 477 (1965).
8. M. D. Armstrong, K. N. F. Shaw, P. E. Wall, *J. Biol. Chem.* **218**, 293 (1956).

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Brood Care in Halictine Bees

Abstract. *Four species of the halictine bee genus* Evylaeus *keep their brood cells open during most or part of the development of the larvae. In the colonial summer phase, house bees care for the young and keep brood cells clean from feces and exuviae. Progressive feeding of nector is present at least in* Evylaeus malachurus, *whose fully fed larvae are, on an average, 60 percent heavier than the egg-and-pollen stage. Interactions between the two generations of social Halictinae are of general occurrence, and their intensity corresponds to the level of social behavior attained.*

Societies of ants, bees, and wasps usually consist of a queen and her daughters, and parental care of the young appears to be the main preadaptation for social behavior (*1*). Growing up in the same nest leads to a degree of mutual tolerance which forms the basis for further social interactions among nest mates. The peculiar haploid-diploid mode of hymenopteran sex determination seems to have supplied a genetic mechanism which gives selective advantage to societies made up of closely related individuals (*2*).

Michener (*3*), while accepting the importance of parental care in the emergence of such societies as that of the termites, ants, and wasps, believes that a different evolutionary path was followed by most bees; he assumes that social organization of bees was established among groups of adults. His conclusions are based mainly on studies of Halictinae, a worldwide subfamily of primitive bees with such a wide range of solitary and social members that they can be regarded as an illustration of how insect societies may have originated.

Honey bees, ants, and some wasps show a variety of interactions between larvae and adults, including the exchange of food (trophallaxis) and social grooming. Both were thought to be characteristically lacking in the mass-provisioning halictines, which seal each cell after it is supplied with pollen and nectar and an egg is laid. Females of solitary species usually die before the emergence of their progeny, and contact with the immature stages is generally prevented by the location of the cells at the end of long, soil-filled laterals (*4*). However, the social species investigated construct cells which are easily accessible from the main burrow. Several of these halictines maintain at least occasional contact with their brood after the cells have been sealed. The reopening of closed cells for inspection has been observed in *Dialictus versatus* and *D. zephyrus*, two Nearctic species with a primitive social organization (*5*).

The evolutionary importance of this phenomenon can best be evaluated through studies of the many species of the genus *Evylaeus* which together cover a remarkably wide spectrum of behavior. Strictly solitary species have relatives with a fairly complicated social behavior and a nest structure suitable for complex societies. The socially most advanced *E. marginatus*, *E. linearis*, *E. malachurus*, and *E. cinctipes* deliberately leave their cells open or reopen them during the development of the larvae (*6*). The nature and intensity of interaction between the two generations vary widely in these species, but all are concerned with aspects of cell sanitation and progressive feeding of the brood. The Mediterranean *E. marginatus* forms the only perennial society known among the Halictinae. Queens live up to 5 years, producing annual clutches of physiologically distinct workers (*7*). On excavation, cells are open and free of larval exuviae and feces. Because *E. marginatus* has not been studied in the laboratory, it is excluded from this discussion.

The overwintered queens of the three annual species provision a few cells in early spring and await the emergence of their workers within the closed nests. During this phase, only *E. cinctipes* removes exuviae and feces from the brood cells, which remain open throughout the development of the young bees. *Evylaeus linearis* and *E. malachurus*, in sharp contrast, do not remove the feces prior to the closure (capping) of the cells. All three species respond unambiguously to the contents in the cells, since they recognize dead and introduced larvae, which they bury in the cell or remove. Cells without contents or feeding instars are never capped by *E. malachurus* or *E. linearis*. The trait to remove dead or "abnormal" larvae from their cells is an important social innovation in these species. As societies increase in size with higher social development, epizootics become a greater threat under the more crowded conditions. A mechanism for the elimination of the contagion is therefore clearly adaptive. In the honey bees, for example, only strains efficient in removing sick or perished larvae can check the spread of infectious diseases, and often achieve spontaneous recovery (*8*).

Colonies are formed in early summer with the arrival of the first workers. A semipermanent division of labor is soon established in the more populous societies, where most eggs are laid by the queen. Some workers forage for pollen and nectar in the field while others guard the nest and care for the larvae. Brood cells in these nests are frequently inspected and all debris is removed from them continuously. Cell closure, which has not been developed in *E. cinctipes* to any extent, has become a very precise mechanism in the two Palearctic species. In all the nests excavated or observed in the laboratory, feeding instars were found in the open cells, and prepupae and older stages were located in the capped cells. This fact was suggestive of progressive feeding since females of *D. zephyrus* had already been observed to apply their tongue to provisions in previously closed cells (*9*), and the house bees in the observation nests of the "open cell" species visited the larvae too frequently for mere routine inspection of the cells. A regular addition of nectar would cause the feeding larvae to become progressively heavier throughout their development. Such a weight increase was observed in *E. malachurus,* when nests in an aggregation near Marseilles were excavated during the spring of 1967 and their cell contents were weighed (Fig. 1). The average weight gain of 60 percent during larval development seems too large to be caused solely by the hygroscopic nature of the pollen, but rather supports Batra's (*9*) suspicion that progressive nectar feeding is present in some halictine bees.

Sanitation and a very primitive type of trophallaxis are then firmly established in the cells of the most advanced of social *Evylaeus* species. The Halictinae are in a phase of rapid evolution, as indicated by the great number and morphological similarity of forms. Their social development, not suprisingly, lags behind and is still at a low level; but the few species investigated so far illustrate the many attempts toward greater social integration. Some of the pathways have nearly come to the end, as in *E. marginatus,* where slow larval development prevents the annual production of queens and thereby a scarcity of the bee throughout its distributional range. The *linearis–malachurus* and perhaps similar lines are complementary to the apine social evolution and oppose Michener's (*3*) strict dichotomy between trophallactic (subsocial) and nontrophallactic (semisocial) primitive insect societies. The inference now is that intimate relations between generations in halictine bees start as soon as some social behavior becomes established and increase in importance as higher social levels are attained by the species.

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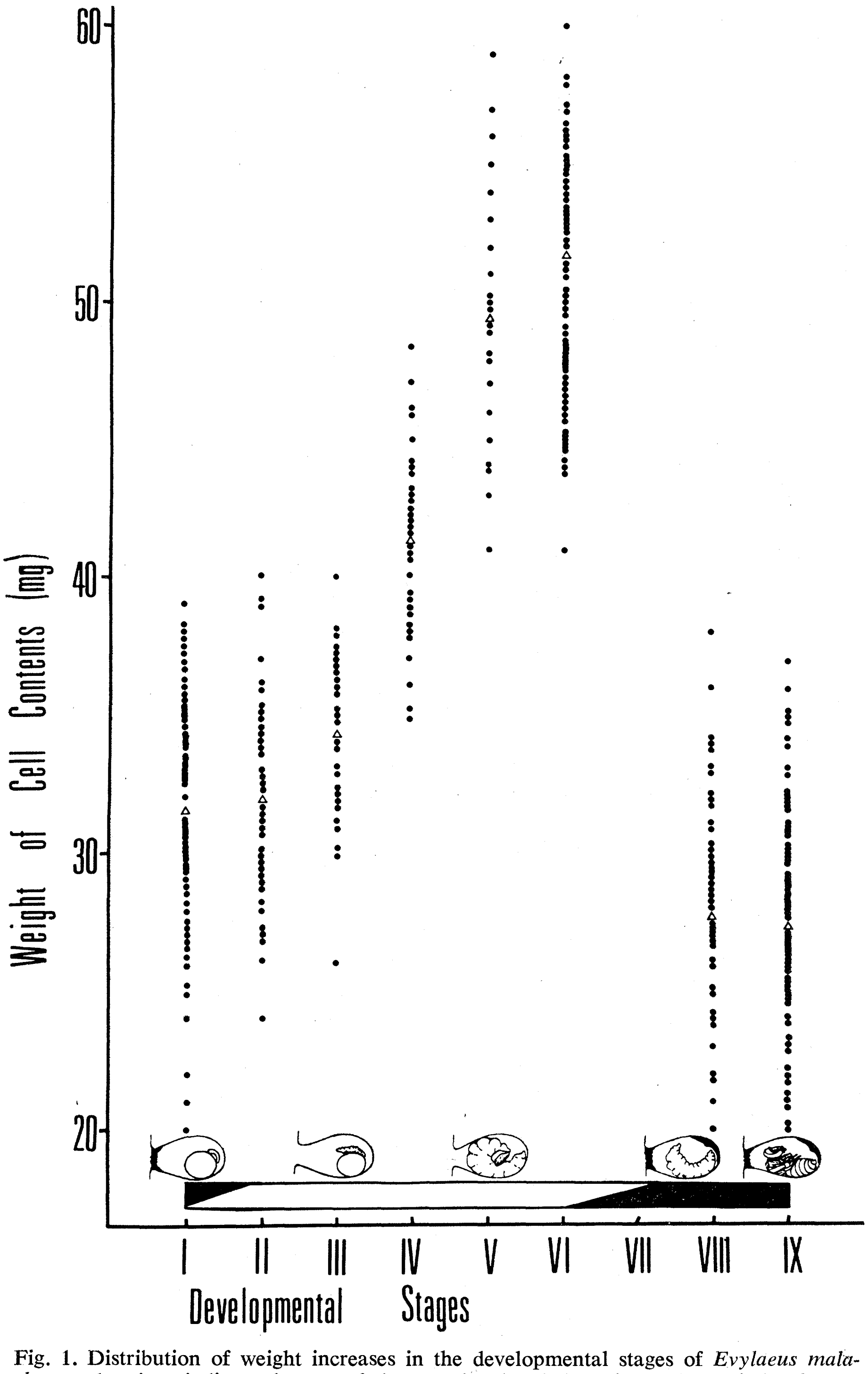

Fig. 1. Distribution of weight increases in the developmental stages of *Evylaeus malachurus*; drawings indicate the age of the samples; bar below shows the periods of open (white) and closed (black) cells. Sampling was done near Marseilles throughout the spring to avoid a seasonal bias.

References and Notes

1. O. W. Richards, *The Social Insects* (MacDonald, London, 1953).
2. W. D. Hamilton, *J. Theoret. Biol.* **7**, 1 (1964).
3. C. D. Michener, *Proc. Intern. Congr. Entomol. 10th* **2**, 441 (1958).
4. G. Knerer, *Insectes Soc.*, in press.
5. S. W. T. Batra, *J. Kans. Entomol. Soc.* **41**, 120 (1968).
6. G. Knerer and C. Plateaux-Quénu, *Compt. Rend. Acad. Sci.* **263**, 1622 (1966). *Evylaeus cinctipes* is the only Nearctic species among the four; the others are Palearctic.
7. C. Plateaux-Quénu, *Année Biol.* **3**, 326 (1959).
8. W. C. Rothenbuhler, *Anim. Behav.* **12**, 578 (1964).
9. S. W. T. Batra, *Insectes Soc.* **11**, 159 (1964).

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