PROC. ENTOMOL. SOC. WASH.
87(3), 1985, pp. 597–605

REPRODUCTIVE BEHAVIOR OF MALE *AMMOPHILA HARTI* (FERNALD) (HYMENOPTERA: SPHECIDAE)

BARBARA J. HAGER AND FRANK E. KURCZEWSKI

Department of Environmental and Forest Biology, S.U.N.Y. College of Environmental Science and Forestry, Syracuse, New York 13210.

Abstract.—The behavior of male *Ammophila harti* (Fernald) was observed during the summers of 1982–1984 on a sand-gravel ridge in Cayuga County, New York. Daily and seasonal activity patterns (general and reproductive) were delineated. At least two generations occurred per year. Males lived approximately three weeks and were usually present at the beginning of each generation. Male activity was bimodal daily with high levels of activity in the morning and late afternoon. Copulatory activity and position were defined. Males were subjected to interference from conspecific males while mating. Reproductive behavior components are discussed and compared with those of other members in the genus.

Studies on the behavior of male solitary wasps lag far behind those on female behavior. This discrepancy is probably due to the inconspicuous nature of the males; they are smaller than the females, usually live one-third to one-half as long, and do not exhibit elaborate, sometimes stereotypic, hunting, nest construction, or provisioning behavior. Few papers have dealt specifically with male behavior until rather recently (see Lin, 1963; Kurczewski, 1966; Alcock, 1975a, b, c; Steiner, 1978; Gwynne, 1978; Evans and O'Neill, 1978; O'Neill, 1979, 1983; for synopsis of male reproductive strategies, see Alcock et al., 1978).

STUDY SITE AND METHODS

We observed *A. harti* (Fernald) males near Auburn, Cayuga Co., New York on a 150 m^2 sand and gravel ridge sparsely covered with grasses, horsetails (*Equisetum* spp.), clovers (*Melilotus alba* Desr., *Trifolium* sp.), Queen Anne's lace (*Daucus carota* L.), milkweed (*Asclepias* sp.), and goldenrod (*Solidago* sp.) (Fig. 1). Observations of males were made almost daily, 2 June–29 Aug. 1982 and 21 June–22 Aug. 1983. Additional, periodic observations were made in June and July 1984. Daily hours of observation ranged from 0800 to 1730 (EDT).

We observed general (flying, feeding, grooming) and reproductive behavior of the males. Reproductive behavior included: (1) attempts by a male to grasp a conspecific (male or female) and initiate mating; and (2) actual coupling of a male and female. We collected and color-coded the males in order to follow them daily. Hourly records were kept of the number of males performing general and reproductive behaviors. These two categories were averaged for day, week, and year. In order to compensate for differences in sampling effort, the number of wasps observed performing a particular behavior is reported as observations/hr. This

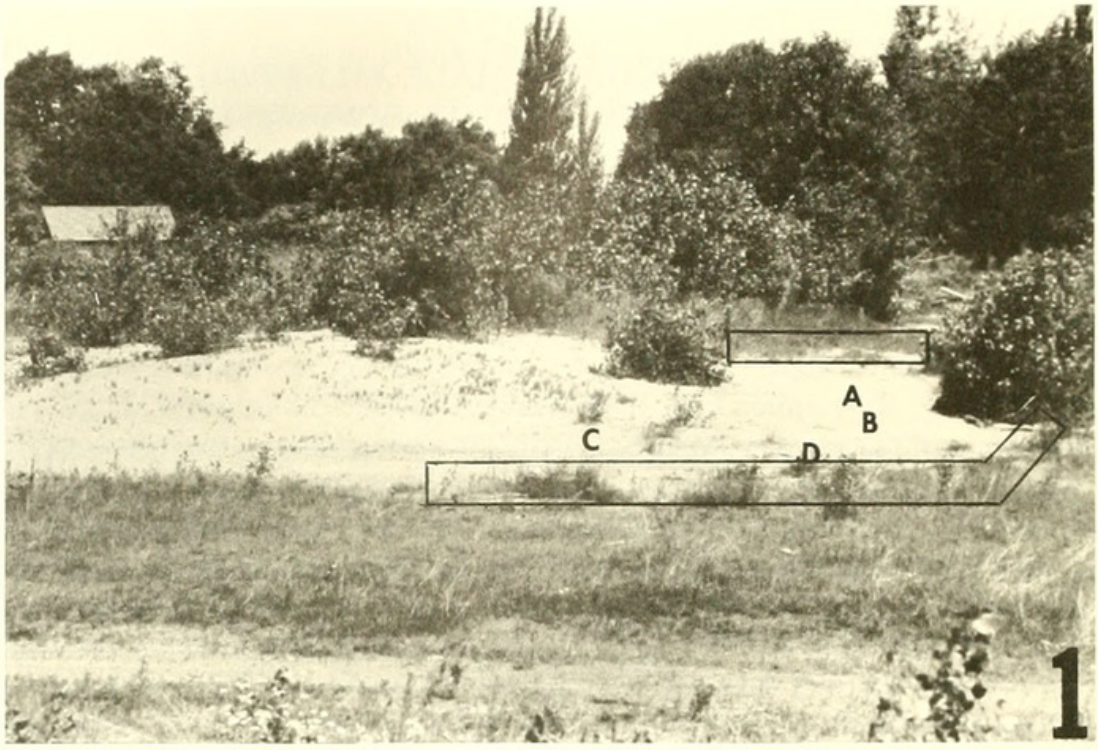


Fig. 1. Study site near Auburn, NY. Letters (A, B, C, D) indicate quadrats within main nesting area of *A. harti*. Male patrol flight areas are designated by rectangles.

enables a comparison of the levels of behavior at different times of the day and season.

Emergence and Longevity

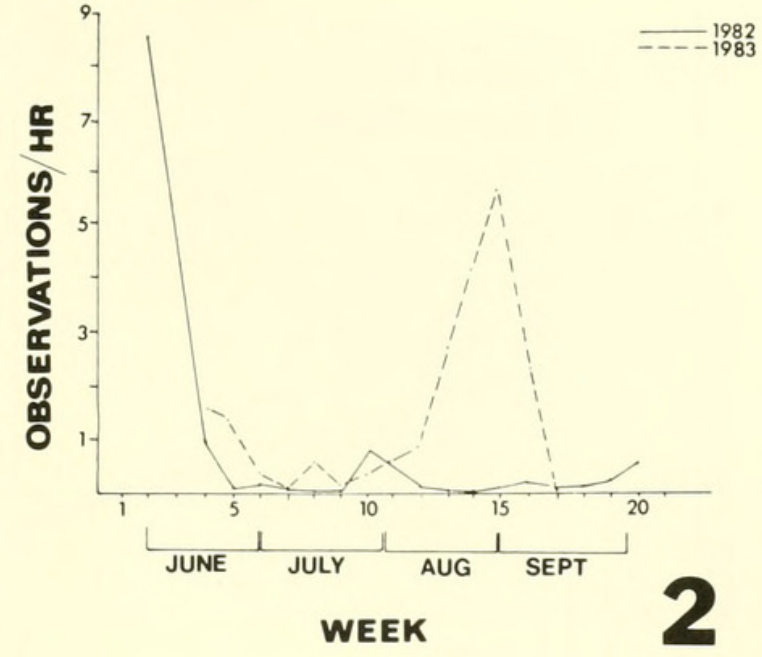
A. harti is slightly protandrous. In 1982 we sighted the first males on 2 June, six days before the first female was seen constructing a nest. In 1983 males were first seen on 18 June, three days before the first nesting females. In 1984 we observed a male on 6 June, 15 days before the first female. The differences in the emergence dates preclude analyzing the data by calendar date (Fig. 2). In order to pool the data across years, the calendar date is adjusted to reproductive date. Reproductive date 1 corresponds to the first day of observed activity (Fig. 3).

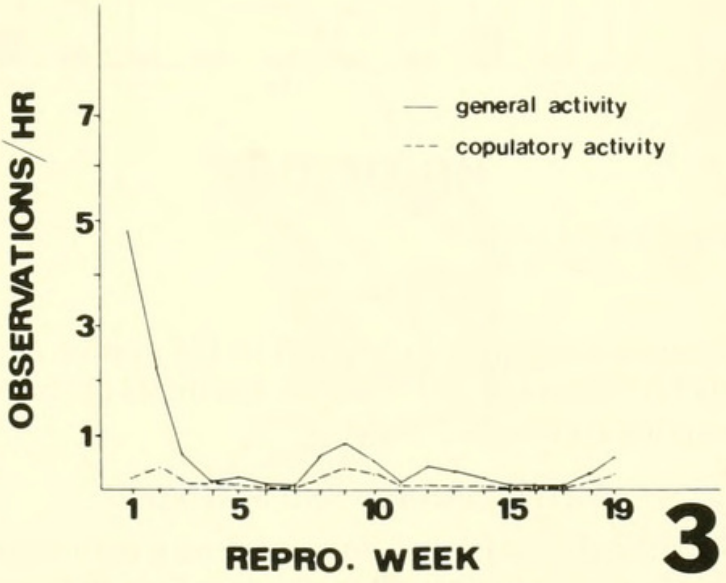
Based on the emergence records of reared wasps, longevity records of females and field observations, there are two overlapping generations of *A. harti* per year; the first occurs in June and the second in Aug. (Fig. 2). In addition there is a weather-dependent, partial third generation in Sept.–Oct. In 1982 the last male was observed on 10 Oct., and in 1983 a male emerged on 30 Sept.

Male longevity was not determined accurately. Males were most numerous for a two–three week period at the beginning of each generation (Fig. 3) and this might well represent their life span. Marked males were never recaptured after this period of time and the male population declined abruptly after three weeks.

Activity Patterns

The mean number of males observed/hr fluctuates significantly among weeks, with two major peaks corresponding to the two generations (ANOVA $F = 1.87$, 15;382 df, $P < .05$, Fig. 3). (Degrees of freedom are reported as: numerator;





Figs. 2–3. 2, Seasonal activity of male *A. harti* (1982–1983) based on calendar date. 3, Seasonal activity of male *A. harti* (1982–1983) based on reproductive date. Reproductive data 1 corresponds to the first day of male activity. Copulatory activity follows the pattern of general activity.

denominator.) Reproductive activity (attempted copulations) follows the pattern of total male activity but with no significant difference among weeks.

The daily pattern of male activity does not differ significantly between generations. The greatest activity occurs in the morning (0800–1100) and late afternoon (1500–1700) (Fig. 4). At these times males fly in quick, sinuous, patrolling flights through the vegetation at the periphery of the nesting area and occasionally enter the nesting site. These flights are mildly reminiscent of the "sun-dances" of some nyssonine wasps (see Evans, 1966). Males flying early in the morning (0800–0900) often land in sunny areas where they rest on the sand and groom. Attempted copulation takes place at all times except in early morning. These attempts take place at both the periphery of the nesting aggregation and within it. During midday

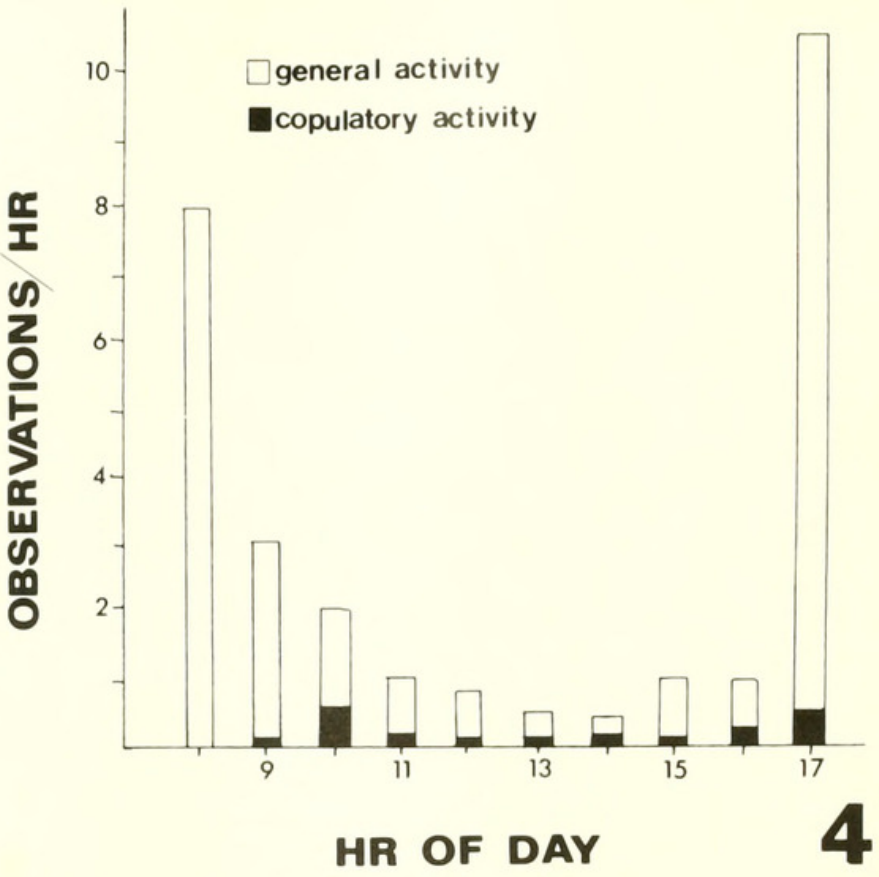


Fig. 4. Daily activity of male *A. harti*.

most observed copulatory attempts occur within the nesting site. Patrol flights decrease drastically between 1100 and 1500; the few males observed at these times were usually attempting copulation.

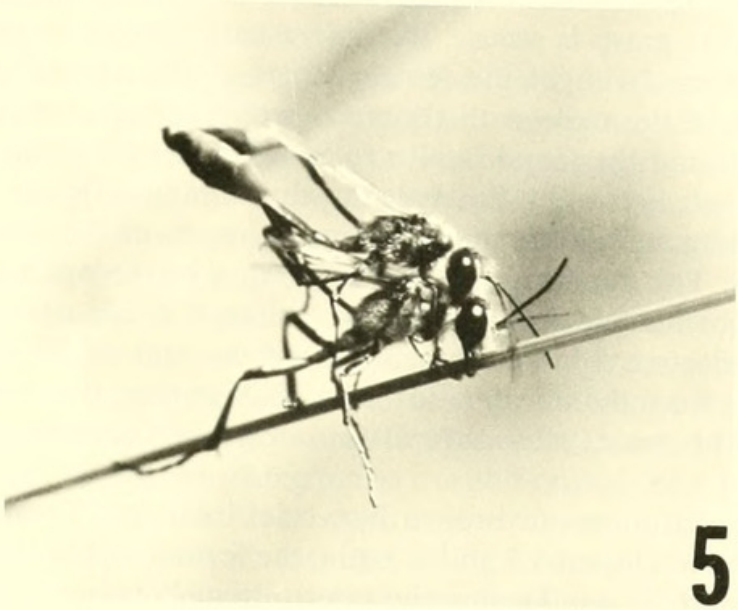
Patrol Flights and Mating

Males are non-territorial; that is, they do not defend a particular site. However, marked males are often recaptured in the area in which they are first collected and marked. Patrol flights occur 10–35 cm above the ground and the male may pursue any flying insect within sight or pounce upon wasp-like objects on the ground. The flight of one male may precipitate others to follow in a "chain reaction." When a wasp on the ground is encountered, the patrolling male attempts to grasp it behind the head with its mandibles. If this fails, the male flies away or lands on the sand nearby and grooms. This suggests that recognition of a potential mate is visual and successful copulation may depend upon the use of tactile and/or olfactory stimuli.

During the initial stages of copulation, the male flies in and grasps the female

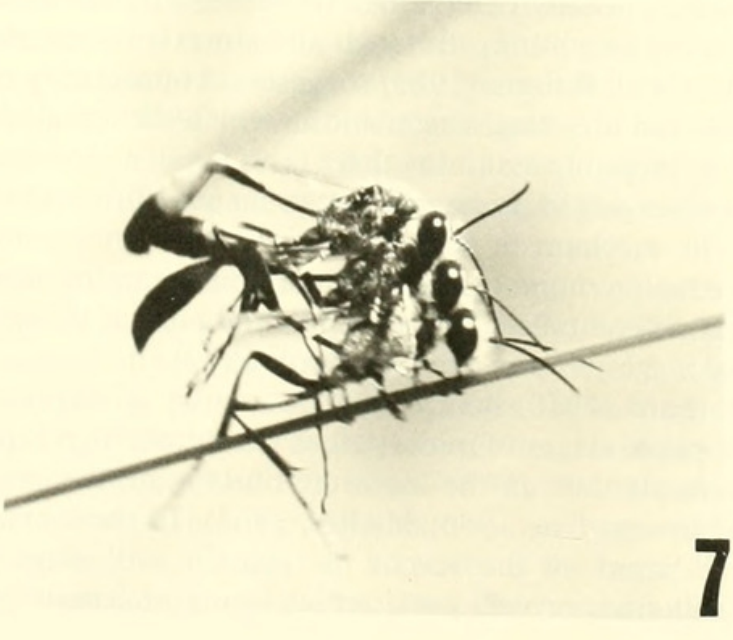
→

Figs. 5–7. 5, Copulatory position of *A. harti* with the male atop the female. Note the twisted abdomen of the male. 6, Second male attempting to copulate with the female. He is using his mid- and hindtibiae to push the first male's abdomen away from the female. 7, Second male successfully copulates with female. The first male's abdomen is extended outward from the pair.



5

6



7

by the back of her neck with his mandibles. He also grasps her mesosoma with his front legs. If the grasp is secure, the pair usually moves to vegetation either by flying or walking. In flight the female hangs at about a 45° angle from the longitudinal axis of the male with the male retaining his grasp of the female's cervix. On the ground the female walks to and climbs up vegetation.

After arriving on vegetation, the male taps his antennae on top of the female's head while opening and closing and probing the apex of the female's abdomen with his claspers. The female grasps the vegetation between her mandibles and, when receptive, bends her abdomen into a z-shaped configuration or extends it upward. The male twists his abdomen around the side of hers and clasps the female's genitalia from the side or below (Fig. 5). If unreceptive, the female lowers her abdomen. The male, after several minutes, may abandon his attempt to copulate.

Copulation is continuous or broken into brief intervals. Two copulations observed from inception lasted 3.3 and 4.5 min; the former was broken into intervals of 31, 108, 40, and 20 sec. During the intermittent "resting" periods, the male rubbed his abdomen with his hindlegs, the female rubbed her abdomen with her hindlegs, and the male rubbed his abdomen along the female's abdomen.

Matings are subject to interference from other males. "Mating balls," consisting of more than one male and a single female, were observed several times. Such behavior terminates with either a single male remaining atop a female or separation of all wasps. A single, interfering male may achieve a brief coupling with the female by displacing the original, coupled male (Figs. 6, 7). In such a case, the female's abdomen is extended at about a 75° angle to her body axis and the male atop the first male is able to push the other male's abdomen away and clasp the female's genitalia. A male already mating may try to prevent access to a female's genitalia by extending his hindfemora parallel and above the female's abdomen with his hindtibiae and hindtarsi spread to protect the sides of the female's abdomen (M. G. Spofford, 1984, pers. comm.). A pair disturbed while mating may fly off in a tail to tail position to avoid further interference.

Discussion

Male solitary wasps usually emerge before the females (Evans, 1966; Bulmer, 1983). *A. harti* is no exception, although the time between male and female emergence may be short. Bulmer (1983) suggests that protandry occurs in insects which have a restricted breeding season and in which the females mate only once soon after eclosion, probably assuming there is no incidence of sperm precedence. Therefore, males emerging early have a better chance of reproducing than males emerging later. The mechanism generating early male emergence may take the form of either producing more males early in a generation [protarrhenotoky (Jayakar, 1963)] or via differentiation in developmental rates of the sexes in the larval, prepupal or pupal stages (Evans and Eberhard, 1970).

Evans and Eberhard (1970) believe that protandry is the result of faster development of the pupal stages of males rather than protarrhenotoky. Evidence to support their claim abounds in the literature on twig-nesting wasps (Krombein, 1960, 1964; Medler and Fye, 1956; Medler, 1964). In these species, the female regulates cell size based on the sex of the egg she will place in the cell. An examination of cell sizes reveals preferential laying of female eggs early in the

generation (deuterarrhenotoky), yet the males laid later emerge before the females and thus they must develop at a faster rate.

Cocoon length is related to sex of wasp in *A. harti* (Hager and Kurczewski, in prep.). Although the overall sex ratio based on cocoon size is biased in favor of females (1:2.71, male : female), there is no significant trend in the exclusive production of one sex at any time in a generation. Differential development of the sexes is therefore suspected and data on emergence shows a faster rate for the pupal stage in the male (Hager and Kurczewski, in prep.).

Much of the behavior of male *A. harti* is directed toward reproduction. The primary function of the non-territorial, patrolling flights appears to be to obtain matings. Patrol of the nesting area also occurs in the Palearctic *A. pubescens* Curtis (Baerends, 1941) and the Nearctic *A. azteca* Cameron (Evans, 1965) and *A. aberti* Haldeman (Powell, 1964). Searching males use abdominal color patterns to locate females (Teschner, 1959). In most species of *Ammophila* the two sexes have different abdominal color patterns (Menke, 1965). Males of *A. harti* generally have a lighter, orange-colored abdomen than do the females.

Patrolling behavior in solitary wasps is associated with clumped nest distribution in open areas (Alcock, 1975b; Alcock et al., 1978). Alcock et al. (1978) define clumped nesting as occurring when an observer can readily view at least ten nest entrances from one vantage point. Patrolling a clumped nesting site is advantageous for males whether the females are monogamous (males copulate with emerging virgin females) or polyandrous (males mate with inseminated nesting females). Copulatory attempts occurring within and at the periphery of the nesting site confirm their importance as mating areas. In those species of *Ammophila* that nest solitarily (dispersed), flowers and hunting and sleeping sites are the primary areas of reproductive activity (Alcock et al., 1978).

Copulation has been observed and described for several species of *Ammophila* (Turner, 1912; Baerends, 1941; Olberg, 1959; Powell, 1964). *A. harti* differs slightly from the basic copulatory position exhibited by other species in the genus in that the abdomen of the male is twisted while coupling occurs from the side (with the female's abdomen slightly twisted) or from below. The female's abdomen is usually bent into a z-shaped configuration. In other species of *Ammophila* the females hold their abdomen straight or extend their abdomen upward at an angle. Successful copulation in *Ammophila* depends on the cooperation of the female; she must raise her abdomen in order to make her genitalia accessible to the male (Powell, 1964; Menke, 1965). Powell (1964) attributes the necessity of raising her abdomen to the female's larger size. Likewise, the bending of *A. harti*'s abdomen may be related to size differences between the sexes. Males average 85% the length of the females.

Repeated coupling and uncoupling during a mating bout occur in *A. pubescens* (Baerends, 1941) and *A. sabulosa* (L.) (Olberg, 1959). Baerends (1941) observed one copulation lasting almost an hour, with 10 couplings during this period.

Interruption of mating by conspecifics appears to be a common strategy in *Ammophila*. "Mating balls" have been observed in *A. sabulosa* (Olberg, 1959), *A. procera* Dahlbom (Bohart and Knowlton, 1953), and *A. pubescens* (Baerends, 1941). Males successful in interrupting a mating pair may receive either an immediate or delayed benefit. Copulation takeover is the immediate benefit. If the "intruding" male separates the coupled pair but does not copulate with the female,

he still may benefit if he later encounters the female and mates with her. However, simply preventing another male from mating may increase the chances of the "intruder's" genes being expressed while decreasing the chances of the other male's genetic contribution to the population.

Most incidences of interrupted mating in *A. harti* appear to take place in bare or sparsely vegetated sand. By moving to vegetation surrounding the nesting site the chances of discovery of the pair by other males may be diminished.

Acknowledgments

We gratefully acknowledge A. S. Menke, Systematic Entomology Laboratory, Agricultural Research Service, USDA for confirming the species of wasp. We thank M. G. Spofford for her assistance in the field and D. J. Peckham for Fig. 1 of the photos. The senior author is especially indebted to W. M. Shields for his influence and constructive criticism of the field work and M.S. thesis, of which this is a small part.

Literature Cited

Alcock, J. 1975a. The behaviour of western cicada killer males, *Sphecius grandis* (Sphecidae, Hymenoptera). J. Nat. Hist. 9: 561–566.

———. 1975b. Territorial behaviour by males of *Philanthus multimaculatus* (Hymenoptera, Sphecidae) with a review of territoriality in male sphecids. Anim. Behav. 23: 889–895.

———. 1975c. Male mating strategies of some philanthine wasps (Hymenoptera, Sphecidae). J. Kans. Entomol. Soc. 48: 532–545.

Alcock, J., E. M. Barrows, G. Gordh, L. J. Hubbard, L. Kirkendall, D. W. Pyle, T. L. Ponder, and F. G. Zalom. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. J. Linn. Soc. 64: 293–326.

Baerends, G. P. 1941. Fortpflanzungsverhalten und orientierung der Grabwespe *Ammophila campestris*. Tijdschr. Entomol. 84: 68–275.

Bohart, G. E. and G. F. Knowlton. 1953. Notes on mating, prey provisioning and nesting in *Sphex procerus* (Dahlbom). Proc. Entomol. Soc. Wash. 55: 100–101.

Bulmer, M. G. 1983. The significance of protandry in social Hymenoptera. Am. Nat. 121: 540–551.

Evans, H. E. 1965. Simultaneous care of more than one nest by *Ammophila azteca* Cameron (Hymenoptera:Sphecidae). Psyche 72:8–23.

———. 1966. Behavior patterns of solitary wasps. Ann. Rev. Entomol. 11: 123–154.

Evans, H. E. and M. J. W. Eberhard. 1970. The Wasps. Univ. Mich. Press, Ann Arbor, Mich., 265 pp.

Evans, H. E. and K. O'Neill. 1978. Alternative mating strategies in the digger wasp *Philanthus zebratus* Cresson. Proc. Natl. Acad. Sci. USA. 75: 1901–1903.

Gwynne, D. T. 1978. Male territoriality in the bumblebee wolf *Philanthus bicinctus*. Z. Tierpsychol. 47: 89–103.

Jayakar, S. P. 1963. "Proterandry" in solitary wasps. Nature 198: 208–209.

Krombein, K. V. 1960. Biological notes on some Hymenoptera that nest in sumach pith. Entomol. News 71: 29–36, 63–69.

———. 1964. Results of the Archbold Expeditions. No. 87. Biological notes on some Floridian wasps. Am. Mus. Novit. 2201: 1–27.

Kurczewski, F. E. 1966. Comparative behavior of male digger wasps of the genus *Tachysphex* (Hymenoptera:Sphecidae, Larrinae). J. Kans. Entomol. Soc. 39: 436–453.

Lin, N. 1963. Territorial behavior in the cicada killer wasp *Sphecius speciosus* (Drury) (Hymenoptera: Sphecidae). Behaviour 20: 115–133.

Medler, J.T. 1964. Biology of *Rygchium foraminatus* in trap-nests in Wisconsin. Ann. Entomol. Soc. Am. 57: 56–60.

Medler, J. T. and R. E. Fye. 1956. Biology of *Ancistrocerus antilope* in trap-nests in Wisconsin. Ann. Entomol. Soc. Am. 49: 97–102.

Menke, A. S. 1965. A revision of the North American *Ammophila* (Hymenoptera:Sphecidae). Ph.D. dissertation. Univ. of Calif., Davis, 247 pp.

Olberg, G. 1959. Das verhalten der solitaren Wespen Mitteleuropas (Vespidae, Pompilidae, Sphecidae). Dtsch. Verlag Wiss. Berlin, 401 pp.

O'Neill, K. 1979. Territorial behavior in males of *Philanthus psyche* (Hymenoptera:Sphecidae). Psyche 86: 19–43.

———. 1983. The significance of body size in male territorial interactions of beewolves. Anim. Behav. 31: 404–411.

Powell, J. A. 1964. Additions to the knowledge of the nesting behavior of North American *Ammophila* (Hymenoptera:Sphecidae). J. Kans. Entomol. Soc. 37: 240–258.

Steiner, A. L. 1978. Observations on spacing, aggressive and lekking behavior of digger wasp males of *Eucerceris flavocincta*. J. Kans. Entomol. Soc. 51: 492–498.

Teschner, W. 1959. Starrheit und Variabilitat in Verhalten von Sandwespen. Zool. Beitr. (n.s.) 4: 411–472.

Turner, C. H. 1912. The copulation of *Ammophila abbreviata* Fabr. Psyche 19: 137.