

LATITUDINAL VARIATION
IN PROTANDRY AND PROTOGYNY
IN POLISTINE WASPS *

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Emergence order of males and females has recently received attention because of its importance as a form of sexual selection (WIKLUND & SOLBRECK, 1982) and in the evolution of sociality (BULMER, 1983a; SEGER, 1983). Here we describe widespread protogyny (female before male emergence) in the autumn broods of Texas *Polistes*, a genus of primitively social wasps. Protogyny in Texas contrasts with protandry (male before female emergence) reported for populations farther north (WEST-EBERHARD, 1969; METCALF, 1980).

Protandry is widespread in insects (WIKLUND & FAGERSTRÖM, 1977). It probably evolved through sexual selection since it is most common in seasonal species where males mate multiply and females mate only once upon emergence, so a male emerging before most of the females emerge would encounter and mate with more receptive females (WIKLUND & FAGERSTRÖM, 1977; WIKLUND & SOLBRECK, 1982; BULMER, 1983b; IWASA et al., 1983).

In Hymenoptera (wasps, bees and ants) protandry facilitates what may have been the first step towards eusociality: daughters remaining to help their mothers rear additional siblings (ALEXANDER, 1974; BULMER, 1983a; SEGER, 1983). Haplodiploidy, the genetic system shared by all Hymenoptera, results in females on average sharing 0.75 of their genes with sisters and only 0.25 with brothers so that female Hymenoptera will

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be selected to rear siblings more readily if they are sisters rather than brothers (HAMILTON, 1964, 1967). Protandry (producing daughters last) provides early females with the opportunity to rear sisters rather than brothers and therefore may facilitate the evolution of eusociality (BULMER, 1983a; SEGER, 1983).

In seasonal colonies of social insects the queen rears mainly workers (females) when she is alone at the beginning of the season. Workers rear additional progeny of the queen, which will become workers or reproductive males and females. Both queens and workers may influence emergence order of reproductives. Queens may do so by laying fertilized (female) or unfertilized (male) eggs. Workers may influence emergence order of males and females by eating or not caring for brood of one sex at certain times, by laying eggs of their own or by not working and becoming future queens.

There are at least four hypotheses which address the evolution of emergence order of reproductive females and males in social Hymenoptera. Males may emerge before reproductive females because by doing so they have greater mating success, just as in solitary insects (METCALF, 1980; BULMER, 1983a). This hypothesis requires that females mate once close to the time of emergence, and that some males mate multiply (WIKLUND & FAGERSTRÖM, 1977). Under these circumstances males emerging before most of the females would have more mating opportunities.

Another hypothesis, which applies only to social Hymenoptera, is that by laying male eggs before female eggs, the queen forces workers to rear brood exhibiting an even sex ratio (BULMER, 1981). These workers would prefer to invest up to 3 times more in sisters than brothers because they are 3 times more closely related to sisters than to brothers (TRIVERS & HARE, 1976). Note that this situation differs from the hypothesis on the early steps of sociality discussed above, where the queen herself rears the first brood of males. Here the first brood consists of workers.

Protogyny, or female emergence which on average precedes male emergence, may be the result of greater male than female mortality before mating (M.G. BULMER, pers. comm.). If males are more likely than females to die before mating, later emergence of males may be selected because it shortens the period in which they are subjected to high mortality. Many differences in behavior between males and females could result in greater male mortality before mating. On the other hand if females are more likely to die before mating, protandry, and not protogyny would be selected.

Protogyny may evolve in environments where the number of days available for brood production in a given year is both variable and hard to predict early in the season. If a female can be either a worker or a

reproductive, a colony producing females before males can delay the decision to end brood production. Females can contribute to brood care, but males never do, so additional brood in a colony that has begun to produce many males will not be tended. In a good year females emerging late will be workers and subsequently rear even greater numbers of males and females. In a poor year where conditions are not favorable for late rearing of brood, females of the flexible generation will be reproductives, not workers, and brood production will end earlier. Prey availability may be highly variable and have a great effect on late brood production. This hypothesis is based on the argument that the number of reproductives a colony produces is maximized by producing workers before reproductives (MACEVICZ & OSTER, 1976; OSTER & WILSON, 1978).

Polistes is an especially interesting genus in which to investigate the evolution of emergence order for several reasons. The lack of morphological castes and the ability of workers to mate and become queens mean that conflicts of interest may be especially apparent in *Polistes*. Variation in emergence order with latitude in *Polistes* provides an opportunity for testing hypotheses. Finally this is an especially well-studied genus that has many aspects of its life history described (e.g. PARDI, 1943; RAU, 1946; WEST-EBERHARD, 1969; GIBO, 1978; NOONAN, 1978, 1981). This paper will focus on those North American species for which emergence order has been studied and females have been separated by caste into workers and future queens. These species are *P. metricus* Say and *P. variatus* Cresson in Illinois (40° N; METCALF, 1980), *P. fuscatus* (Fabr.) in Michigan and Ontario (42° N; WEST-EBERHARD, 1969; GIBO, 1978; NOONAN, 1978, 1981) and *P. metricus*, *P. exclamans* Viereck, *P. bellicosus* Cresson, *P. carolinus* (L.) and *P. dorsalis* (Fabr.) in Texas (30° N; STRASSMANN, 1979, 1981a, 1981b, 1984, 1985; LESTER & SELANDER, 1981; STRASSMANN et al., 1984 and unpubl.). In the rest of this paper the Michigan, Illinois and Ontario populations will be referred to as northern and the Texas populations will be referred to as southern.

COLONY CYCLE OF POLISTES

Nests are started in spring by one or more mated females. These females establish a queen or principal egg layer by fighting among themselves (PARDI, 1942; WEST-EBERHARD, 1969). Workers emerge 1½ to 2 months later. In most southern populations a few males also emerge at this time. After zero to four broods of workers reproductive males and females are produced. In northern populations worker to brood relatedness is high (coefficient of relatedness, $r = 0.66$ for *P. metricus*, METCALF & WHITT, 1977), while it is often quite low in southern populations ($r = 0.39$ for *P. exclamans*; $r = 0.43$ for *P. apachus-bellicosus*, LESTER & SE-

LANDER, 1981). Low relatedness of workers to brood in southern populations is the result of death of the original queen who is replaced by a mated worker, satellite nests founded by workers, and multiple egg layers (STRASSMANN, 1985). In northern populations re-nesting upon nest destruction is often impossible because not enough time remains in the season. However in most southern populations, only very few nests survive from spring to autumn; the majority of successful nests are built after the beginning of the season by females whose original nest was destroyed [STRASSMANN, 1981b; but see QUELLER & STRASSMANN, 1986 for *P. annularis* (L.)].

Sex ratios of reproductives adjusted for weight differences in males and females are 1:1 in the northern species (NOONAN, 1978; METCALF, 1980) and female-biased in a southern population of *P. exclamans* (STRASSMANN, 1984). Studies of *P. metricus*, *P. variatus*, *P. apachus* Sausure and *P. fuscatus* found that males emerge before females on average (Table 1; WEST-EBERHARD, 1969; METCALF, 1980; METCALF & FINER in BULMER, 1983a). *P. exclamans* in Texas exhibits protogyny; all females typically emerge before the first males of the autumn brood from any given nest, though all nests in the population are not completely synchronized (STRASSMANN, 1984).

Future queens that are about to mate and hibernate differ from workers in time of emergence, behavior, fat body appearance and ability to tolerate cold (EICKWORT, 1969; WEST-EBERHARD, 1969; METCALF, 1980; STRASSMANN et al., 1984).

Males leave the nest before females and go to hibernacula (RAU, 1929; WEST-EBERHARD, 1969). At or near the hibernaculum some males set up mating territories while others patrol for mates (WEST-EBERHARD, 1969; LIN, 1972; TURILLAZZI & CERVO, 1982; POST & JEANNE, 1983). Sometimes males wait around the entrance to a hibernaculum and pounce *en masse* on arriving females (RAU, 1929). Females arrive before the onset of cold weather, mate and then cluster in groups over winter (RAU, 1931, 1946; WEST-EBERHARD, 1969; STRASSMANN, 1979). Wasps present at a hibernaculum together number from 10 to several thousand (RAU, 1928, 1930, 1931 and pers. obs.). Electrophoretic evidence from *P. metricus* indicates that while some females mate more than once, one male accounts for 90% of the daughters (METCALF & WHITT, 1977).

METHODS

P. metricus Say, *P. carolinus* (L.), *P. bellicosus* Cresson and *P. dorsalis* (Fabr.) (Hymenoptera Vespidae) were investigated in 1983 and 1984 at Brazos Bend State Park, 42 miles southwest of Houston, Texas. Concurrent studies on *P. exclamans* Vierek are not included because the results did not differ from those previously reported for a population of this species in Austin, Texas (STRASSMANN 1981a, 1984).

Table 1.
Emergence dates of northern American Polistes.

Species	Reproductive females		Males		Location	Reference
	Mean emergence date	Range	Mean emergence date	Range		
<i>P. fuscatus</i>	1 Sept.	1 Aug.-10 Sept.	10 Aug.	1 Aug.-5 Sept.	Michigan	WEST-EBERHARD, 1969
<i>P. variatus</i>	5 Sept.		28 Aug.		Illinois	METCALF, 1980
<i>P. metricus</i>	5 Sept.	mid. Aug.-mid Oct.	28 Aug.	mid Aug.-early Oct.	Illinois	METCALF, 1980
<i>P. apachus</i>	early Oct.	mid Aug.-mid Nov.	mid Sept.	mid Aug.-mid Nov.	Davis, Calif.	METCALF & FINER in BULMER, 1983

Nests were studied mainly in wooden nest boxes that were nailed to trees or on metal stakes about 4 ft high in tallgrass coastal prairie and oak bottom lands (STRASSMANN et al., unpubl.). In 1983 nests were censused weekly. In 1984 nests were censused monthly. The 1983 census dates that are reported were chosen to match those available for 1984.

The autumn brood of males and females is defined as those females that will mate, hibernate and begin new nests the next spring, and males that mate with these females. The autumn brood was distinguished from males that emerged earlier and female workers by emergence date, lack of further brood in the nest when the autumn brood was emerging, and lethargic behavior of females of this brood.

In September, 1984, emergence order of males and females in the autumn brood was determined by counting numbers of newly-emerged individuals of each sex (determined by their black eye color). Status of the females as reproductives and not workers at this time was determined by examining the fat bodies of a sample in the field. This can be done using a handlens and is a reliable indicator of caste (STRASSMANN et al., 1984). Females emerging at this time were found to be reproductives that will mate and overwinter before beginning nests.

RESULTS

P. carolinus nests did not produce males until August (Fig. 1, Table 2). In September and October on average four to 15 males emerged from those nests producing males (Fig. 2). *P. metricus*, *P. bellicosus*, and *P. dorsalis*, produced males along with early broods of worker females (Fig. 1). Eight to 29% of nests produced an average of one to three males in May and June (Fig. 1). However the majority of males were produced at the end of the colony cycle in August through October (Fig. 2). *P. metricus*, *P. bellicosus* and *P. dorsalis* also exhibited protogyny in the autumn brood (Fig. 3). This was most surprising for *P. metricus* because it is protandrous in Illinois (Table 1; METCALF, 1980). Most nests did not produce further females after males began to emerge (Fig. 3). Two *P. metricus* and two *P. bellicosus* nests were producing only females at this time, and had probably not yet begun to produce males. Thus only two nests of *P. bellicosus* and one nest of *P. carolinus* were producing a majority of females in the autumn brood after male emergence had begun. In addition to these data, observations of nests at the time of other censuses in 1983 and 1984 indicated that nests producing males of the autumn brood generally had ceased producing females. When young (black-eyed) males were present on a nest, young females were usually absent, and there was an abundance of inactive reproductive females that had already emerged.

It appeared that brood production ended earlier in *P. metricus*, *P. bellicosus* and *P. dorsalis* than in *P. carolinus* (Table 2; STRASSMANN et al., unpubl.).

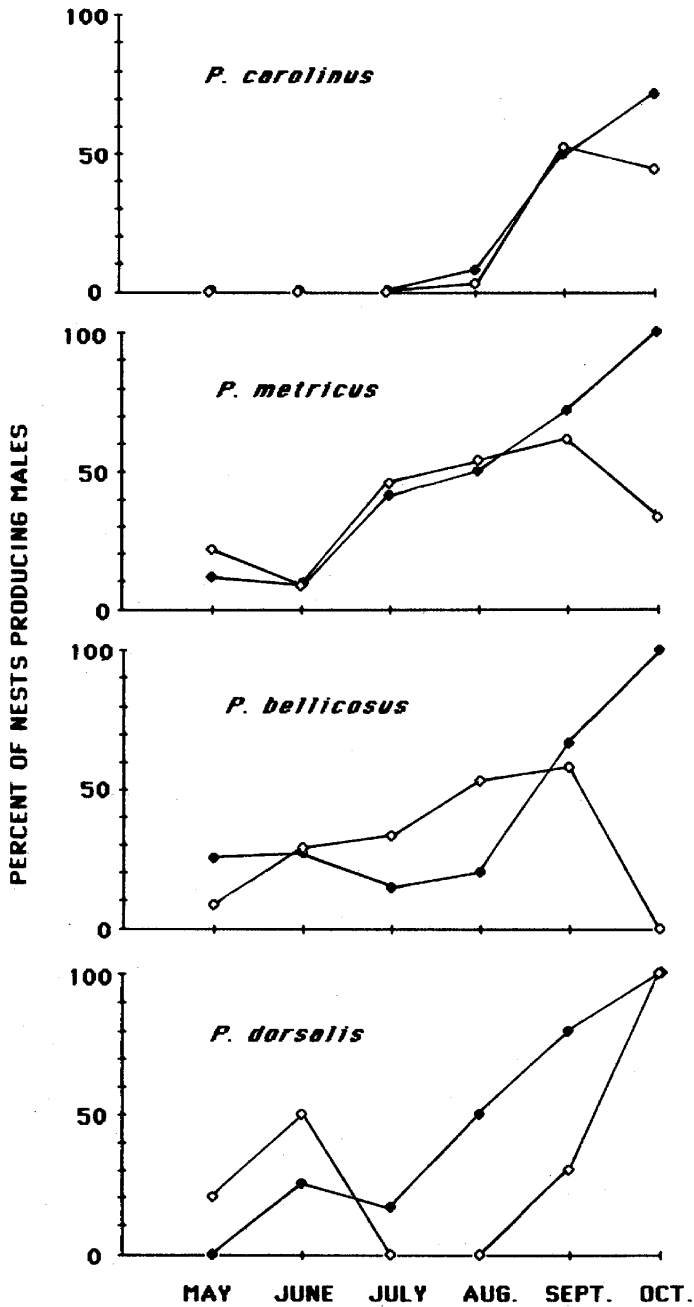


Fig. 1. — Percent of all nests producing males. Solid dots are for 1983 and open dots are for 1984. All censuses were taken during the last 10 days of each month. Sample sizes are given in Table 2.

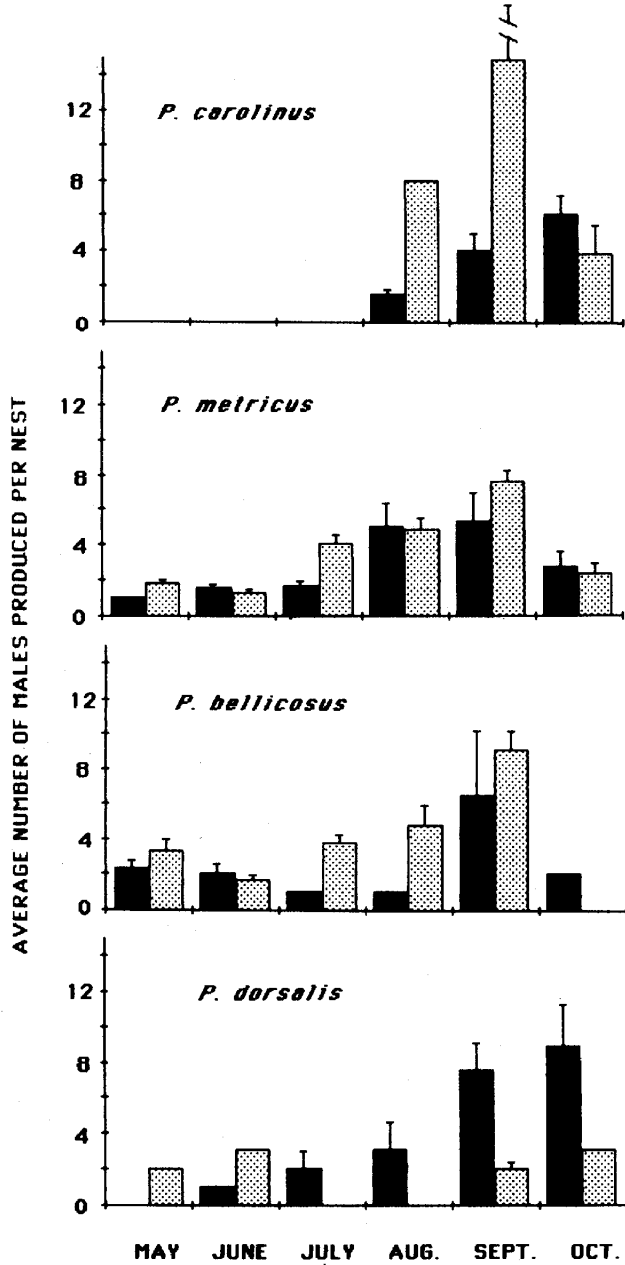


Fig. 2. — Mean numbers of males emerging from nests producing males. Solid bars are for 1983 and shaded bars are for 1984. Standard errors are indicated. All censuses were taken during the last 10 days of each month.

Table 2.
Numbers of nests censused at each date.

Species	Year	May	June	July	Aug.	Sept.	Oct.
<i>P. carolinus</i>	1983	25	25	24	25	16	14
	1984	27	24	12	34	23	9
<i>P. metricus</i>	1983	26	25	17	16	7	3
	1984	111	86	33	54	46	9
<i>P. bellicosus</i>	1983	12	11	7	5	3	1
	1984	36	31	15	15	36	5
<i>P. dorsalis</i>	1983	6	8	6	6	5	4
	1984	4	2	2	2	10	1

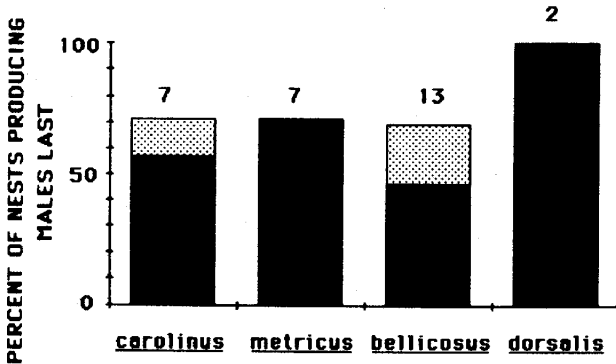


Fig. 3. — Percent of nests producing only males after male production is initiated in the autumn brood is given by the solid bars. Shaded areas indicate nests producing a majority of males at this time. Sample sizes are given over the bars.

Females of all species observed remained on their nests until late October or November when they went to hibernacula, usually after one or two cold fronts of below 10 °C. Mating takes place some time afterwards since mated females were never found on their nests in autumn. That mating may take place well into the winter is suggested by the considerable abilities of males to tolerate cold (STRASSMANN et al., 1984).

DISCUSSION

The best hypothesis on the evolution of emergence order in *Polistes* should predict protandry in the north and protogyny in the south. It is likely that the explanation will involve environmental differences since all

southern species thus far studied are protogynous, even though they come from two different subgenera, one of which is the only subgenus represented in the northern studies (*P. fuscatus*, *P. variatus*, *P. metricus*, *P. carolinus*, *P. bellicosus* and *P. dorsalis* in *Fuscopolistes* and *P. exclamans* in *Aphanilopterus*, RICHARDS, 1978), and because of the differences within *P. metricus*. The hypotheses that will be discussed are sexual selection, relative male and female mortality before hibernation, worker-queen conflict over investment in males and females, and temporally variable environments.

Since *Polistes* females do not mate on emergence, but wait until they retreat to hibernacula and then mate at roughly the same time, males emerging earlier will not encounter more receptive females. Females sometimes mate multiply (METCALF & WHITT, 1977). Thus the preconditions of the sexual selection hypothesis for protandry are not met in *Polistes*. Only if early emergence increases the ability of a male to obtain a high quality territory at a hibernaculum or provides some other mating advantage could sexual selection explain protandry in these species. Since there are no reported differences in mating between northern and southern species (WEST-EBERHARD, 1969; LIN, 1972; TURILLAZZI & CERVO, 1982; POST & JEANNE, 1983), this hypothesis would predict protandry for both locations.

Males of southern populations spend more time as adults before females are available for mating at hibernacula than is the case in northern populations. Greater male than female mortality before mating in southern populations would select for protogyny in the south. While hard to measure, it is reasonable to suppose that males are more vulnerable before hibernation than females. Males leave the natal nest before females, and so may suffer greater mortality from predators. Males are often seen dead in spider webs. Females by contrast remain largely quiescent on their natal nests until hibernation, leaving them only to forage for nectar.

Workers will be in greater conflict with the queen over the sex ratio of the brood in northern populations where siblings of the workers are reared on a majority of nests, than in southern populations where workers on most nests are rearing nieces and nephews. This is because a female is asymmetrically related to brothers ($r = 0.25$) and sisters ($r = 0.75$) and similarly related to nieces and nephews ($r = 0.375$). Therefore in northern populations workers will prefer to invest as much as 3 times more in sisters than brothers while the queen will prefer equal investment in the sexes (TRIVERS & HARE, 1976; PAMILO, 1982; BULMER, 1983c). Since workers are equally related to nieces and nephews, the most common brood in southern nests, their sex ratio preferences will not differ from those of the queen. According to this hypothesis protandry is predicted in northern and not southern populations, as is observed.

If a female can become a worker or a future queen on emergence, producing females before males means the decision to end brood production can be delayed for 2 or 3 weeks longer than it could if males were produced simultaneously with females, or before females. Under unpredictable conditions for brood rearing at the end of the season such flexibility may result in greater numbers of reproductives produced. This is because total numbers of reproductives produced by a colony is maximized when workers emerge before reproductives (MACEVICZ & OSTER, 1976). However if the colony is unlikely to survive to reproductive emergence, more overlap between workers and reproductives may result in maximum production of progeny (GREENE, 1985). This hypothesis requires that southern populations experience more variable conditions than northern ones.

No one hypothesis predicts both protogyny in the south and protandry in the north. The hypothesis that protandry is the result of queens forcing workers to invest equally in brothers and sisters agrees with observed north-south differences in emergence order and relatedness. Further studies on autumn behavior of males and females are necessary to investigate sexual selection and relative male and female mortality as explanations for emergence order. Such studies should measure male and female mortality after emergence but before mating, the role of age in male mating success, details of mating behavior, and latitudinal variation in these variables. To investigate whether or not an unpredictable number of days for brood production has resulted in protogyny, latitudinal variation in rainfall, prey availability and other variables important in brood production need to be measured.

SUMMARY

Polistes wasps (Hymenoptera Vespidae) are protogynous in the south (30°N) and protandrous in the north (42°N) of America. Sexual selection is unlikely to account for protandry because females do not mate soon after emergence, and sometimes mate multiply. North-south differences in both emergence order and relatedness of workers to brood fit the hypothesis that protandry is the result of worker conflict with the queen over the sex ratio. Protandry allows the queen to determine the sex ratio.

Protogyny could be the result of greater male than female mortality prior to mating. It could also be the result of a variable and unpredictable number of days for brood production, if females can become either workers or reproductives until late in their development. In this case protogyny would allow the decision to produce reproductives rather than workers to be delayed for a few more weeks.

Texas populations of *P. metricus* Say, *P. bellicosus* Cresson, *P. dorsalis* (Fabr.) and *P. exclamans* Vierek all produce males in May, June and July and in greater numbers in August, September and October. *P. carolinus* (L.) has not been found to produce males before August. The early males mate with workers that become queens on many nests in the middle of the season. Some of these males may survive to mate with future queens in autumn.

RIASSUNTO

Nelle vespe del genere *Polistes* (Hymenoptera Vespidae) dell'America del Nord le femmine compaiono prima dei maschi («protoginia») a Sud (30°N), mentre a Nord (42°N) i maschi compaiono prima delle femmine («protandria»). Che la «protandria» risulti da una selezione sessuale è improbabile, dal momento che le femmine non si accoppiano immediatamente dopo lo sfarfallamento e, in qualche caso, si accoppiano più volte. Le differenze fra Nord e Sud, sia nell'ordine di sfarfallamento che nel grado di parentela delle operaie con le larve, sono in accordo con l'ipotesi che la «protandria» risulti da un conflitto tra operaie e la regina per la sex ratio. Con la «protandria» è la regina a determinare la sex ratio.

La «protoginia» potrebbe derivare da una maggiore mortalità dei maschi rispetto alle femmine prima dell'accoppiamento, oppure da una durata variabile, impossibile da predire, dello sviluppo delle larve, se le femmine fossero in grado di divenire tanto operaie quanto regine fino a sviluppo avanzato. In tal caso, la «protoginia» permetterebbe di ritardare per qualche settimana ancora la decisione di produrre regine piuttosto che operaie.

Le popolazioni texane di *P. metricus* Say, di *P. bellicosus* Cresson, di *P. dorsalis* (Fabr.) e di *P. exclamans* Vierek producono tutte maschi in maggio, giugno, luglio e, in maggior numero, in agosto, settembre, ottobre. *P. carolinus* (L.), per quanto si sa, non produce maschi prima di agosto. I maschi comparsi precocemente si accoppiano a metà della stagione con operaie che divengono regine su molti nidi. Alcuni di questi maschi possono sopravvivere fino ad accoppiarsi in autunno con le future regine.

REFERENCES

- ALEXANDER, R.D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. & Syst.* 5: 325-383.
 BULMER, M.G. 1981. Worker-queen conflict in annual social Hymenoptera. *J. theor. Biol.* 93: 239-251.
 BULMER, M.G. 1983a. The significance of protandry in social Hymenoptera. *Am. Nat.* 121: 540-551.

- BULMER, M.G. 1983b. Models for the evolution of protandry in insects. *Theor. Populat. Biol.* 23: 314-322.
- BULMER, M.G. 1983c. Sex ratio evolution in social Hymenoptera under worker control with behavioral dominance. *Am. Nat.* 121: 899-902.
- EICKWORT, K. 1969. Separation of the castes of *Polistes exclamans* and notes on its biology (Hym.: Vespidae). *Insectes soc.* 16: 67-72.
- GIBO, D.L. 1978. The selective advantage of foundress associations in *Polistes fuscatus* (Hymenoptera: Vespidae): a field study of the effects of predation on productivity. *Can. Ent.* 110: 519-540.
- GREENE, A. 1985. Production schedules of vespine wasps: an empirical test of the bang-bang optimization model. *J. Kans. ent. Soc.* 57: 545-568.
- HAMILTON, W.D. 1964. The genetical evolution of social behaviour, I. *J. theor. Biol.* 7: 1-16.
- HAMILTON, W.D. 1967. Extraordinary sex ratios. *Science, Wash.* 156: 477-488.
- IWASA, Y., F.J. ODENDAAL, D.D. MURPHY, P.R. EHRLICH & A.E. LAUNER 1983. Emergence patterns in male butterflies: a hypothesis and a test. *Theor. Populat. Biol.* 23: 363-379.
- LESTER, L.J. & R.K. SELANDER 1981. Genetic relatedness and the social organization of *Polistes* colonies. *Am. Nat.* 117: 147-166.
- LIN, N. 1972. Territorial behavior among males of the social wasp, *Polistes exclamans* Viereck. *Proc. ent. Soc. Wash.* 74: 148-155.
- MACEVICZ, S. & G.F. OSTER 1976. Modeling social insect populations. II: Optimal reproductive strategies in annual eusocial insect colonies. *Behav. Ecol. & Sociobiol.* 1: 265-282.
- METCALF, R.A. 1980. Sex ratios, parent-offspring conflict and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. *Am. Nat.* 116: 642-654.
- METCALF, R.A. & G.S. WHITT 1977. Intra-nest relatedness in the social wasp, *Polistes metricus*. *Behav. Ecol. & Sociobiol.* 2: 339-351.
- NOONAN, K.M. 1978. Sex ratio of parental investment in colonies of the social wasp, *Polistes fuscatus*. *Science, Wash.* 199: 1354-1356.
- NOONAN, K.M. 1981. Individual strategies of inclusive-fitness-maximizing in *Polistes fuscatus* foundresses, pp. 18-44. In: R.D. Alexander & D.W. Tinkle, Edits. *Natural selection and social behavior: recent research and new theory*. New York: Chiron, 532 pp.
- OSTER, G.F. & E.O. WILSON 1978. *Caste and ecology in the social insects*. Princeton: Princeton University Press, 352 pp.
- PAMLO, P. 1982. Genetic evolution of sex ratios in eusocial Hymenoptera: allele frequency simulations. *Am. Nat.* 119: 638-656.
- PARDI, L. 1942. Ricerche sui polistini. V. La poliginia iniziale di *Polistes gallicus* (L.). *Boll. Ist. Ent. Univ. Bologna* 14: 1-106.
- PARDI, L. 1943. Ricerche sui Polistini. 6. Sulla sproporzione numerica dei sessi nei nidi dei Polistini. *Processi verb. Soc. tosc. Sci. nat. Pisa* 52 (2): 1-9.
- QUELLER, D.C. & J.E. STRASSMANN 1986. Reproductive success and group nesting in the paper wasp, *Polistes annularis*. In: T. Clutton-Brock, Edit. *Reproductive success*. Chicago (in press).
- POST, D.C. & R.L. JEANNE 1983. Male reproductive behavior of the social wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). *Z. Tierpsychol.* 62: 157-171.
- RAU, P. 1928. Autumn and spring in the life of the queen *Polistes annularis* and *P. pallipes*. *Bull. Brooklyn ent. Soc.* 23: 230-235.
- RAU, P. 1929. At the end of the season with *Polistes rubiginosus* (Hym.: Vespidae). *Ent. News* 40: 7-13.

- RAU, P. 1930. The behavior of hibernating *Polistes* wasps. *Ann. ent. Soc. Am.* 23: 461-466.
- RAU, P. 1931. An additional note on the behavior of hibernating *Polistes* wasps. *Ann. ent. Soc. Am.* 24: 515-518.
- RAU, P. 1946. The nests and the adults of colonies of *Polistes* wasps. *Ann. ent. Soc. Am.* 39: 11-27.
- RICHARDS, O.W. 1978. The social wasps of the Americas excluding the Vespidae. London: British Museum (Natural History), 584 pp.
- SEGER, J. 1983. Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature, Lond.* 301: 59-62.
- STRASSMANN, J.E. 1979. Honey caches help female paper wasps *Polistes annularis* survive Texas winters. *Science, Wash.* 204: 207-209.
- STRASSMANN, J.E. 1981a. Evolutionary implications of early male and satellite nest production in *Polistes exclamans* colony cycles. *Behav. Ecol. & Sociobiol.* 8: 55-64.
- STRASSMANN, J.E. 1981b. Parasitoids, predators and group size in the paper wasp, *Polistes exclamans*. *Ecology* 62: 1225-1233.
- STRASSMANN, J.E. 1984. Female-biased sex ratio in social insects lacking morphological castes. *Evolution, Lawrence, Kans.* 38: 256-266.
- STRASSMANN, J.E. 1985. Worker to brood relatedness in the social wasp, *Polistes exclamans*. *Z. Tierpsychol.* 69: 141-148.
- STRASSMANN, J.E., R.E. LEE JR., R.R. ROJAS & J.G. BAUST 1984. Caste and sex differences in cold-hardiness in the social wasps, *Polistes annularis* and *Polistes exclamans* (Hymenoptera: Vespidae). *Insectes soc.* 31: 291-301.
- WEST-EBERHARD, M.J. 1969. Social biology of polistine wasps. *Misc. Publs Mus. Zool. Univ. Mich.* 140: 1-101.
- TURILLAZZI, S. & R. CERVO 1982. Territorial behaviour in males of *Polistes nimpha* (Christ) (Hymenoptera, Vespidae). *Z. Tierpsychol.* 58: 174-180.
- TRIVERS, R.L. & H. HARE 1976. Haplodiploidy and the evolution of the social insects. *Science, Wash.* 191: 249-263.
- WIKLUND, C. & T. FAGERSTRÖM 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* 31: 153-158.
- WIKLUND, C. & C. SOLBRECK 1982. Adaptive versus incidental explanations for the occurrence of protandry in a butterfly, *Leptidea sinapis* L. *Evolution, Lawrence, Kans.* 36: 56-62.

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