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## VESTIGIAL PLEOMETROSIS IN THE NORTH AMERICAN *POLISTES PALLIPES* LEPELETIER.

By J. BEQUAERT, New York, N. Y.

In the October-December, 1919, issue of this BULLETIN my esteemed friend, Mr. Wm. T. Davis, has published some observations of the common American social wasps, a most welcome addition to the scanty literature of the subject in America. Among other interesting points, he relates several cases in which two, three, or four queens of the common Eastern *Polistes pallipes* Lepeletier (= *metrica* Say; *variatus* Say) had worked together in establishing a new colony, though in this as in other species of *Polistes* each queen as a rule starts her nest alone.

The founding of a new colony among social Hymenoptera by two or more fecundated females is nowadays usually called "pleometrosis," following Wasmann's terminology. When it occurs among strictly monogynous wasps, as with *Polistes*, it is well worthy of careful investigation, since it evidently is then one of those vestigial instincts whose study is of great value for a proper understanding of the evolution of animal behavior (Wheeler, 1908).

During the spring and summer of 1918, Mr. John Treadwell Nichols, Curator of Ichthyology at the American Museum of Natural History, observed the nesting habits of *Polistes pallipes*, and he has very kindly communicated his notes to me for publication. The several nests found by him and described below were all located under boards in a grassy field at Mastic, Long Island, N. Y.

1. A first group of three *Polistes* nests was found on May 12 under one of the boards. The weather being foggy and cold, the

Behavior (social)  
Hymenoptera - Vespidae - Vespinae

mother wasps were clinging around the pedicel of their respective nests and could be captured without difficulty. All three nests had been recently started. The first was about 8 mm. in diameter and consisted of five cells of the usual width, but only about 5 mm. high, each containing an egg placed vertically in the bottom; it was attended by *one* female. The second, also occupied by *one* female wasp, measured about 11 mm. in diameter, consisting of seven cells not over 6 mm. high and each with an egg. The third nest, however, was considerably larger than its neighbors, reaching 14 mm. in diameter, with eleven cells, each with its egg, the central cell 8 mm. high; *two* queen wasps were found on this nest, which fact probably accounts for the larger size of the structure.

2. Another group of four *Polistes* nests was discovered under another board in the same field on May 19. At my suggestion, these nests were left with their inhabitants, their condition being noted from time to time by Mr. Nichols, with a view of ascertaining whether the presence of more than one queen is really of some advantage to the progress of the community. The history of each of these four nests is as follows:

Nest (*a*) consisted on May 19 of ten cells and was occupied by *two* queens, each cell containing an egg. On May 27, fourteen cells. On June 8, seventeen cells, some with rather large larvae. On June 22, nineteen cells, one of them closed above the full-grown larva. On June 29 the nest was in much the same condition, but it had fallen to the ground and only one of the queens was present. It was not observed after that date.

Nest (*b*) on May 19 of eight cells, attended by *one* female. On May 27, eleven cells with eggs or very small larvae, and a twelfth cell just started. This nest was not further observed.

Nest (*c*) on May 19 of seventeen cells, with *two* females. On May 27, nineteen cells. On June 22, nineteen cells with eggs or very young larvae, the two queens still present. On June 29, twenty cells with larvae, two queens. On July 16, some of the cells were sealed above full-grown larvae; two queens present. On August 19, many of the cells were sealed up and, in addition to the two mother wasps, five newly hatched workers were present. This nest was taken home at that date and a number of males were bred from it at the end of August.

Nest (d) on May 19 of eight or nine cells, with one female. On May 27, fourteen cells. On June 8, nineteen cells, some with rather large larvae. On June 22, twenty-one cells, two in the center being closed with a cap and one of them empty; a newly hatched worker was found on the nest together with the queen. On June 29 the nest was in much the same condition and it was not observed after that date.

The advantages gained by the presence of two mother wasps in one colony are not very striking in these cases, but the observations are too fragmentary to warrant any conclusion. It would be extremely interesting to have such experiments repeated on a much larger number of colonies and over several successive years, so as to eliminate the possible influence of seasonal conditions. At any rate, Mr. Nichols' observations tend to show that pleometrosis must be of rather common occurrence with *Polistes pallipes*. Yet this way of starting a new colony has been but rarely mentioned in this species, perhaps because most observers did not deem the fact worth noticing. In addition to Mr. Davis' observations mentioned above (1919), I have only been able to find the following remark by G. and E. Peckham (1898, p. 177): "We have, in several instances, seen two or three queens of our *Polistes fusca*<sup>1</sup> join together and utilize a nest of the preceding year, each one clearing up three or four cells wherein to start her colony, while close by other queens were starting new nests, each building one for herself, being unable to find anything that suited her among the numerous old ones that hung about the place." In connection with this remark, I want to point out that in all of Mr. Nichols' observations two queens were associated in building new nests afresh and not in appropriating old ones. Miss Enteman (1902, p. 340, footnote; and 1904, pp. 17-19), in Illinois, also observed that two and even three females of *Polistes variatus* Cresson, a color form of *P. pallipes*, coöperated in the founding of a nest; she describes in detail the color variation of the offspring of two nests, each founded by two queens.

The starting of a new nest by two or several females has re-

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<sup>1</sup> This name probably refers to one of the forms of *P. pallipes* Lepeletier. [J. B.]

peatedly been observed in other, exotic members of the genus *Polistes*, though always as an exception. Concerning the common European species, *Polistes gallicus* (Linnaeus), C. T. v. Siebold (1871) states that in four years' observations he found among several hundreds of nests in southern Germany only two colonies with two queens each. P. Marchal (1896, p. 21) observed even three and four queens on some nests. Janet (1903, p. 65) and C. Schmitt (1919, p. 117) have recorded further instances of pleometrosis in this wasp. In a very interesting case, described by Ferton (1901, pp. 128-129), the females of eight nests of this *Polistes* were apparently mixed, so that they would go indifferently from one nest to another. Of the South American *Polistes versicolor* Fabricius, H. von Ihering (1896) says that in Rio Grande do Sul, Brazil, he repeatedly found in the spring a female together with workers on a newly started nest. I believe that these, too, were cases of pleometrosis, since in the tropical *Polistes* it is often hardly possible to distinguish externally workers from fertile females, and in some of the species it is even doubtful whether a differentiated worker caste is present.

Pleometrosis has also been recorded by P. and N. Rau (1918, pp. 286-288) for the large North American *Polistes annularis* (Linnaeus). Near St. Louis, Missouri, they found on one occasion in the spring several females of this wasp congregating on old nests, as many as 16 being seen clustering on one nest. I doubt, however, whether these wasps intended starting new colonies in that manner; but in the vicinity of these old nests the Raues also observed four new ones, one of these with one queen, one with two, and two with four queens.

The term "pleometrosis" used in the title of this note was originally defined by Wasmann (1910) as "the occurrence of several queen ants of the same species or race in one colony." It can, however, be conveniently extended to other social Hymenoptera and is then the equivalent of "polygyny." Reuter (1913) and Roubaud (1916) have called "polygyny" a condition where several fertile females are present in one colony of wasps, regardless of the manner in which the nest originated, there usually being in such cases no morphological nor physiological differentiation into castes. In monogynous wasp societies, on the other hand, but a

single queen is found in each nest, since there is a difference in structure, or in function, or in both between the fertile females and the worker caste.<sup>1</sup> Polygynous insect societies need not of necessity be founded by several fertile females, as is shown by the African wasps of the genus *Belonogaster*, in which there are apparently no true workers, all the females of the nest being externally alike and physiologically equal, capable of being fecundated and of producing mature eggs. Yet in *Belonogaster* a new nest is, as a rule, started by an isolated female, though often two or more queens may associate to found a new society: the single female who started the colony is then joined by other, foreign females at an early period in the construction of the nest; new nests may even originate through swarming, a number of fecundated females leaving together an old nest in order to start a new one (Roubaud, 1916).

Wasmann distinguishes between primary pleometrosis, in which two or more females of the same species or race unite to found a new colony, and secondary pleometrosis. This latter condition may arise either through inbreeding of queens newly hatched in the colony and fecundated in or near the nest; or through subsequent adoption of foreign queens from other colonies of the same species or race; or again through fusion of several neighboring colonies.

The known methods by which a new colony may arise among social Hymenoptera can all be grouped under one of the following three headings (see Crawley and Donisthorpe, 1913):

(1) *Haplometrosis* (Wasmann): a single fecundated female, or queen, seeks a suitable shelter, starts a nest, and raises a new brood of workers alone. This is by far the most common method among the Formicidae, where the female, after the marriage flight, drops her wings, retires into hiding, and founds a new formicary. It is also the rule among many monogynous social bees (*Bombus*) and wasps (*Vespa*, *Polistes*, etc.).

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<sup>1</sup> The terms "polygyny" and "monogyny," as applied to social insects, were proposed by Reuter (1913) to replace those of "polygamy" and "monogamy" used with a similar meaning by R. and H. von Ihering. Reuter's terminology is evidently more appropriate and less misleading.

(2) *Primary pleometrosis*: two or several fecundated females start a new colony together. A number of such cases have been described among ants (Wheeler, 1917), but with these insects they are exceptional, and in most cases such formicaries become later monogynous again; one of the queens kills the others, or the colony divides up into two or more societies each with its own queen. It is, however, of rather common occurrence with many of the tropical social Vespidae of the subfamily Polybiinae (Epiponinae), where new colonies are often started by swarms of females and workers leaving the old nest.

The honey-bees (*Apis*) and the Meliponidae also found new communities through swarming, but the procedure in this case is somewhat intermediate between haplometrosis and pleometrosis. Though in these social bees each new colony is, as a rule, founded by a single fecundated queen, she is nevertheless accompanied in the swarm by a detachment of workers, or sterile females, who help considerably in establishing the new hive. It would thus seem that swarming is a primitive habit of social Hymenoptera and dates back from a time when there was as yet no differentiation into castes and pleometrosis was the rule. Among tropical social bees, owing to favorable climatic conditions permitting perennial colonies, swarming was retained and even used to new ends after a worker caste had been developed.

(3) *Allometrosis* (Forel): the female seeks a nest of another species and succeeds in being adopted by this strange colony, whose members bring up her brood. Such cases of social parasitism are thus far only known among ants: they may be temporary, the host colony dying out in course of time after the host queen has been eliminated, so that a pure colony of the intruding female remains; or permanent, the mixed character of the colony being kept up, this condition also presenting various modifications.

I am much in favor of H. von Ihering's and Roubaud's opinion that, among the Vespidae at least, the evolution of solitary into social instincts did not proceed from the habit commonly observed in many solitary wasps of building their nests in close proximity, the isolated nests of different females thus tending to merge gradually, so to speak, into larger, common structures cared for by



several females; but that it was rather the outcome of a tendency of the young wasps to stay with their mother upon emerging from the nest (see also Wheeler, 1922, XV, p. 131). These primitive polygynous societies, upon becoming more populous, tended to divide by pleometrosis, the haplometrotic or monogynous condition being much more specialized and of a later date. In true solitary Vespidae (Eumeninae and Zethinae), each mother wasp cares alone for her nest: in the immense majority of species the egg is laid, the food for the young stored, and the cell closed up in a very short time, and the mother rarely, if ever, comes in contact with any of her offspring. Only when certain forms took to nursing, or to provisioning their cells gradually, bringing in prey as the growth of the larva progressed, was an opportunity given to the building up of family groups where the newly hatched offspring could be induced to remain with their mother and coöperate in keeping up the care of the nest. Along the evolutionary road which led from these crude associations to the complicated societies of some of the present-day species the splitting up of a colony into new social units through pleometrotic swarming must have been an important milestone. For this reason it is worth while to investigate whatever vestiges of pleometrosis may be left in the behavior of the present haplometrotic species.

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