Social Aspects of Facultative Gravidity and Agravidity in Hymenoptera.

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This presentation is concerned with the environmental initiation of (1) gravidity and of agravidity in the normal, well-nourished female of certain ectoparasitic and social Hymenoptera and (2) the distinctive behavior pattern that accompanies each state.

Gravidity is characterized by ovigenesis, the ovaries containing viable oocytes and/or eggs; agravidity is characterized by the absence of ovigenesis, the ovaries lacking viable oocytes and eggs. Agravidity is synonymous with "phasic castration"[1] but not with "cessation of ovigenesis" such as occurs in the endoparasite, Metaphycus helvolus (Compere); a superficially similar condition not involving differential behavior but the mere cessation and resumption of ovigenesis effected by the absence and presence of hosts[2,3].

The facultative realization of gravidity and agravidity is effected either by a delayed (ontogenetic) response or an immediate (imaginal) response to environmental conditions. The ability of the female adult to change alternately from a gravidic to an agravidic state with each state characterized by a distinctive behavior pattern is presumably an adaptation to biotic environmental conditions that alternate in suitability and unsuitability for the successful development of the female's progeny. It is an adaptation apparent in many ectoparasitic and in most, if not all, social Hymenoptera.

The critical physiological mechanism involved in this adaptation is the egg-resorption process[4]. It is this process which, on one hand exhausts the female adult of oocytes as an immediate response to environmental conditions and on the other hand early in the ontogeny of the female supposedly precludes the presence of oocytes in her ovaries when newly-emerged.

The fact of ovisorption as a regular and integral process in the economy of many species of Hymenoptera whose females when newly emerged are always gravidic was noted by the writer[2] in his study of ovigenesis in the Encyrtidae. Portions of the egg chorions of many encyrtids are not resorbed, remaining for the life of the female as identifiable remnants within the ovarioles. Since such remnants do not interfere with either ovigenesis or ovulation, they attest to the normality of the ovisorption process.

The role of this phenomenon in the ecology of a hymenopterous parasite was reported by Schneider[5]. He observed that the chalcidid Brachymeria euploeae Westwood, a parasite of the pupa of the gambir

moth, Oreta carnea Butler, when reproducing at the rate of 2 generations to 1 host generation tends to cause the host population to be so even-brooded that there occurred, periodically, a scarcity of host pupae. This scarcity, in turn, initiated ovisorption and cessation of ovigenesis in the parasite regardless of her age, this being a form of phasic castration as an immediate response. Eggs were resorbed despite the female's fat-body being fully developed.

Apparently, Schneider[5] was first to point out that this ovigenic condition in parasitic Hymenoptera is comparable to that characterizing the worker caste of social species. He noted that in both groups the vigor of the female tended to increase with the cessation of ovigenesis.

For many years circumstantial evidence has indicated that in a number of species the delayed ovulation of the ripe egg and its consequent exposure to incipient resorption extracts sufficient nutrients to give that egg an agravidic (caste) bias. Generally, this bias is subject to counteraction after the female becomes adult. However, in the high social species in which morphological differentiation of the female adult prevents mating, this bias is subject to counteraction by special feeding during the late larval stages.

In all such Hymenoptera, reproduction is usually biparental; the adult life of the reproductive female is at least twice the length of her minimum developmental period and the deposition of her eggs is largely, if not entirely, restricted to sites (positions) suitable for progeny development. Agravidic bias as a resorptive effect can be realized only if the amount of nutrient material remaining in the egg at the moment of its deposition is sufficient for the development of a healthy embryo. It is significant that the entire complement of eggs deposited by an apparently healthy queen honeybee with normal hive relations may fail to hatch[6]. This failure, presumably, is an effect of delayed ovulation being genetically so prolonged that the resorptive process extracts from each egg the amount of yolk needed for the complete development of the embryo.

The process by which the female Hymenoptera attains an agravidic state either as a delayed response ("alimentary castration" of the embryo) or as an immediate response ("nutricial castration" of the adult) has been discussed, in part, by Wheeler[1] under "phasic castration". Castration, broadly speaking, is any process that interferes with or inhibits the production of "ripe" ova or "ripe" spermatozoa.

Phasic castration, as a delayed and as an immediate response, was observed in 1933 and 1934 by the writer[7] in 4 species of pteromalids; Dibrachoides sp., a pupal parasite and Eutelus sp., Peridesmia sp., and Spintherus sp., egg-predators of the alfalfa weevil, Hypera postica (Gyllenhal).

The material available for study consisted of about two thousand parasite adults, males and females, obtained as immature individuals from southern Europe through the cooperation of the U.S.D.A. Mating occurred soon after emergence. All adults were held at room temperature (15-28° C) and fed bee honey. Those not used for reproduction and study were released in California alfalfa fields. Most of the newly emerged females of each species received from Europe were in an agravidic condition (as a delayed response).

However, about one-third of the Dibrachoides received in July 1933 were gravidic upon emergence and so could immediately reproduce. Nevertheless, all the newly emerged female progeny of these were agravidic, presumably because parental ovulation was delayed and permitted incipient ovisorption to occur.

During February 1934, one female of this agravidic group after 7 months in the laboratory at room temperature began to host-feed and soon became gravidic. After being permitted to deposit 1 egg on each of 10 host pupae, an examination of her ovaries revealed that ovigenesis had occurred in only one ovary, the other having remained in an agravidic state. At the moment of dissection, the gravidic ovary contained 8 yolk-replete eggs and 3 in the process of resorption[8].

Nine of the 10 deposited eggs became adult females but, of these, upon emergence, only the first and last were gravidic, the other 7 being agravidic. Evidently, the ripe eggs within an ovary are differentially influenced by environmental factors, possibly by host availability relative to the rate of ovigenesis.

In the spring of 1934 another shipment of immature parasites from Europe yielded 250 female Peridesmia. During an emergence period of 21 days, the percentage of females in a gravidic state gradually decreased from 90 to 25. Correspondingly, of course, the females that emerged in an agravidic state increased from 10 to 75 percent. The food consumed by the larval instars of the various Peridesmia females was probably uniform in quality since the food supply of each larva consisted of a single cluster of host eggs.

In the imported populations of the pteromalid species the proportions of gravidic and agravidic females presumably reflected the phenotypic conditions under which their parents oviposited, as the season advanced, ovulation being more and more delayed.

Dissections were not needed to determine the presence of the two types of females, studies in 1933 having demonstrated that the female's host-feeding responses were completely adequate for this purpose. The cessation of host-feeding proved to be an accurate indication of the cessation of ovigenesis and the lack of developing oocytes. Conversely, host-feeding is an accurate indication of ovi-

genesis. When an agravidic female becomes gravidic, host-feeding commences when the largest oocyte attains a size equal to or larger than the mass of its attendant nurse cells. The fact that the germaria in all the agravidic females examined appeared viable and healthy indicated a capacity to resume ovigenesis.

The study of these 4 species of Hymenoptera show that females which possess the capacity for phasic castration are characterized by short developmental periods (life-cycles) and long adult lives. The larval feeding period of Spintherus, for example, is only 1 week, but 1 agravidic female that emerged from the European shipments in July 1933 was held at room temperature until February 1934. Subsequently, this female became gravidic and deposited 27 eggs during an 18-day period.

It seems significant that the ectoparasitic ichneumonid Hymenoptera, supposedly representative of the ancestral forms of the aculeates[9], exhibit similar but primitive behavior patterns. The gravidic female parasite searching for egg-deposition sites frequents host habitats and utilizes the sting for host-feeding and host mutilation as well as for oviposition. The agravidic female on the contrary may frequent flowering plants feeding on nectar and in some cases give her progeny maternal care.

Experimental evidence that the condition of the ovaries of a hymenopterous female directly determines the patterns of her behavior other than that of mere oviposition was reported by Thorpe and Caudle[10]. They found that the female ichneumonid Pimpla ruficollis Gravenhorst, a solitary parasite of the pine shoot moth, Rhyacionia buoliana (Schiffermüller), when agravidic frequented flowering plants, being repelled by the odor of Pinus sp., whereas, when gravidic, being attracted by this odor, it frequented the foliage of pine trees.

In the braconid Cedria paradoxa Wilkenson, a gregarious ectoparasite, the differential behavior patterns of the female have been observed to change according to her gravidic and agravidic states. As reported by Beeson and Chatterjee[11], and J. Chu[12], the female has an adult life of 23 days when the prevailing temperatures vary between 25° C and 30° C. During this period, a female produced in succession 2 distinctive broods of progeny with each brood subsisting on 1 host individual and attaining adulthood in 11 days. Between oviposition periods, however, the parental female exercises maternal care of her developing offspring. In this case also it was noted that host-feeding occurred only during the period of oviposition. A circumstance indicating that ovisorption was involved was the fact that when the female's host relations were so manipulated that she deposited a 3rd brood of eggs all such eggs were nonviable, presumably because of embryonic starvation[13].

In the evolution of highly social Hymenoptera the requirements of social life and population control in colonies consisting of great numbers of workers (agravidic females) per queen (a gravidic female), all being derived from eggs having an agravidic bias, apparently made necessary a morphological differentiation of the female adult to prevent mating and thus, in effect, to fixate the female's agravidic state.

This fixation appears to have been accomplished as in the army ant and the honeybee by extrinsically enforced inanition of the late larval instars and the more or less synchronous imposition of morphological differentiation; a differentiation realized in the adult by reduced reproductive organs and the loss and acquisition of secondary sexual characters. Species reproduction, being biparental, required that this fixation be subject to preclusion, a preclusion accomplished nutritionally by the agravidic females themselves according to the needs of the colony. Queen production based on larvae which lack agravidic bias was replaced by queen production based on nutritional counteraction of larval agravidic bias.

This phenomenon may have evolved from colony conditions now represented by the stingless honeybees of the genus Melipona in which caste is obviously determined in the egg, the brood cells of the queens (gravidic females) and of the workers (agravidic females) being identical, intermixed, and mass provisioned with equal amounts of food[14]. Unlike the higher social species there is no "undernutrition" of the agravidic larvae to bring about distinctive structures in the adult.

In normal colonies under optimum conditions the ratio of queen cells to worker cells may be as high as 1 to 4. However, when conditions are not optimum a high proportion of queens are replaced by workers, a circumstance that indicated to Michener[15] that in Melipona trophic conditions play a role in caste determination. Apparently, the proportion of workers reflects the proportion of deposited eggs which have an agravidic bias as an effect of delayed ovulation and the consequent ovisorption, a proportion that increases as colony conditions deteriorate. In Melipona, therefore, queen production is not based on nutritional counteraction of agravidic bias but on eggs that escape incipient resorption.

It is probable that in the social species more highly evolved than Melipona most, if not all, the ovulated eggs are thus biased. However, observations by Fyg[16] indicate that in the honeybee a few ovarian eggs may escape the resorptive process and retain their gravidic bias so that when underfed as larvae they become the "dwarf" queens. Agravidic ontogonies in species without structurally distinctive females yield agravidic adults regardless of either the quantity or quality of the food consumed as larvae.

Despite the fact that Melipona larvae are mass-provisioned, Kerr and Nielson[17] "suspected" that the queen became irrevocably different from the worker during her late larval instars. However, the only trophogenic hypothesis that appears to adequately account for the situation in Melipona is (1) the embryonic undernutrition (alimentary castration) of a portion of the brood predisposing the diploid individual to become when newly emerged an agravidic adult, and (2) the absence of embryonic undernutrition in a portion of the brood so that some diploid individuals are gravidic soon after emergence. Although gravidic when newly emerged the Melipona queen possesses few developing oocytes, presumably because of the relatively small amount of food consumed during her larval instars.

In the semi-social bee Augochloropsis sparsilis (Vachal), the fixation of worker structure by larval nutrition does not occur, since only a portion of the embryonic brood may be undernourished. Caste is determined according to Michener[15], after the female is an adult. Probably it is brought about by nutricial (threptic) castration. It is manifested only by division of labor; one female, the queen, doing most of the egg laying; the others (workers), most of the foraging. Both queen and the workers are fecundated by the male.

In Bombus, which has the maximal physical caste differences known in primitively social bees, there are records of mated workers and of colonies headed by workers[15]. Underfeeding of female larvae merely miniaturizes the adult female therefrom. The queen may inhibit ovigenesis in the workers, perhaps directly, by means of a pheromone. However, when oviposition by a queen ends, one or more of the agravidic workers begins oviposition several days later. (In the Hymenoptera, a primary oogonium can become a mature, ripe egg in less than 70 hours[2].) Such workers when thus relieved of their threptic duties, become gravidic with noticeably distended abdomens. They remain in the nest instead of foraging for nectar and pollen, rarely flying forth to defend the colony. Each one tends to crawl about on the cells that contain its own progeny[18].

Evolutionary increase in colony size to that exhibited by the higher social species is apparently dependent on a capacity to nutritionally counteract the agravidic bias of a very few young larvae and to establish in the great majority the fixation of worker structures thus assuring an ability to control the nest environment and the permanence of queen/worker ratios, upon which the welfare and reproductivity of large colonies depend. Such fixation apparently permitted mass provisioning of larvae to be replaced by progressive feeding.

It appears, therefore, that in the higher aculeates, agravidic larvae become "worker-fated" if subjected to forced underfeeding during their late instars, this being accomplished by the restriction of larval development either to progressively-provisioned, relatively

small brood cells as in the honeybee or to prolonged periods of high-brood/worker ratios as in the army ant and that such underfeeding merely tends to fix by morphological differentiation a line of development already initiated by alimentary castration of the embryo.

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