

THE BEHAVIOR PATTERNS OF SOLITARY WASPS¹

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Some of the more conspicuous features of wasp behavior were reported more than two centuries ago, but it was not until the publication of the first volume of Fabre's *Souvenirs Entomologiques* in 1879 (66) that the attractiveness of this field of investigation became widely apparent. The classic work of Fabre and those of Ferton (68), Adlerz (1), G. W. & E. G. Peckham (159), and P. & N. Rau (173) are widely known and have provided a broad foundation for the natural history of wasps. More recently, the influence of the "European school" of ethologists, exemplified particularly by Tinbergen and Baerends, has been strongly felt. In a sense, the modern era of wasp ethology may be said to have begun with Baerends' extended study of *Ammophila pubescens* Curtis in 1941 (5) and with Iwata's "Comparative Studies on the Habits of Solitary Wasps" in 1942 (88), for both of these papers have had an important impact on research in this field in the past 25 years. These two papers are accepted as points of departure for the present review; these and other papers cited below contain bibliographies which collectively cover much of the very extensive literature in this field. I have omitted mention of many strictly descriptive studies, not because these are unimportant as contributing to the comparative ethology of wasps, but simply because a very large volume would be needed to survey this field fully. Attention will here be directed to behavior patterns common to all solitary wasps (more especially to fossorial species) and to some of the important questions being asked about them by contemporary workers.

I have omitted consideration of wasps parasitic upon other wasps, including both parasitoids (such as Mutillidae) and cleptoparasites (cleptobionts, *arbeitsparasiten*) [such as *Evaetes* and *Ceropales* in the Pompilidae, *Nysson* and *Stizoides* in the Sphecidae (30, 37, 63, 73, 156, 220)]. Solitary wasps are defined as species in which there is no cooperation involving division of labor between mothers and daughters or between females of the same generation. All social wasps belong to a portion of the superfamily Vespoidea, to the family Vespidae as defined by Richards (177); he regards the social wasps as probably monophyletic, although this opinion has not been universally accepted in the past. The nonparasitic solitary wasps considered here belong to seven families commonly placed in five superfamilies, as follows: Bethyloidea: Bethylidae; Scoliidea: Tiphidae, Scoliidae; Vespoidea:

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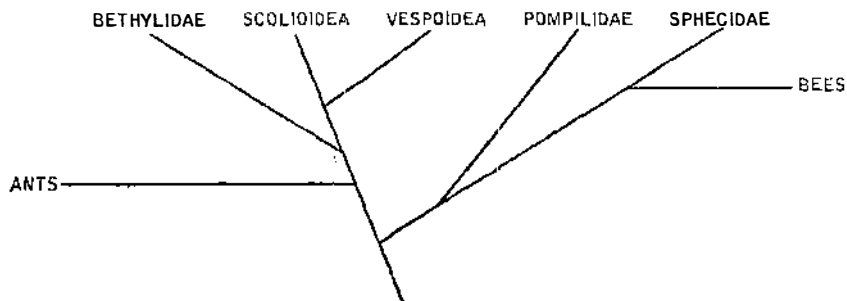


Fig. 1. Dendrogram showing probable relationships of the major groups of aculeate Hymenoptera.

Masariidae, Eumenidae; Pompiloidea: Pompilidae; Sphecoidea: Sphoridae (including Ampulicinae as a subfamily). The probable relationships of these superfamilies to each other and to the ants and bees is shown in Figure 1.

GENERAL FEATURES OF BEHAVIOR

Solitary wasps are of generally local distribution, populations tending to remain for successive years in areas providing an abundance of their hosts or suitable nesting sites, or both (99). Persistence of nesting aggregations at one site for many years has been reported for several species (36, 67, 154, 167), although it is also evident that decline or emigration of populations may occur when conditions become unfavorable [e.g., as a result of parasitism (38) or overgrowth of bare soil by vegetation (154, 204)]. Whether localization is the result of imprinting or of trial and error selection of certain attributes of the substrate remains a moot point (38, 46, 194). Thorpe's (194) statement that odor may be responsible for colony localization appears based on faulty evidence (46), but on the other hand, Kullenberg (121) believes that "marking scents" produced from mandibular glands may be instrumental in keeping populations together. Olberg (156) believes that "pseudocolonies" of solitary wasps are largely the result of the quality and availability of suitable nesting situations.

Feeding by adults.—The food of adult wasps is derived from a variety of sources, most commonly from flowers or extrafloral nectaries. Short-tongued wasps (Tiphidae, Eumenidae, Pompilidae, many Sphecidae) forage chiefly on Umbelliferae, Euphorbiaceae, and other flowers with shallow corollas, while wasps with more elongate mouthparts (e.g., *Bembix* and *Ammophila* in the Sphecidae) are able to exploit a great variety of flowers (156). The longest mouthparts of any wasp occur in the sphecid genus *Steniolia*; members of this genus are primarily associated with Compositae, although able to utilize flowers of at least 23 families (60). Gillasp (74) has postulated that the long tongue of this genus may have evolved in xeric habitats in association with critical moisture requirements and strong competition for the available blossoms.

In contrast, many wasps rarely or never visit flowers. Some of them obtain carbohydrates by licking up honeydew deposited on vegetation by homopterous insects; this is so for many Bethyridae (56) and many of the smaller members (and some larger members) of other groups (110, 156). Feeding at flowing plant sap has been recorded for a few species (36), while at least one species is reported to make lesions in plants and feed on the exuding sap (105). Wasps which capture flower-feeding insects may at times feed upon the crop contents of their prey ("honey robbing"). Species of *Bembix*, for example, have been observed stopping en route to their nest and feeding from the oral opening of syrphid flies (204).

Females of certain species feed upon the body fluids of their prey, either instead of or in addition to nectar or honeydew. At times this involves simple imbibing of the blood which exudes from the puncture made by the sting (18, 108). More commonly, the wasp squeezes or chews a portion of the prey with its mandibles and feeds upon the exuding blood [malaxation; see especially Thomas (191)]. Malaxation following prey immobilization has been reported for many different wasps [Bethyridae (15); Tiphiidae (25, 96); Pompilidae (65); Eumenidae (39); Sphecidae (40, 156, 187)]. Certain wasps have been reported to feed directly upon prey which is then rejected rather than carried to the nest [hypermalaxation, Huber (85)]; this is reported, for example, for the bethylid *Cephalonomia waterstoni* Gahan (69), for the tiphid *Elaphroptera atra* Guerin (96), for the eumenid *Rygchium dorsale* (Fabricius) (171), for the pompilid *Priocnemis cornica* (Say) (65), and for the sphecid *Mellinus arvensis* (Linnaeus) (126). Rathmayer (163) found that both hypermalaxation and honey-robbing occur in the sphecid *Philanthus triangulum* (Fabricius). The factors which release malaxation or honey-robbing in normally flower-feeding wasps have not been studied; Nielsen (154) believes that the wasps may suddenly require fluids while in the course of hunting or provisioning activities and hence utilize their prey. Huber (85) found that *M. arvensis* is especially likely to "hypermalaxate" the prey when it is unable, for some reason, to place the prey in the nest; he interprets most instances of chewing and rejection of prey as displacement activities.

Sleeping.—Solitary wasps, like many other insects, spend nights and periods of inclement weather in a state of akinesis conveniently termed "sleep," which does not imply a close similarity to human sleep. Wasps sleep either in the soil or on plants. In the latter case they assume locations and poses, often characteristic of genera, in which the substrate is held so fast by the mandibles or legs, or both, that even a strong wind will usually not dislodge them. Characteristic poses of sleeping wasps are shown especially by Rau (169), by Evans & Linsley (64), and by Linsley (131). As these authors point out, a particular site may be used again and again by aggregations of wasps and bees of several species, although nearby plants of very similar appearance are never used; this suggests that the presence of one or a few resting Hymenoptera may serve as a stimulus to others [even occasionally to Diptera (131)]. The more compact sleeping aggregations of some wasps generally contain only a single species; such clusters may be bisexual

or may consist only of males. Large sleeping aggregations of males of the tiphiid genus *Myzinum* are well known (172); males of the sphecid *Sphex latreillei* Lepeletier are reported to form large clusters on plants in Chile (95). The large, compact sleeping clusters of the sphecid genera *Bembecinus*, *Zyzzyx*, and *Steniolia* are bisexual, although at certain times one sex may predominate; in all three of these genera, massive clusters containing several hundred individuals have been reported (43, 60, 95).

The function of sleeping aggregations remains obscure. There is no evidence that temperature is increased materially inside the clusters or that protection from physical or biotic factors in the environment is increased. In *Steniolia*, mating occurs when the wasps assemble in the evening (60), but the facilitation of mating seems to be an insufficient explanation of all examples of gregarious resting on plants. The possibility that this behavior represents an early stage in the origin of sociality has been considered by Grassé (78) and by Schremmer (179). Lindauer (129) believes that these insects "simply have a drive to sleep together."

The list of wasps known to sleep on vegetation includes females of some species known to provision their nests progressively (e.g., species of *Ammophila*), but the majority of more advanced solitary wasps sleep in their nests. In some cases both sexes sleep in the nest [e.g., *Chitemnestra gayi* (Spinola) (95)]; in other cases the females sleep in the nests, the males in vegetation [*Sphex latreillei* (95)]; in still other cases, the females remain in the nests and the males in special sleeping burrows which they dig themselves [*Bembex* spp. (46)]. In *Microbembex monodonta* (Say) both males and females dig special sleeping burrows, even though the females maintain brood nests for a period of days (59).

Grooming.—Wasps groom the body, wings, and appendages by certain stereotyped movements which have been so well described and illustrated for certain Sphecidae by Olberg (156) and by Huber (85) that there seems no need to discuss them here. There is need for a comparative study of grooming behavior among Hymenoptera, in fact, among insects in general. Grooming occurs periodically during the activities of the wasp, especially following feeding, mating, prey carriage, or emergence from the burrow; the stimulus is presumed to be provided by foreign particles on the body or appendages. Grooming may also occur when the wasp is prevented from completing certain phases of its behavior or in cases of conflicting drives (85, 156); such grooming is suggestive of displacement preening in birds.

Reproductive behavior.—Proterandry (= hysterogyny; emergence of males one to several days before the females) is virtually universal among solitary wasps. Males commonly remain within the area where they emerged, often flying back and forth or in circular or irregular patterns. Such prenuptial flights have been described for wasps of several families [Scoliidae (25, 147); Pompilidae (61); Sphecidae (161); Eumenidae (168)]. When populous, these flights have often been called "sun dances," a name introduced by Rau & Rau (173) although used earlier for similar flights of certain bees.

Baerends (5) found that marked males of *Ammophila pubescens* flew

about an area measuring about 2×50 meters, within which they pounced not only upon conspecifics but also upon other insects and even inanimate objects. In some digger wasps the males take up perches on or near the ground to which they return repeatedly and from which they fly off from time to time and grapple with neighboring males; this has been noted in *Astata minor* (Kohl) by Minkiewicz (146), in *S. latreillei* Lepeletier by Janvier (95), and in *Tachytes elongatus* Cresson and *Sphecius speciosus* (Drury) by Lin (127). In *Sphecius*, reactions of males to intruders in their territories were found to terminate in one of four ways: (a) unsuccessful pursuit, (b) threat (pursuit broken off within striking distance), (c) butting, and (d) grappling. Grappling occurred only among *Sphecius* males, mostly those in adjacent territories, while the other three reactions involved *Sphecius* males as well as various other insects.

In the sphecid wasp *Oxybelus sericeum* Robertson, males set up territories at the entrances to active nests and pursue approaching insects, including dipterous parasites and other male *Oxybelus* [Bohart & Marsh (12)]. When the female arrives at the nest the male copulates with her, such matings often occurring many times in a single day. In wasps of the genus *Trypoxylon*, subgenus *Trypargilum*, the male characteristically remains within the nest when the female is absent, acting as a guard, and mounting the female when she enters the nest; in this genus the male may participate slightly in nest care, although such behavior is otherwise unknown among wasps (81, 112, 176).

In most solitary wasps, mating is most often successful with newly emerged females. In certain gregarious Bethyridae, the males crawl over the cocoons and may actually chew into them and mate with females before emergence (15, 160). In some Sphecidae males attempt to dig into the soil at points where females are detected emerging (156, 204). There are many reports of females which have begun their nesting activities failing to mate with males which approach them; such females curve their abdomen in such a way that contact of the genitalia is prevented or brush off the male with their hind legs (46, 85, 156); in some cases a characteristic flight of the female may apparently serve as a signal to the male that she is unreceptive (127). However, in some instances, females will interrupt nest digging or provisioning in order to mate; for example, Gillaspay (72) observed matings of 2 to 3 min duration by *Sphex tepanecus* Saussure while females were bringing prey. Repeated mating by *Tiphia morio* Fabricius over a period of days has been reported by Janvier (98).

According to Baerends (5), the male *A. pubescens* pounces upon the female from a distance of about 30 cm, the response apparently being to a form of about the size, shape, and color of the female (not necessarily in motion). This was determined by experiments using various wooden models and dead wasps. In this species the black and red abdomen of the female (as opposed to the dorsally black abdomen of the male) may serve for species and sex recognition. In *Crabro cribrarius* (Linnaeus), Kullenberg (121) found that a moving, dark object having pale bands simulating those of the female served as an effective visual releaser. In the tiphiid subfamily, Thynninae,

the females are reported to assume an immobile, inverted "waiting posture" on the trunks of trees and to be attractive to the males only when in this position, the stimulus perhaps being visual (96).

There is evidence that at least in some cases the female secretes a pheromone from the apical portion of the abdomen which acts as an attractant to males of that species. When the sting apparatus is removed from female *Scolia bicincta* Fabricius in the field, males are attracted to the site in considerable numbers (59). Kullenberg (121) found that if the abdomen of a female *C. cribrarius* is pressed with the fingers, males are attracted from their mating flights. This author used dried *C. cribrarius* females, washed in ether and scented artificially, in an effort to determine the nature of the sex attractant. He found that, of the compounds tested, citronellal acted as the best sexual excitant, the related compound isopulegol as the strongest attractant. In the case of *Argogorytes mystaceus* (Linnaeus), Kullenberg (121, 122) found an odor between farnesol and hydroxycitronellal to resemble most closely that of the female. The males of this wasp are attracted to the flowers of the orchid *Ophrys insectifera* (Linnaeus) by an odor which mimics that of the female; having arrived at the flower, the male is stimulated by the dark color and microtopography of the labellum to bite the base of the labellum and to undertake pseudocopulation, thus acting as a pollinator of a flower which has "parasitized" certain releasing mechanisms of the wasp [Baerends (6)]. The orchid *O. speculum* Link appears to have a similar association with the scolid wasp *Campsoscolia ciliata* (Fabricius) in Morocco (122).

Copulation has been described in detail in only a few cases, most particularly in the vespid *Ancistrocerus antilope* (Panzer) (28), and in sphecids of the genera *Ammophila* (5, 156), *Bembix* (46, 154), *Mellinus* (85), and *Sphecius* (128). In *Ammophila*, the pair may remain together for a considerable time, and may fly together, but copulation is of short duration and occurs from time to time while the pair is at rest; in one case Baerends (5) observed 10 copulations of one pair in an hour. In the majority of cases the male is in a dorsal position, straddling the female and holding her with his mandibles (*Ammophila*), legs (*Bembix*, *Mellinus*), or both [*Ancistrocerus*; *Tiphia* (100)]. Antennal contact plays an important role in *Tiphia*, *Ancistrocerus*, *Mellinus*, and some species of *Ammophila*. Mating in flight has been reported in a variety of species, but in many cases actual contact between the genitalia has not been confirmed; most species apparently copulate while at rest on plants or on the ground. In *Sphecius speciosus*, the male mounts the female in the usual manner but immediately after inserting his genitalia dismounts and faces in the opposite direction; in this case the pair remain attached for 45 minutes or more and if disturbed may fly about considerably, the larger female carrying the male behind her (128). Much this same behavior has been noted in the eumenid wasp *Monobia quadridens* (Linnaeus) (168).

Mating in flight over a considerable period of time is well known in several groups of wasps in which the female is wingless; in this case the male carries the smaller female about, the pair being attached by their genitalia.

This is apparently the case in at least two genera of Bethyridae (56), in the mutillid genus *Timulla* (130), and in Tiphidae of the subfamilies Myrmosinae (114) and Thynninae (76). In the last group, the male may carry the female to a feeding site (usually honeydew or extrafloral nectaries) where the pair feed; or the male may feed the female. In the latter case, the male may feed the female by regurgitation at the feeding site or may carry a food bolus to a female in the breeding habitat in a fringed concavity beneath the head. Given (76) has described the several structural and behavioral modifications involved and their probable evolution.

NESTING BEHAVIOR

Wasps are entomophagous in their immature stages (with the exception of most Masaridae, as discussed in the next section), and are presumed to have been derived from a now extinct group of parasitoid Hymenoptera. They differ from parasitoids in that the ovipositor is modified to form a sting, the egg being deposited directly from the genital aperture. Certain groups of primitive wasps otherwise behave much like parasitoids, leaving the prey *in situ* following temporary immobilization and oviposition. Such behavior is common among bethylids (221) and tiphids (25) and occurs in a few pompilids (106) and sphecids (93, 211). Other wasps prepare a nest which, in its simplest form, is a mere crevice into which the prey is dragged (69, 219) or the burrow of the host [e.g., in *Chlorion lobatum* (Fabricius) as described by Iwata (92); in *Aporus hirsutus* (Banks) as described by Williams (218)]. Simple nests which are prepared after the prey is captured are characteristic of most Pompilidae (65) and of a few sphecids, such as *Prionyx* (49) and *Podalonia* (189). A few pompilids prepare the nest before taking prey, and this pattern is very common in the Sphecidae and universal in Vespoidea. In these wasps the nest becomes the focal point in their behavior, to which they return repeatedly with prey, often for a series of cells (152).

The Scoliodea are fossorial wasps, as are the basic stocks of the families Eumenidae, Masaridae, Pompilidae, and Sphecidae, although there are elements in all four of these families which prepare nests above the ground. The building of free mud nests has evolved independently in all four families, at least twice in the Sphecidae (Sceliphronini and Trypoxylonini). In many Eumenidae and a few Masaridae some of the ground-nesters build elaborate mud entrance-tubes to their nests [see especially Móczár (149)]. Much has been published on various aspects of the construction of mud nests, and the matter will not be pursued further here [see, e.g., (77, 88, 103, 123, 212)]. Some Eumenidae cover their mud nests with a paper-like substance prepared from wood fibers (91) while some Discoeliinae (= Zethinae) make use of bits of leaves and moss as well as paper [summary in Wheeler (214)]; such use of paper foreshadows that of the social Vespidae.

The families Eumenidae, Pompilidae, and Sphecidae also each contain elements which have independently evolved behavior resulting in the construction of nest cells (usually in series) in cavities in plants. In the Sphecidae, xylicolous stocks have evolved from ground-nesters in several sub-

families; even the widespread fossorial genus *Ammophila* contains a xylicolous species (210). Merisuo (144) has made an interesting comparison of wood-nesting versus ground-nesting Sphecidae in Finland with respect to their taxonomic affinities, adaptive structures such as pygidia and tarsal combs, burrow patterns, and types of prey. It is possible that terricolous species or genera have evolved from xylicolous forms in certain cases (153).

A few plant-inhabiting species bore holes in living stems and remove the pith (11, 14, 94, 119), but the majority of species remove the pith from dead twigs or the pruned stems of roses and other plants (99, 101, 116) or make holes in rotten wood (79, 101, 207). Many species utilize natural cavities or borings made by beetles or other insects (104, 138); in such cavities several species may succeed one another, even in a single series of cells (31, 32). Certain species utilize tubular cavities either in wood, in the soil, or in abandoned mud dauber nests [e.g., *Trypoxylon clavatum* Say (165)]. The use of trap nests, consisting of hollow sections of bamboo or sticks containing artificial borings, has greatly increased our understanding of twig-nesting wasps and has resulted in some fascinating contributions to ecology and behavior which, unfortunately, cannot be reviewed here [see especially (27, 28, 29, 92, 109, 113, 114, 142, 143)]. Partitions between cells commonly consist of mud, but many other types of materials may be used [see review in Iwata (88)]. A few species are reported to omit cell walls either occasionally or regularly, so that several larvae develop together in a large chamber, usually without cannibalism (155, 209); however, fairly frequent cannibalism is reported in *Isodontia pelopoeiformis* (Dahlbom) (181). Krombein (119) found that several species nesting in vertical plant stems always pupated with the anterior end upward, suggesting that the spinning larva orients itself with respect to gravity. However, Cooper (29) found that species of diverse taxonomic affinities nesting in horizontal borings oriented their cocoons with the anterior end toward the rough, outer wall and the posterior end toward the smooth, concave inner wall. He speaks of this as "digital communication" between mother and offspring by way of the cell wall. It would seem likely that this behavior is inherited from ground-nesting ancestors, since ground-nesters typically pupate facing the rough (formerly open) end of the cell.

Nesting in fossorial species.—Fossorial wasps most commonly nest in bare, friable soil, but many examples are known of species nesting in hard-packed soil or among vegetation. The majority of species utilize flat or gently sloping surfaces, while some nest only in vertical banks and a few nest either in vertical or horizontal surfaces [e.g., *Philanthus gibbosus* (Fabricius) (62)]. Quite a number of Pompilidae [examples in (65)] and a few Sphecidae [examples in (47, 61)] start their burrows from those of mammals or of other wasps. Re-use of borrows of the previous generation, at least in some cases, is reported in *Mellinus* (85) and in *Cerceris* (77). Burrows may terminate in a single cell or may eventually contain several to many cells; in the latter case, the cells assume a variety of configurations. Minkiewicz (145) recognized 11 types of terrestrial nests in the Sphecidae and applied special names to each

[see also (33, 135, 152)], but most workers have been content to describe or sketch the nest profile and to present data on depth and on cell size. In any case, the proposed classifications by no means suffice to cover the infinite variety of nests found among fossorial wasps. For example, pompilids of the genus *Tachypompilus* prepare a bowl-shaped depression in the powdery soil in which they nest (188, 217). Another unusual nest, involving a "preliminary burrow" which is later filled up and abandoned, as well as an unusually long brood chamber, has been described for the sphecid *Bembix pruinosa* Fox (46). While nest type is generally more or less fixed within a species, often within a genus, instances are known in which a species typically makes simple, unicellular nests but in some cases (and in some areas) makes branched, multicellular nests (180, 204). In multicellular nests, the first cell is commonly farthest from the entrance, additional cells being added on short side burrows progressively back toward the entrance [e.g., in *Crabronini* (79)]; but the reverse may be true [e.g., in *Cerceris* (117) and in *Philanthus* (62)]. Some wasps make only one multicellular nest which serves them throughout their lives (85).

Wasps commonly precede the construction of their nest (especially their first nest) with short periods of "appetitive digging" at various sites in the nesting area. During these periods the nesting drive is believed to increase in intensity; as the threshold of reaction is lowered the wasp eventually remains at a site presenting certain soil attributes and completes a nest (5, 85). Once the nest is started, the soil may be removed in one of several ways, for which convenient terms have recently been coined by Olberg (156). "Rakers" scrape the soil beneath the body by vigorous strokes of the front legs, which are curved toward the midline so that the spines comprising the pecten (= tarsal comb) are directed downward. The front legs may move alternately (Pompilidae) or synchronously (most Sphecidae). In the latter case the abdomen commonly moves up on the downstroke (allowing space for the sand to shoot out beneath the body), down on the upstroke; in the former case the abdomen usually remains in the "up" position throughout periods of digging [see Olberg's book (156) for examples and illustrations]. "Pushers," on the other hand, back out of the burrow pushing the soil behind them, often with the aid of a strong pygidial plate on the apical abdominal segment, the resulting mound coming to surround the nest entrance [e.g., in *Cerceris* (133)]. "Pullers" back out of the entrance bearing a mass of soil between the back of the head and the front legs; the soil may be deposited almost immediately [e.g., in *Mellinus* (85)] or dragged several centimeters from the entrance [e.g., in *Tachytes mergus* Fox (120)].

The final type recognized by Olberg, "carriers," differs in that the lump of soil is actually lifted from the ground and deposited at some distance from the nest, either by walking over the ground [e.g., in *Ammophila wrightii* Cresson; see review in Powell (162)] or by flying off and releasing the load at varying distances from the nest [e.g., in other species of *Ammophila* (58, 162)] and in many Eumenidae (118, 153). In some carriers, the posterior surface of the head [*Anacrabro* (7)] or the palpi [*Pterochelus* (153)] bears a

strong fringe of setae (psammophore) which assists in holding the bolus of earth. Eumenids often carry water to the nesting site, using it to soften the earth prior to digging (88); such behavior may have served as a precursor to the construction of free mud nests by other eumenids. The sphecid *Podium flavipenne* Lepeletier is also reported to be a water-carrier, again presaging the construction of free mud nests in the related genera *Trigonopsis* and *Sceliphron* (218).

It should not be assumed that the four types of digging are mutually exclusive; for example, *Tachytes mergus* starts the nest as a "raker," then becomes a "puller" when it reaches damper sand; *Bembix* spp. may be pullers when handling small stones, although typically rakers *par excellence*; *Ammophila* spp., although carriers, often do a certain amount of raking when opening or closing the nest [see also Steiner (185)]. Nor should it be assumed that all examples of one type behave identically. For example, although most rakers build up a pile of soil at the nest entrance, others dig in such a way that the soil particles are sprayed over a wide area [e.g., *Bicyrtes quadri-fasciata* (Say) (113); *Aphilanthops frigidus* (Smith) (52)].

In many species (other than carriers) a conspicuous mound of soil (= tumulus, spoil heap) accumulates at the nest entrance. In many cases this mound remains intact except for weathering and for use of some of the soil for closures. In a few cases the wasp undertakes elaborate leveling movements at the nest entrance, resulting in partial or complete dispersal of the mound. Several types of leveling behavior have been described in species of *Bembix* (46, 51). Wasps which provision the nest with more than one prey often close the nest entrance when they are away or at least during the night or periods of inclement weather (temporary or provisional outer closure). Rakers usually merely scrape a small amount of soil into the entrance and then scrape it away upon returning. In *Ammophila* an object of correct size to block the lumen of the burrow [the *Hauptverschlussklumpchen* of Baerends (5)] is selected, often after "trying several for size," and additional lumps and loose soil are placed over this object (58, 189). Many examples are known of species which omit temporary closure either occasionally or regularly. In *Bembix* most species prepare a temporary "inner closure," separating the cell from the burrow, either instead of or in addition to the outer closure (46).

After the cell or nest is fully provisioned, it is sealed off permanently (final or definitive closure). Carpenter (19) has compiled data on the manner in which 92 species pack the soil in the nest entrance. As a rule, Pompilidae employ the dorsum of the apical abdominal segment for pounding soil; in certain species, such as *Poecilopompilus interruptus* (Say), these pounding movements are especially strong and prolonged (111). In the Sphecidae, it appears that most groups also use the tip of the abdomen for packing soil, but the subfamily Sphecinae differs sharply in that the front of the head is employed (113, 124, 156). The manner of nest closure in *Ammophila* has been much studied, and it is now well established that some species hold a small pebble in the mandibles while pounding (5, 50, 58). Following final nest

closure, some species move sticks, leaves, or other objects over the site [examples in (58, 65, 124, 180)].

It has been noted that in certain wasps much of the soil for closure is dug from one or a few spots near the entrance, resulting in a small depression (quarry, false burrow) [see e.g. (2, 43)]. In some species, false burrows are a fixed and permanent feature of their behavior; they are often dug before the initial closure or after the final closure, indicating that they do not serve as quarries for soil for closure. Neither is there evidence that they serve as nest markers, for sleeping, or for storing prey. Various parasites have been reported entering or ovipositing in false burrows, and it seems probable that these burrows, having originated as quarries, have become divorced from their original function and position in the behavioral sequence and have become more elaborate and stereotyped, i.e., they have become displaced and ritualized [for examples and discussion, see Tsuneki (201, 209), and Evans (46, 57)]. All things considered, behavior patterns relating to leveling, closure, and concealment are rich in details which cannot be explored fully here but which provide the comparative ethologist with an inexhaustible supply of research problems.

Orientation.—Wasps which capture prey before making a nest may move about considerably in their search for hosts; there is some evidence that predators on locusts may even follow swarms about (83). Some wasps “hide” their prey in situations where it is protected from ants and other predators while they dig their nest. “Hiding places” include crotches of plants, various crevices in the soil, and even burrows prepared for storing the prey temporarily; examples include Bethyridae (217), Pompilidae (65, 148), and Sphecidae (40, 49). Such wasps may make several trips between nest and prey and are often readily disoriented by disturbance to landmarks.

Wasps which prepare the nest prior to hunting commonly make one or more orientation flights (=locality studies) during or following preparation of the nest. These flights show much variation in detail depending upon the terrain and the species of wasp involved, and the literature is replete with descriptions of such flights. During these flights the wasp learns visual cues which guide it upon its return flight (=homing or recognition flight). A single orientation flight lasting only a few seconds may in some cases suffice for successful homing (195), but some species tend to reinforce their recognition of the nest site by short orientation flights over the first two or three days (85). Reorientation flights commonly occur following major disturbances to the nest area (86). The classic studies of Baerends on *Ammophila pubescens* (5) and of Tinbergen and his co-workers on *Philanthus triangulum* (10, 195, 199, 200) are too well known to require detailed comment here [several summaries in English are available (20, 21, 194, 197, 198)]. Tinbergen (197) regards the last phase of the homing flight as a telotaxis, although of a special type (pharotaxis, menotaxis), since the stimulus situation has been acquired by conditioning and consists not of individual elements but of a configuration or gestalt. Tsuneki (202) demonstrated that pompilid wasps

are able to utilize the direction of solar light in maintaining their course (menotaxis), and it is probable that this will be found to be true of many wasps.

Thorpe (194) has summarized experiments on wasps which carry their prey over the ground with respect to their response to obstacles placed in their path. Thorpe himself (193) performed such experiments on *A. pubescens* and found that in each case the wasp, without hesitation, diverged just enough to clear a metal screen placed in its path and to return to its original direction, thus quickly solving a simple problem without losing course. This species is known to maintain two or three nests at one time, remembering the location of each nest over a period of days, although "forgetting" those which have received the final closure and adding new nests from day to day [behavior now known to occur also in a North American species, *A. azteca* Cameron (58), but not reported for other solitary wasps].

Chmurzynski (23, 24), following several earlier workers, has distinguished three major stages in the orientation of Hymenoptera, these stages being defined on the basis of specific behavioral features. These stages are: (a) distant orientation (departure in the correct direction), (b) proximate orientation (recognition of nest surroundings), and (c) immediate orientation (finding the nest entrance). By releasing nesting females at various distances from the nest, he was able to demonstrate that the outer limit of distant orientation in *Bembix rostrata* (Linnaeus) is between 0.5 and 0.7 km. In *A. pubescens*, Baerends (5) found this distance to be much less, about 40 m; but, on the other hand, *P. triangulum* is exceedingly wide-ranging and may return to the nest from distances of over 1 km (200). Earlier experiments by Rau (166) demonstrate that wasps of diverse groups are able to return to their nests from distances of 1 to 2 miles. The outer limits of distant orientation tend to be irregular, depending upon the location of nesting, feeding, and hunting sites, nature of the terrain, and other factors.

Orientation in wasps occupying broad expanses of shifting sand may differ in some ways from that of species occupying sites rich in landmarks. Thus, van Iersel (86) found that, in proximate orientation, *B. rostrata* utilizes markers without respect to their height but only to their total surface area; furthermore, this species appears to employ concentric girdles of landmarks, parts of which effectively guide it to the nest even when other parts are severely disturbed. The entire background, including even objects on the horizon, as seen from a position facing the nest, may be utilized by Bembicini at least when the immediate area of the nest is disturbed (87, 204). *Bembix niponica* Smith (204) and *Microbembex monodonta* (59) land precisely at nest entrances and attempt to dig even when sheets of glass or transparent plastic are placed over them. Chmurzynski (23) believes that touch may play a role in immediate orientation, but there is no evidence that odor plays a role, as has sometimes been postulated [e.g., by Parker (157)]. Chmurzynski (22) has studied color preferences in homing *B. rostrata*, and Tsuneki (208) has studied color and form discrimination in *Odynerus frauenfeldi* Saussure (Eumenidae) returning to nests in tubular cavities.

PROVISIONING THE NEST

The only exception to the statement that wasps are entomophagous in the larval stage is provided by the vespoid family Masaridae. A member of one of the more primitive subfamilies of masarids, the Euparagiinae, is known to be predaceous on beetle larvae, but all members of the other two subfamilies, so far as studied, provision their nests with pollen and nectar. Many masarids are oligolectic, restricting most or all of their foraging to one or a few genera of plants (e.g., the smaller species of *Pseudomasaris* to *Phacelia*, the larger species to *Penstemon*; many members of the *Quartinia* group to Compositae, etc.). Masarid wasps have no special structural devices for carrying pollen, the female merely carrying it in the mandibles as a pellet. However, the labium shows much modification in the various genera, possibly correlated with the extraction of nectar from flowers of different structure (9, 26, 177).

All other solitary wasps are entomophagous as larvae, and all are predators as adults (other than parasitic species, not considered here). Predatory wasps are believed to have been derived from parasitoids, and because of the unusual features of their behavior they may properly be termed "predatoids" (54). These unusual features may be summarized as follows: (a) the prey is utilized primarily as larval food, the adults feeding upon carbohydrates (exceptions noted earlier); (b) predation is sex-limited, being part of the provisioning behavior of the female; and (c) nearly all wasps exhibit a certain measure of host-specificity and their hunting and stinging behavior is closely adapted to the type of prey. In several families, host-specificity is on the family level. For example, all records of Pompilidae indicate restriction to spiders, and to forms approximating the wasps in size, since all use a single spider per cell (42). Bethyliidae employ coleopterous or lepidopterous larvae occurring in cryptic situations [wood, soil, galls, leaf-rolls, etc. (56, 221)]. Scoliidae and Tiphiidae are predators on the larvae of soil-inhabiting Coleoptera (Scarabaeidae, Cicindelidae), while Eumenidae employ plant-inhabiting eruciform larvae, chiefly Lepidoptera but sometimes Coleoptera or Hymenoptera (25, 88). Within each of these families, the genera and species exhibit varying degrees of further host-specificity, in some cases involving profound structural modifications [e.g., aptery in many hypogeic Bethyliidae and Tiphiidae; head and foreleg modifications in pompilid predators on trap-door spiders (182, 218)]. Instances are known of eumenid wasps exploiting insects inhabiting a specialized habitat (e.g., leaf mines) although prey of diverse affinities occupying that habitat are accepted (104, 118).

The remaining family, Sphecidae, stands in strong contrast to the others, for this group has radiated to exploit adult and immature insects of nearly all orders (exceptions: Thysanura, Diplura, Zoraptera, Anoplura, Siphonaptera, Embioptera) as well as springtails and spiders. In this family, specificity is mainly on the subfamily, tribal, generic, or even specific level, so that prey type often provides a useful taxonomic character [see especially de Beaumont (8)]. Lists of prey and associated predators in specific regions have been

presented by several authors (33, 84, 144, 156), and Iwata (88) has presented a general review of this subject.

Most species of Sphecidae are narrowly to rather broadly oligophagous, taking members of one or several genera or related families occurring in a particular habitat. A relatively broad spectrum of prey is employed by certain Crabronini, some species being known to utilize insects of three orders (79). In the genus *Microbembex* (Bembicini), a complete breakdown in specificity has occurred. Janvier (95) reported *M. sulfurea* (Spinola) as preying upon arachnids and upon insects of five orders. *M. monodonta* employs an even broader array of arthropods than this, but takes only specimens already dead or disabled (157); this species will even employ centipedes, millepedes, and terrestrial Crustacea when they are placed on the ground near the nest (59).

Examples of monophagy or near-monophagy are also uncommon. Perhaps the best examples in the Sphecidae are to be found in ant predators of the genera *Tracheliodes* (158) and *Aphilanthops* (52), the various members of which attack only one or a few closely related species of ants, and in each case only one sex and caste. Many apparent examples of monophagy are the result of the fact that in one area a species may appear to specialize, when, in fact, records from other areas indicate that it is capable of utilizing quite different hosts. Individual nests of broadly oligophagous wasps often contain only one or a few species of prey, suggesting that [contrary to the statement of Tinbergen (197)] some conditioning probably occurs with respect to hunting sites (17, 85, 209). Within a given area, the wasps may appear to "divide up" the available prey to a certain extent (competitive exclusion principle) (14, 151). On the other hand, instances have been cited of broad overlap in prey of species nesting side by side, perhaps the result of the fact that populations of these species are kept at suboptimal levels by parasite pressure (57). *Bembix u-scripta* Fox appears to escape direct competition for prey by hunting at dusk and taking flies at rest on vegetation (51).

A considerable degree of host specificity is exhibited by most Scoliidae (25) and some Pompilidae (65). Certain Bethyridae are relatively polyphagous; for example, Bridwell (15) was able to rear *Scleroderma immigrans* Bridwell on a wide variety of beetle larvae and also on hymenopterous larvae and even termites. In contrast, experiments with the bethylid *Cephalonomia waterstoni* revealed that this species shows a different degree of preference for each of several species of *Laemophloeus*; however, when confined with a less preferred host, the threshold of attack is lowered to the extent that populations can maintain themselves on these hosts [Finlayson (70, 71)]. Finlayson was unable to demonstrate an appreciable degree of preimaginal conditioning, a concept little employed since espoused by Wheeler (214) as an explanation of host restriction in Hymenoptera [but see discussion in Thorpe (194)].

Prey capture.—Hunting and prey capture have been described in general terms in a wide variety of wasps. It seems probable that odor stimuli, received by the antennae, play important roles in prey detection in all wasps [see e.g. (17, 183, 211)]. It is for this reason that wasps are not "deceived"

by visual mimics; for example, fly predators often use flies which mimic bees, while bee predators do not accept such flies (59, 80). Tinbergen (196) found that deantennated *Philanthus triangulum* females did not take prey, even though able to orient to the nests correctly; also they would attack certain dummies when covered with the scent of the prey, but only when they were so scented. However, such dummies were not accepted unless presented at the appropriate stage in the reaction chain. Tinbergen found that the wasps first fly from flower to flower and approach moving objects of appropriate size; at this stage they respond only to visual cues, and are not attracted to bees placed out of sight in open tubes. After the wasp approaches the potential prey from downwind at a distance of about 10 to 15 cm, odor suddenly becomes important, and, if the proper stimulus is received, the wasp leaps upon its prey, although stinging occurs only upon reception of additional stimuli, probably of a tactile nature (196, 197).

Rathmayer (163, 164) has studied prey immobilization in this same species of sphecids. He found that the sting is inserted only once, in the membrane behind one of the fore coxae. He has described and figured the sensilla on the sting and sting sheaths which guide the sting by tactile cues to the coxal membrane. By a series of experiments and preparations, Rathmayer demonstrated that the poison is not usually injected into a ganglion and does not act as a neurotoxin blocking the ganglia; rather it diffuses through the blood to the leg musculature. He found that many insects besides the normal prey of *Philanthus* succumb to its sting; however, some element in the blood renders *Philanthus* immune to its own venom. *Palarus variegatus* (Fabricius), a wasp which preys upon *Philanthus* and other wasps and bees, is also immune to *Philanthus* venom (although *Philanthus* is not immune to *Palarus* venom).

Observational data from many sources indicate that many wasps which prey upon Hemiptera or upon adult holometabolous insects typically insert the sting but once, on the venter of the thorax close to the major organs of locomotion, probably much as in *Philanthus*. However, Orthoptera hunters typically apply three or four stings. Steiner's (187) studies of *Liris nigra* (van der Linden) reveal that the first sting is applied to the cricket prey in the membrane at the base of the hind (jumping) legs, three additional stings at the base of the front legs, middle legs, and in the "neck" region, in that order. Various abnormal and incomplete sequences of stinging occur under certain conditions of reduced motivation or unusual stimulus situations. By an ingenious series of experiments involving surgical displacement of body parts, Steiner showed that the wasp is guided visually by the form and movements of the prey, but that each insertion of the sting is guided by tactile stimuli received by the sting apparatus, these stimuli prevailing over other factors.

Predators on insect larvae commonly sting the prey several times, presumably a reflection of the lesser concentration of locomotory function in larvae. Caterpillars are stung several times along the venter of both the thorax and abdomen both in sphecids (5) and eumenids (39). Certain

Tiphiidae (98) and Bethylidae (215) may sting their prey a great many times and over many parts of the body. Cessation of movement on the part of the host may be an important factor in discontinuance of stinging in many wasps.

Full recovery of the host from the effects of the sting is common in Tiphiidae and occurs occasionally in Bethylidae [for references see Clausen (25)]; recovery is also reported for certain Pompilidae (65) and a very few Sphecidae (93). Linsley & MacSwain (132, 133) believe that in the species of Cercerini which they studied, either the prey is not paralyzed until some time after it is taken into the nest or the toxin has a delayed effect. In the majority of wasps, the prey is paralyzed in such a way that it remains alive but immobile until consumed by the larva, although one often notices variation in the depth of paralysis even within the prey of one individual (80). Steiner (186) discusses variation in paralysis as a result of an incomplete series of stings in *Liris nigra*. Some species of *Bembix* apparently kill the first fly (the egg pedestal) although later flies are merely paralyzed (204); but killing of all the prey is usual in some other species of *Bembix*, especially cell cleaners such as *B. texana* Cresson (46, 59). Iwata (88) reviewed much of the literature on stinging and on the effects of the sting published prior to 1942.

Early reports that some *Bembix* kill their prey by crushing have been shown to be incorrect (154). However, Janvier (97) believes that *Pemphredon* does not sting its aphid prey but paralyzes it by pinching the thorax with its mandibles. This may also be the case in the related genus *Xylocelia* (161). Deleurance (39) reports that in *Eumenes*, following stinging, a fairly lengthy pinching of the prey in the vicinity of the nerve ganglia occurs; he believes that this is essential for complete paralysis and that it presages maceration of the prey in the Vespidae [Wheeler (214) cites other cases of prey maceration in Eumenidae].

Various other cases of mutilation or luxation of the prey following stinging have been reported, but these apparently serve either to release blood which is then lapped up (malaxation, discussed earlier) or to render the prey more suitable for carriage, storage, or oviposition. For example, several species of the sphecid genus *Ampulex* are reported to cut off the antennae of their cockroach prey (105, 219) while, in the Pompilidae, some species dislocate the legs of the spiders (182) and most if not all Auplopodini amputate the spider's legs at the coxae (34, 65, 174). In *Bembix*, one wing and one or two legs on the same side of the fly are dislocated prior to oviposition, the result being that the fly remains securely on its back after deposition of the relatively large egg at the base of the dislocated wing [see, especially, Tsuneki (204)]; but flies brought in after the initial one are not so treated.

A comparative study of the venom of Hymenoptera has yet to be made. The work of Molitor (150) and of Rathmayer (163) suggests that there may be a certain amount of venom specificity. Welsh & Batty (213) have tested the venom of solitary wasps of several families (Scoliidae, Mutillidae,

Sphecidae) and found it to lack serotonin, an important constituent of the venom of social wasps and bees.

Carriage of prey to nest-cell.—The manner in which the prey is grasped for carriage to the nest is subject to little or no variation within genera, and often within subfamilies or even families. The major types of prey carriage have been reviewed by Iwata (88), by Bristowe (17), and, most recently, by Evans (53), so that no detailed discussion seems necessary. Three major types, each with two or more subtypes, may be distinguished: (a) mandibular (i.e., the wasp grasps the prey with its mandibles, sometimes also with some of its legs); (b) pedal (grasp is with the middle or hind legs, or both); and (c) abdominal (prey is impaled on the sting or held by special modifications of the apical abdominal segment). The first type may involve carriage over the ground, either backward or forward, or in flight, while the second and third types are primarily concerned with carriage in flight. Types *b* and *c* occur only in the Sphecidae, in fact in only a few specialized stocks of that family. *Oxybelus* is one of the few genera in which two types occur, some species employing the hind legs and others the sting. Tsuneki (203) observed that in *O. strandi* Yasumatsu three different types of grasp were employed; he believed that smaller flies were impaled on the sting, but that heavy flies were carried by the hind legs or even by one of the middle legs (the last grasp being characteristic of certain Crabronini). However, as he points out, most species of this genus employ either the sting or the hind legs, with no apparent correlation with the size of the prey [see also Krombein (118)].

Prey carriage represents one of the more stereotyped elements of wasp behavior and in general bears little relationship to the type of prey carried (e.g., the scavenger wasp *Microbembex monodonta* carries a diverse assortment of dead arthropods with its middle legs, a grasp characteristic of all Bembicini). Nevertheless, some latitude of execution is possible in many species. For example, certain Pompilidae, as well as Sphecidae such as *Ammophila*, will at times carry large prey over the ground and smaller prey in flight, and variation has been noted in the part of the prey grasped by the wasp [examples in (65, 156)]. Wasps which normally carry the prey directly into the nest may, upon arriving with an unusually large prey, leave it at the entrance and draw it in from the inside. Certain wasps characteristically turn around in front of the entrance and draw the prey in backwards; "turning around" behavior has been the subject of detailed study in *Ammophila* by Teschner (189) and in *Mellinus* by Huber (85). In *M. arvensis* "turning around" is released and directed by the stimulus "dark opening in the tumulus," but is occasionally performed in the absence of such stimulus, as a "vacuum activity" [Huber (85)].

Several genera of Sphecidae characteristically do not take the prey directly to the cell, but store it in the burrow, often in a plug of soil or "holding cell," moving it to a (usually newly prepared) cell only after several prey have accumulated. Such behavior is highly characteristic of the subfamilies Astatinae (45) and Philanthinae (52, 62, 132, 133). Linsley &

MacSwain (133) reported that pollen and detritus are cleaned from the beetle prey of *Cerceris californica* Cresson before the wasp places them in the cell.

Wasps which stock their cells fully, lay their egg, and close the cell within a short period of time, such that closure occurs at least before hatching, are said to exhibit "mass provisioning." If, however, a waiting period is interposed such that there is contact between mother and larva, provisioning thereafter being spaced so that the larva receives additional prey each day in accordance with its increasing size, the species is said to exhibit "progressive provisioning." Tsuneki (204) feels that the term "progressive mass provisioning" should be applied to this phenomenon, since the prey is not fed directly to the larva but merely piled in the cell. However, the term progressive provisioning has been widely employed, and the term "direct feeding" is available to describe the typical condition in social wasps. It is apparent that mass provisioners are sometimes required to wait for a period before completely filling the cell (e.g., because of inclement weather); if such delay is long enough, there may be fortuitous contact between mother and larva. Such "delayed provisioning" [Evans (50)] is not always clearly distinguishable from progressive provisioning in the field, although, in fact, there are several fundamental differences (an obligatory "waiting period" as well as stimulation of the mother by the larva being characteristic of true progressive provisioning) [see Tsuneki (204-206)]. However, most theories of the origin of sociality in wasps require the development of progressive provisioning from delayed provisioning (48, 136, 214).

Progressive provisioning appears to have arisen from mass provisioning several times independently; it is reported in a few Masaridae (177), in a few Eumenidae (39, 214), and in the sphecid tribes Ammophilini, Stizini, and Bembicini (43, 50). Direct feeding of prey which is at least partially macerated is reported among solitary wasps only in a few Eumenidae [see summary in Wheeler (214)].

Oviposition.—All Bethyridae, Scoliidae, and Pompilidae, as well as the majority of Sphecidae, lay their egg on the paralyzed prey. In the Bethyridae, position of the egg may vary within one species (108). In some members of this family, several eggs are laid on one host by one female. Kearns (107) reported from one to nine eggs per host in *Cephalonomia gallicola* (Ashmead), more eggs being laid per host in conditions of low host density. Kishitani (108) reported one to seven eggs per host in *Goniozus japonicus* Ashmead, more eggs as a general rule being laid on larger specimens. Iwata (89) reported rarely up to 16 eggs on one prey in this same species. Females of the bethylid genera *Laelius* and *Allepyris* are reported to bite off the hairs of their dermestid hosts on the areas where the eggs are attached (221).

In other wasps a single egg is deposited on the prey, and the position of the egg tends to be relatively constant in a given species, often within a genus or group of genera. Clausen (25) figures the typical egg position of several species of Tiphiidae and Scoliidae; in the former group, the egg is glued closely to the integument after an extensive kneading of the body

surface, while in the scoliids it is glued in an erect position [see also (100, 147)]. Janvier (100) noted a limited amount of variation in egg position in *Tiphia morio*. Considerable variation in egg position occurs in some species of the sphecids genus *Ammophila* (58), although this is exceptional. Steiner (187) found that egg position in *Liris nigra* is constant, but that if that portion of the body on which the egg is laid is excised, a lowering of threshold occurs and the egg is deposited elsewhere. Iwata (88) recognized 23 "oviposition types" among solitary wasps; these types are illustrated by seven excellent plates of drawings [for other good illustrations of egg positions, see (77, 92, 137)].

Oviposition in the empty cell, before commencement of provisioning, has developed in several stocks of Sphecidae independently; in this case the egg is fastened erect to the bottom of the cell or, less commonly, laid loosely on the bottom or against a wall [type 18 of Iwata (88); see also Evans (43, 46)]. All Vespoidea oviposit in the empty cell, the majority suspending the egg by a filament as described by Hartman (82), although some members of both the Masaridae and Eumenidae are said to deposit the egg loosely in the cell, while a few Eumenidae apparently fix the egg directly to the cell wall, as in social forms (88).

It is generally believed that the female is able to determine the sex of the egg at the time of deposition, presumably by means of a sphincter which controls fertilization (males being haploid as in other Hymenoptera). It is said that some Bethyridae lay male and female eggs side by side on the host (160). Many Eumenidae and Sphecidae appear to lay male eggs in smaller cells containing fewer prey [see e.g. (27, 142, 170)]; this is particularly marked in the cicada killer, *Sphecius speciosus*, in which Dow (41) found that cells provisioned with one cicada always yielded males, while cells with two cicadas nearly always yielded females. Jayakar (102) found that both a sphecids, *Sceliphron madraspatanum* (Fabricius), and a eumenid, *Eumenes esuriens* (Fabricius), prepared a series of cells containing male eggs followed by a series containing female eggs. Calculations from his data indicated that the overall probability of this occurring by chance in the two species was 2×10^{-6} . He believes that the order in which the eggs are laid may be responsible for the phenomenon of proterandry, but data accumulated by several persons working with twig-nesters (116, 119, 141, 142) lead one to doubt that "protarrhenotoky," as he calls it, is especially common or that it bears any important relationship with proterandry.

CURRENT PROBLEMS AND APPROACHES

Studies of wasp behavior in the past three decades demonstrate well a statement of Konrad Lorenz (134) that the main thing we have learned about animal behavior is that it is much more complicated than was once supposed. Glib "explanations" of wasp behavior, running the gamut from "chain reflexes" to "intelligence," are no longer in vogue. Rather, behavior patterns are regarded as parts of complex systems also involving structural and biochemical components, each the result of a long evolutionary history and each

both adaptive and adaptable, that is, closely attuned to the niche of the species by means of constant interplay between genome, phenome, and environment. No general survey of current behavioral thinking will be attempted here; several reviews from varying points of view are available (6, 21, 129, 134, 178, 197).

Behavioral formulae.—It is obvious that several typical sequences of behavioral acts occur among wasps; it was noted above, for example, that all Vespidae build and oviposit before provisioning (nest-egg-prey) while all Pompilidae oviposit on the prey (prey-nest-egg, less commonly, nest-prey-egg). Particular sequences may characterize all members of a family or genus; exceptionally one finds more than one sequence within a genus [e.g., *Bembix* (46)] or even in a more limited sense within a species [e.g., *Ammodiplosis infesta* Smith (205)]. The usefulness of a shorthand for designating the order in which actions are performed is demonstrated by the fact that at least four workers have developed their own formulae compounded of symbols for each unit of behavior (Table I). Iwata (88), who first used such a system extensively, spoke of these as "habit-types," but it would seem more

TABLE 1. SYMBOLS USED FOR UNITS OF WASP BEHAVIOR BY SEVERAL AUTHORS

	Preparation of nest	Searching for prey	Paralysis of prey	Transport of prey	Placing prey in nest	Oviposition	Final closure
Iwata (88)	I (insinuare)	V (venari)	P (pungere)	T (transferre)	-	O (ovum parere)	C (claudere)
Arens (4)	a	b	c	d	e	f	g
Tsuneki (205)	B (burrowing)	H (hunting)		T (transporting)	S (storing)	O (oviposition)	C (closing)
Oberg (156)	N (Nestbau)	J (Jagd und Eintragen)			-	E (Eiablage)	V (Verschliessen)

appropriate to call them behavioral sequences, especially since the word "habit" is falling into deserved disuse in favor of the more noncommittal word "behavior."

The use of such formulae permits ready comparison of the gross behavior of groups of wasps; for example, in Iwata's system the nesting behavior of the sphecid genus *Prionyx* may be formulated as PTIOC, the related, but presumably more advanced, genus *Sphex* as IPTO(PT)^aC. Phylogenetic schemes employing behavioral formulae have been employed especially by Iwata (88, 90) and by Evans (42, 43). Such symbols are also useful as a framework for analyses such as those of Tsuneki (205) (see also Fig. 2). If students of wasps are to continue to use such a shorthand, it is essential that it be standardized. This writer suggests using Iwata's original symbols with some (but perhaps not all) of the refinements added by Iwata himself (90), as well as other refinements suggested by Evans (43) and by Tsuneki (205). A measure of simplicity must, of course, be retained; it is probable that persons studying in depth one or a few related species will find more symbols useful than will persons comparing major stocks of wasps. Behavioral formulae have no intrinsic value except as a useful tool in comparative studies.

Treatment of whole behavior patterns.—Few persons have had sufficient data at hand to attempt an analysis of whole behavior patterns in terms of presumed causative factors. The classic endeavors of Baerends (5) with respect to *Ammophila pubescens* are well known and were summarized in part by him in an earlier volume of the *Annual Review of Entomology* (6). In this paper, Baerends criticized the analyses of behavior in species of *Bembix* by Evans (46) and by Tsuneki (205, 206), remarking that “the proper way to detect and distinguish different behavioral systems (instincts) is by statistical and experimental analysis, not by a merely logical classification according to function.” If one substitutes the words “most fruitful” for “proper,” it is difficult to disagree with Baerends. As to what is “proper”: it is surely as proper for a researcher to proceed cautiously within the framework of his opportunities and limitations as it is improper to use statistics to clothe shaky postulates with a sheen of sophistication, as has sometimes been done in this field as in many others.

Analyses which have been attempted thus far have all conceived of the nidification cycle (or instinct) in terms of an hierarchical system which, according to Baerends (5), is under the general influence of an endogenous “brood-rearing drive” (*Brutpflegestimmung*) (with other drives for mating, feeding, grooming, etc.). Although Baerends speaks of these drives as causal factors, others have assumed that the pressure of eggs developing in the genital tract provided the motivation of nesting wasps [see e.g., Wheeler (214)]. Tsuneki (205) considers positive egg pressure (PEP) the driving force in the nesting behavior of *Bembix niponica* and other wasps. This particular point would seem amenable to experiments more stringent than those of Tsuneki, for example, involving careful removal of mature eggs from the female genital tract.

In the hierarchical systems proposed, the major drive is conceived of as setting in motion a series of subsystems or phases, each of these in turn a series of systems of the third order. In most models, these systems of the second or third order are much the same as the units of behavior utilized in the formulae discussed above (e.g., digging, oviposition). Thus, one may speak of a wasp undertaking a hunting flight as a result of a drive which is subordinate to that for this particular phase of its nesting cycle, and, in turn, to the drive controlling nesting and brood rearing in the whole. Most cases of “blindness of instinct” described by various authors are the result of wasps failing to adapt to a given situation when under the influence of an inappropriate drive. Molitor (150) found that some wasps will accept unusual prey (even their own larvae) if presented at the nest entrance, even though these wasps are highly specific in their hunting behavior. Bristowe (17), Olberg (156), and others mention instances in which suitable prey introduced while the wasp is digging the nest is merely “ignored,” and Bristowe (17), Hamm & Richards (80), Evans (46) and many others note cases in which prey accidentally dropped at the nest entrance is not picked up and used, the wasp merely entering the nest “empty-handed” and flying off to take new prey. Since drives are not by any means insulated from external influences, such

wasps may, in fact, adapt to various unusual circumstances, but there is no simple formula for predicting such adaptation: the variables involved include intensity of the drive, quality of the releasers, innate plasticity with respect to that facet of behavior, capacity for learning, etc. Thorpe (194) discusses various types of learning known to occur in wasps and other insects. Olberg (156) and Huber (85) review examples of possible displacement and vacuum activities reported to occur in wasps confronted with conflicting motivations or unusual stimulus situations.

In addition to the several models of whole behavior patterns already mentioned, an especially interesting one has been presented by Thorpe (194) on the basis of data from Baerends (5). Thorpe stresses the relationship

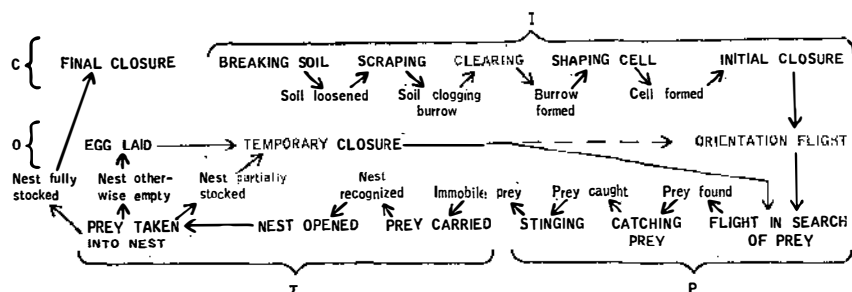


Fig. 2. Much simplified model of behavior associated with a single one-celled nest of a mass-provisioner (such as *Bicyrtes quadrifasciata* Say) having the behavioral formula IPTO(PT)ⁿC. Words in capital letters represent actions, words in small letters presumed releasers. The nesting cycle is presumed to be mediated by the "nesting and brood-rearing drive" or by "positive egg pressure" (see text for further discussion and references to other models).

between appetitive behavior ("search for releasers") and consummatory acts ("fixed action patterns") in the nidification cycle. The model presented here (Fig. 2) is original but not greatly dissimilar to that of Thorpe. Each element in the "reaction chain" is dependent upon that preceding it as well as upon certain factors in the environment (often gestalts), and each act is capable of a certain latitude of execution, consummatory acts less so than others. However, Steiner (187) has shown that consummatory acts such as stinging, prey carriage, and oviposition are of unequal value in terms of capacity for modification. Most contemporary workers conceive of the distinction between appetitive behavior and consummatory acts as being relative rather than absolute; Tsuneki (206) finds it convenient to recognize three "classes of behavior" rather than two. In reality there is a complete spectrum of actions, from those performed in a highly stereotyped manner to those involving irregular searching patterns capable of many modes of performance and often capable of ready conditioning. One species may have a certain aspect of its behavior quite fixed, while in a related species the same be-

havior may be variable; Olberg (156) presents examples and terms these stenoplastic and euryplastic species, respectively.

The problem of fixity versus variability in behavior is an old one, dating at least from the times of Fabre (66) and the Peckhams (159), but it is still very much alive [for recent discussions with respect to solitary wasps, see especially (150, 154, 175, 189, 190)]. Crèvecoeur (35) distinguished between adaptability to varying environmental situations and the development of ethological races as a result of mutation and selection, presenting examples of each. Teschner (189) made a similar distinction in a discussion of fixity and variability in three species of Ammophilini. Teschner regards plasticity as characteristic not only of appetitive behavior and the taxis components of fixed motor patterns, but even of the patterns themselves, a point confirmed in some measure by Steiner (187). Steiner is one of the few persons to have considered maturation and senescence of behavior patterns, a matter of less importance than in longer-lived, nonmetamorphosing animals but nevertheless one which ought not to be ignored. Olberg (156) speaks of latent motor patterns which may be expressed only under certain situations and which add to the apparent plasticity of behavior. The problem of genotype versus phenotype in behavioral variation, and the extent to which behavior may undergo permanent change as a result of canalization of phenotypic plasticity or conditioned responses (if at all), is one of the key problems of ethology (140).

Phylogeny of behavior.—Behavior patterns are to be understood not only in terms of their function and causation but also in terms of their evolutionary history. That certain behavioral features are diagnostic of species, genera, or families of wasps is well established; examples have been cited above, and the literature is replete with others [see e.g. (8, 54, 111, 125)]. The family Pompilidae is more readily definable on ethological grounds than on the basis of structure (42). Recently acquired knowledge of the behavior of that anomalous group of wasps, the Embolemidae, has permitted placement of the group as a subfamily of Dryinidae (Bethyloidea) (16). Spooner (184) has shown a close concordance of structure and ethology in the sphecids tribe Psenini, and Bohart & Menke (13) have shown a similar concordance in the Sphecinae. The sphecids genus *Glenostictia* was recently described principally on the basis of prey choice and type of provisioning (75), and subsequent studies have added still further diagnostic behavioral features (59). Adriaanse's separation of two cryptic species of *Ammophila* on the basis of several aspects of nesting behavior is well known (2, 3). More recently, Bowden (14) has shown that two *Dasyproctus*, formerly regarded as subspecies, quite clearly behave as two species. Evans (42) and Soyer (183) have both shown that certain sibling species of the pompilid genus *Anoplius* are very different ethologically, although, as a matter of fact, the genus *Anoplius* taken as a whole is not at all distinctive in its behavior. Other examples of lack of concordance between structure and behavior have been pointed out in the Eumenidae (44) and in the sphecids tribe Crabronini (207). Such cases

sometimes mean that the wrong morphological characters have been emphasized.

It is self-evident that phylogenetic studies must utilize behavior patterns subject to little variation within the taxa being considered; such patterns may be treated much like structures. The comparative anatomist arranges the various states of his characters in morphoclines, the directions of which can often be deduced by the application of established criteria [Maslin (139)]. In a similar way, the student of behavior may employ ethoclines [Evans (46)] which, when solidly founded, may be highly suggestive with regard to the origin of complex and specialized behavior. Although this approach has been branded as futile by some workers [Thompson (192)], it has proved its value many times over, not only in wasps, but in many other groups of animals. Types of prey carriage in wasps have been shown to form an ethocline of several well-defined stages (53) and the species of *Ammophila* have been shown to exhibit ethoclines with respect to several aspects of nesting behavior (50, 58, 162). In each case, definition of the ethoclines has helped to explain complex behavior otherwise considered enigmatic or presumed to be "intelligent," and at the same time has elucidated structures and other aspects of behavior related to these same adaptive complexes.

The comparative approach has proved especially instructive with regard to the possible origins of social behavior in the Hymenoptera, all of the social groups having apparently had their origins among the wasps (Fig. 1). The Vespidae probably evolved from a stock of Eumenidae, employing progressive provisioning and macerating their prey (48, 136, 214, 215). Intermediate stages between wasps and ants are lacking, but the studies of Given (76) on food transfer in the Thynninae (Tiphidae) are suggestive, as are the studies which have been made on the subsocial Bethyridae (15, 215). The bees are presumed to have arisen from an extinct stock of Sphecidae, and it is of interest to find in existing Sphecidae examples of both types of social evolution occurring in the bees: by way of matrifilial associations arising from progressive provisioning and by way of communal nesting of females of the same generation (55). Communal nests have been reported mainly in the Crabronini, while progressive provisioning is especially characteristic of Bembicini, although occurring also in several other groups. Some of the Cercerini are also of interest in this context. Krombein (115) found that the offspring of *Eucerceris triciliata* Scullen may begin emerging while the mother is still active within the same nest, and he asks whether the daughters might not continue to use the old burrow entrance and dig subsidiary burrows of their own. Grandi (77) has found that this is, in fact, what happens in *Cerceris rubida* (Jurine). This species has two generations during the summer, the females of the second generation, sometimes as many as four or five of them, living together with the mother. They tend to average smaller than the mother, but they carry out normal nesting and provisioning activities with no apparent conflict; there is some division of labor, the females "taking their turn" at guarding the nest entrance. Such species are indeed very close to the nebulous line separating nonsocial from social Hymenoptera.

The flood of literature in the field of wasp behavior within the past three decades leads one to believe that, after a long history of desultory observation and speculation, this field is at last coming of age. Many new techniques are available (although not reviewed here), and recent conceptual advances permit one to pose questions which are truly relevant to problems of causation and evolution. While looking to the future, it is nevertheless fitting to recall a remark made at the turn of the century by that pioneer ethologist Charles Otis Whitman (216): "Observation, experiment and reflection are three in one. Together they are omnipotent; disjointed they become impotent fetishes."

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