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SEASONAL DEVELOPMENTAL CYCLE AND CASTE DIFFERENTIATION IN THE SOCIAL WASP Polistes gallicus L. (HYMENOPTERA, VESPIDAE). I. PHENOLOGY AND LIFE CYCLE REGULATION

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The extensive genus of social wasps *Polistes* Latr. comprises more than 150 species, two thirds of which live exclusively in the tropics. The species of the temperate latitudes, however, have been studied more fully and in greater detail. Polistine wasps are a favorite subject for study of the biology and behavior of social wasps. This is due to their distribution ranges in countries with a temperate climate, and also to a number of features of their biology that facilitate observations of these wasps (the small size of their colonies, the absence of a nest envelope). Moreover, in their social organization Polistine wasps occupy an intermediate position between presocial and semisocial insects on the one hand and groups attaining high degrees of sociality in their evolution on the other (Wilson, 1971). This made it possible for Evans (1958) to call the genus *Polistes* the "key" genus for understanding the evolution of social behavior in wasps. All this explains the mounting interest from the middle of our century in Polistine wasps, the abundance of works devoted to them and the fact that among the social wasps this group at the present time has been most studied (see the reviews: West-Eberhard, 1969; Wilson, 1971; Spradbery, 1973). Some important aspects, however, of the social organization of Polistine wasps are as yet far from having been adequately studied. This applies, for example, to the processes of caste differentiation. The views of individual authors on the causes and factors that bring about the development of individuals of different castes and that are responsible for the characteristics of their behavior and physiology are very varied, which is to be explained by inadequate investigation (especially experimental) of this problem. At the same time study of the mechanisms of caste differentiation is essential for a correct understanding of the evolution of social behavior in wasps and other social insects. To fill this gap the present work has undertaken, which is to be published in the form of a series of papers.

The life cycles of Polistine wasps in a temperate climate are very similar and have the following features: clearly manifested seasonal variation and connected with it synchronism of the development cycles of the individual colonies; a shorter development cycle of the colony, as compared with tropical species; separation of

the incubation periods of workers and reproductive individuals; and survival of young fertilized female wasps, the foundresses of the nests, in the adverse winter period in a diapause condition. All these characteristics are lacking in the tropical species and constitute adaptations to the climatic conditions of the temperate latitudes (West-Eberhard, 1969).

The developmental cycle of the wasp colony from the time it is founded to its complete disintegration at the end of summer can be divided into several periods. We propose the following terms for these periods, which differ somewhat from those employed in the foreign literature (West-Eberhard, 1969; Yamane and Kawamishi, 1975) and which are more suitable for use in the Russian language.

I. The period prior to the appearance of workers (ante-ergate period). This period extends from the time of the establishment of the nest to the emergence of the first adults of the new generation, which are always workers and correspond to the duration of preimaginal development at a given temperature (40-50 days); characteristic of it is the absence in the nest of free cells beneath the pupae.

II. The period of growth and maturation begins with the appearance of the first worker wasps. At this time construction of new nest cells proceeds intensively and the fecundity of the queen attains the maximum. The number of workers also increases. Small peripheral cells with eggs are visible in the nest and also empty cells in the center of the comb.

III. The period of maturity and disintegration begins with the appearance of males and overwintering females, the future foundresses. It is characterized by an increase in the number of empty cells, emergence from the pupae of increasing numbers of reproductive individuals, the gradual disappearance of the brood, and disintegration of the colony. Henceforth for the sake of brevity we shall refer to these as the first, second and third periods.

Furthermore, in the annual cycle of Polistine wasps we can distinguish an autumn period, when pairing and preparation of the fertilized females for overwintering takes place, the overwintering period and the period of spring activation of the foundress-females, their maturation and preparation for nesting. These periods, however, are not a part of the development cycle of the colony and have not been specially studied in this work.

Establishment of the nest may be undertaken either by a single foundress (haplometrosis) or by a group of females (pleometrosis). In the latter case, only one of the wasps becomes the egg-laying queen, while the rest serve as workers. Particularly close attention has been paid to the period of the establishment of the nest and the interrelationships of the foundress wasps prior to the appearance of true workers (Pardi, 1958; Hermann, 1975; Gamboa, 1978; Gibo, 1978). There are, however, also studies of the complete life cycle of different species of Polistes. These have been undertaken mainly in the USA, Italy and Japan. These works have been concerned with the study of *P. antennalis* Peres and *P. fadwigae* Dalla Torre (Yoshikawa, 1954), *P. canadensis* and *P. fuscatus* (West-Eberhard, 1969), *P. biglumis* (Yamane and Kawamishi, 1975), *P. metricus* (Bohm and Stockhammer, 1977), and finally *P. gallicus* (Turrilazzi, 1980). In them data are to be found on the seasonal dynamics of the numbers of eggs, larvae, pupae and adults; the duration of the ontogenesis of single individuals; and the times for the onset of the basic phenological stages. The studies cited were carried out either on single wasp colonies, kept under observation throughout the whole cycle (Yoshikawa, 1954; West-Eberhard, 1969), or by comparing selections of nests, collected in nature at different times for full laboratory study and assessment (Bohm and Stockhammer, 1977; Turrilazzi, 1980). None of these methods enables us to describe precisely the phenological development times of colonies with account taken of their intrapopulation variability. In the present work, therefore, for the first time the method was employed of observations of a sufficiently large number of colonies under natural conditions, with an exact quantitative assessment of their composition throughout the whole development cycle.

In the Polistine wasps living in a temperate climate, the processes of caste

differentiation are closely connected with the seasonal variation of the life cycle (West-Eberhard, 1969) and cannot therefore be studied separately from the factors regulating the seasonal development cycle. Nevertheless, virtually no attention has been paid to the problems of the regulation of seasonal development in the Polistine wasps, with the exception of a few works (Deleurance, 1952; Grinfel'd, 1972; Bohm, 1973). The data obtained, however, are insufficiently full and require verification, which was also the aim of the present work.

MATERIAL AND METHODS

The work was undertaken in 1980 and 1981 within the limits of Kherson from April to October inclusively, which for this locality corresponds to the active period in the annual cycle of these wasps. The temperature conditions for these years are shown in Fig. 1. Below will be described all the basic methods employed in this and subsequent works in this series.

Beginning in the last ten days of April, inspections were made of the usual nesting sites of Polistine wasps, such as lofts, barns, garages, and other structures, and also pipes, caves, empty containers, etc., mainly in the northeastern part of the town. These inspections enabled us to find and take into account 97 and 143 nests in the respective years, although of this number only 42% of the colonies survived and completed the full development cycle. Only the data for these 94 nests have been used to describe the seasonal cycle.

The colonies intended for phenological observations had to be left at the site under natural cover, at the same time making them accessible to regular and careful inspection. For this purpose the nest was grasped by the stalk with forceps, carefully detached from the substrate and fastened to the end of a plywood strip about 20 cm in length. A wire hook was attached to the other end of the strip. By means of it the nest was placed close to the site where it was initially established, suspended from the closest beam, joist, the edge of a roof shingle, or pipe, where the foundress could find it easily. Subsequently on inspection these nests were photographed and brought into the light. In each nest the queen was tagged in color with oil paint. Nests to which access was most difficult were transferred together with the foundress in specially equipped containers to the open balcony. The technique of this operation and also the construction of the containers have been described in detail by Grinfel'd (1972).

Observations of the nest began from the time it was detected, usually in the 2nd-5th diels after its establishment. Transfer operations ensued two weeks later (colonies that were too young because of the tenuous attachment of the queen to the nest withstood transfer badly). Because of this detailed inspection proved to be possible only at the end of May, when larvae were already present in the nests. From this time counts of the numbers of eggs, larvae, pupae and adults were made regularly throughout the whole season, as long as the nest remained occupied.

Nest inspections were carried out once a week in natural habitats and twice a week in the houses. At the time of inspection a map on the nest was made for each colony, assuming the form of stencilled contours of the cells of the nest, in which the content, egg larva or pupa, was indicated by special symbols (Fig. 2). For each nest the series of maps depicts its history, enabling us to trace the fate of each cell. From this can be derived information on the seasonal dynamics of the number of eggs, larvae, and pupae; on their growth and survival in the different development stages of the colony; and on the duration of the specific ontogenetic stages. Moreover, the actual appearance of the nest map makes it possible to define the development stage of the colony and its condition. Thus in round nests the brood of different stages, from egg to pupa, is arranged in alternate concentric rings, from the number of which the age of the nest can be determined (Fig. 2,A,B). At the end of the cycle, with the appearance of reproductive individuals in the colony, the regular sequence is lost (Fig. 2,C), and it is also lacking in weak colonies with a disrupted developmental cycle.

Simultaneously with the completion of the nest map, the numbers and caste

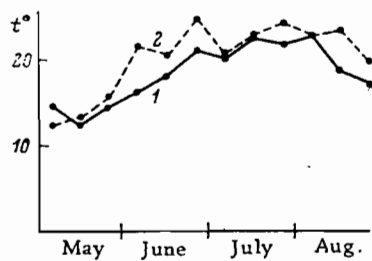


Fig. 1. Mean ten-day air temperatures in April-August 1980 (1) and 1981 (2) (according to the data of the Kherson Meteorological Station).

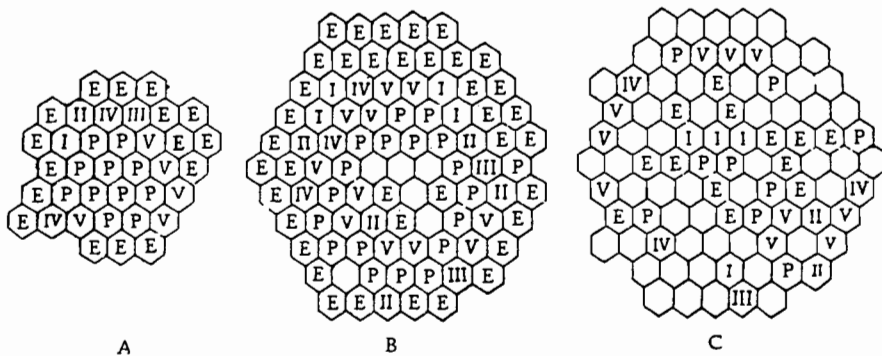


Fig. 2. Nest maps of haplometrotic colony Bd-II of *Polistes gallicus* L. (1980) at different development stages:

- A) 20.VI., period I of cycle (until appearance of workers);
 B) 19.VII., period II of cycle; C) 13.VIII., period III of cycle (beginning of colony disintegration). p - pupa; e - egg; I-V) larvae in different instars.

composition of its adult population were recorded. For determining the caste affiliation of female Polistine wasps the use of the behavioral criterion is accepted (Deleurance, 1952; West-Eberhard, 1969). Individuals that unlike the workers do not engage in foraging are regarded as being overwintering females (the future foundresses). In addition to this, they do not defend the nest, do not respond to the request for food, are on the whole rather sedentary and inclined to group together at the back of the nest, and therefore have greater similarity to males than to workers and the queen. Establishment of caste affiliation according to the full behavioral repertoire requires many hours of observations of each individual, which is impossible with a large number of colonies. Because of this, from the whole complex of the behavioral characters of the caste it was necessary to select a single one, the simplest one, quickly and easily detectable and at the same time persistent and reliable. This requirement is met by the defense reaction of the wasp in the nest. The degree of aggressiveness of the female was determined by a simple test consisting in a five-fold presentation to the wasp of the end of a preparation needle. The reaction was assessed on an 8-point scale: +4 - a high degree of aggressiveness: the wasp clasps the needle with its legs and moving along it bites and stings; +3 - forward rushes at and pursuit of the needle; +2 - rushes without pursuit; +1 - opening of the mandibles without forward rushes; 0 - complete indifference; -1 - movement away from the needle; -2 - retreat to the back of the nest; -3 - the wasp leaves the nest.

Initially 120 individuals were tested, the caste affiliation of which was determined from the full behavioral repertoire. Each individual received 4 series of five-fold presentations of the needle in the course of a month. It was established,

that the character of the defense reaction was in fact a persistent caste character. In workers and future queens it was formed on the 2nd-3rd day of their life (at the beginning of summer activity) and subsequently remained unchanged. At the same time a "positive" reaction (3-4 points) was characteristic of workers, while overwintering females responded exclusively in the range from 0 to -3. The numerous individuals of intermediate type that alternately exhibited a reaction of different signs constituted a special group. In all other characters these wasps were closer to the overwintering females, and at the end of the season their defense reaction usually assumed a persistently negative character.

Subsequently we used the defense reaction as the basic criterion for caste affiliation in females in natural colonies. As auxiliary characters, account was taken of the size of the wasps, their mobility and distribution in the nest. In this context only a few minutes at the most were needed to determine the caste composition of each colony.

In 1980 all the colonies observed (except for two) had a single queen, but in 1981 data were obtained not only for haplometrotic colonies, but also for 16 pleometrotic ones, which we placed in a separate group for analysis.

In 1980 data were obtained for 11 colonies established in cages by the Gibo (1978) method. Latticed cages measuring 430 X 430 X 430 mm were placed under natural climatic conditions on the open balcony. Inside each case was a little house imitating the natural refuges usually selected by wasps when nesting and a food table. The wasp was provided with water, food and building material (strips of cardboard). As food the wasps were presented with live larvae of the wax moth and 5% honey solution. The cages were colonized at the beginning of May with queens caught in nature, which after 6-10 days (later in time than in nature) proceeded to establish nests. Subsequently the colonies in the cages passed through all the stages of the seasonal cycle right up to withdrawal of the fertilized females for overwintering. All these colonies were pleometrotic.

In the houses and cages each wasp had an individual color tag, which made it possible with maximal precision to assess the number of adults and to trace the fate of each individual.

We thus obtained data for the following variants: natural haplometrotic colonies in 1980 (30 nests) and in 1981 (48 nests), natural pleometrotic colonies in 1981 (16 nests) and pleometrotic colonies in cages in 1980 (9 nests).

RESULTS AND THEIR DISCUSSION

In processing the data obtained, the basic phenological dates were determined as follows: a) beginning of the cycle - the time at which the nest was established (corresponding to the appearance of the first eggs); b) end of period I and beginning of II - appearance of the first worker; c) end of period II and beginning of III - beginning of the large-scale appearance of overwintering females (single individuals were not taken into account); d) end of period III and of the whole cycle - complete disappearance of the brood.

Analysis of the phenological data was made by two basic procedures. In the first, for each colony all the phenological dates and the duration of all three periods of the cycle were determined, and these data were then averaged out for each sample. The results are presented in Table 1. In the second, phenograms were constructed (Fig. 3, A-D), wherein for each calendar date the percentage of colonies is shown in which one or other category of individuals is present. On these phenograms the average phenological dates were determined from the presence of the corresponding character (workers, overwintering females, etc.) in 50% of the colonies. They differ slightly from those presented in Table 1 since the distribution of the development times is not strictly normal, and therefore the median does not coincide with the arithmetic mean.

Table 1

Average duration of the periods of the development cycle in 4 samples of colonies of *Polistes gallicus* L.

Periods of cycle	Samples studied														
	1980							1981							
	in cages				in nature				in nature				in nature		
	pleometrotic				haplometrotic				haplometrotic				haplometrotic		
n	\bar{x} (days)	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x}	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x} (clays)	$\pm\sigma$	$\pm m$	CV (%)	
															1
I	9	62	3.3	1.3	5.3	27	52	1.5	0.3	2.9	37	42.2	5.5	0.9	13.0
II	9	47.5	8.7	3.3	49.7	30	38	4.4	0.9	11.6	48	43.5	8.9	2.4	20.5
III	9	30.3	8.9	2.8	29.4	30	22	10.5	2.2	47.7	48	29.3	8.5	2.9	29.0
II+III	9	47.8	6.0	2.03	42.5	30	60	13.3	2.6	21.6	48	72.8	14.3	2.4	19.6
I+II+III	9	40.9	4.5	1.7	4.1	27	111	14	2.9	12.6	37	115	13.0	1.9	11.3

Table 1 (Continuation)

Periods of cycle	Samples studied														Criterion of reliability for Student's differences																						
	1981							Total							1 and 2			1 and 3			1 and 4			2 and 3			2 and 4			3 and 4							
	in nature				pleometrotic			n	\bar{x}	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x} (days)	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x}	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x}	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x}	$\pm\sigma$	$\pm m$	CV (%)	n	\bar{x}	$\pm\sigma$	$\pm m$	CV (%)
	4	1	2	3																																	
I	16	45	5.7	1.4	12.7	89	47.7	7.8	0.8	16.4	7.5***	12.5***	8.9***	4.9***	1.8***																						
II	16	30.9	11.4	2.9	36.9	103	35.7	11.3	1.19	31.7	5.6***	6.4***	3.1**	2.3*	3.5***																						
III	16	49.4	8.6	2.2	14.3	103	24.8	13.0	1.36	52.4	2.2*	0.3	3.1**	0.8	2.7*																						
II+III	16	50.3	12.1	3.1	24.0	103	60.8	16.2	1.7	26.6	3.6**	8.6***	0.7	3.8***	6.0***																						
I+II+III	16	95.3	6.0	1.5	6.3	89	108.5	14.9	1.5	13.7	0.4	2.0*	6.4***	4.8**	8.7***																						

Note. Differences in reliability with probability error: * - 5%; ** - 1%, *** - 0.1%.

The brood on the phenograms according to its subsequent fate traced from the nest maps is differentiated into three categories: that developing into workers; that developing into males and overwintering females; that not undergoing development (perishing at the end of the development cycle of the colony).

On all the phenograms the tendency is clearly discernible to prolongation of the duration of the later phenophases: the establishment (appearance of the first eggs) takes place most synchronously, while the difference in the times at which the last larvae perish at the end of the cycle reaches two months; the first workers appear in the different colonies more synchronously than the first overwintering females etc.

The brood in the first development stages of the colony is represented by immature-stage workers. Subsequently with the appearance of the eggs, larvae and pupae of the next category, this brood gradually disappears. In nature the last workers usually emerge from the pupae before the actual beginning of period III of the cycle. In all 4 samples, the males began to appear virtually simultaneously with the future foundresses. The last eggs developing successfully to adult were laid by the queens at the end of period II - the beginning of III. All eggs laid later than this threshold time and also the larvae and pupae deriving from them perished or were destroyed by the wasps. This phenomenon was studied for the first time by Deleurance (1955), who showed that the appearance in the colonies of a non-developing ("abortive") brood was evidently connected with the aging of the workers and degeneration of their salivary glands. After the disappearance of the brood the adult wasps still remained for some time on the comb and exhibited virtually no forms of social interrelationships. Gradually the workers died, and the males and overwintering females lost their attachment to the nest, forsaking it finally at the end of September.

Nest establishment in 1980 and 1981 occurred almost at the same time, at the beginning of May (Fig. 3), which is evidently to be explained by the similar spring temperatures of these years (Fig. 1) that determine the maturation of the females-foundresses. The duration of period I of the cycle is also probably determined by the temperature conditions that affect the development rate of the first brood. Thus in 1981, which was warmer, it was reliably shorter than in the colder 1980 (Table 1), but in the colonies in cages, it was appreciably longer than in the three other samples (Table 1) since the cages were exposed to temperatures that were lower on the average than in the natural habitats. The duration of periods II and III, however, and also that of the whole development cycle is already not so directly connected with temperature conditions.

Of great interest is period III of the cycle, the duration of which determines the times of maturation of the colony (appearance of reproductive individuals). For the pleometrotic colonies (in nature and especially in the cages), it proved to be appreciably shorter (Table 1). This is undoubtedly connected with the much more profound and significant difference between pleo- and haplometrotic colonies, which is clearly discernible on the phenograms for the brood (Fig. 3). In colonies with a single foundress, the transition from the exclusive rearing of workers to the rearing of overwintering females occurs immediately after the emergence of the first workers from the pupae (Fig. 3,B,C). Not even a single case was noted on the disruption of this regularity. The period of the rearing of the first overwintering females was at the same time almost completely coincidental with period II of the cycle. Their appearance, i.e., the beginning of period III, was not noted earlier than the end of July-beginning of August; it was always on a large scale and signified the maturation of the colony and usually did not alternate with the appearance of workers. In 3% of the nests in 1980 and in 6% in 1981, the earlier appearance was noted of single males (at the end of June), but not a single early overwintering female was detected. A different picture was observed in the pleometrotic natural colonies, where overwintering females may be reared at two times. In these nests already among the first adults of the new generation reproductive individuals made their appearance (their presence is indicated on the phenograms by a dotted line - Fig. 3,D), and these consisted of both males and females. They occurred in all the pleometrotic colonies and were more numerous (up to 7-12 individuals in strong

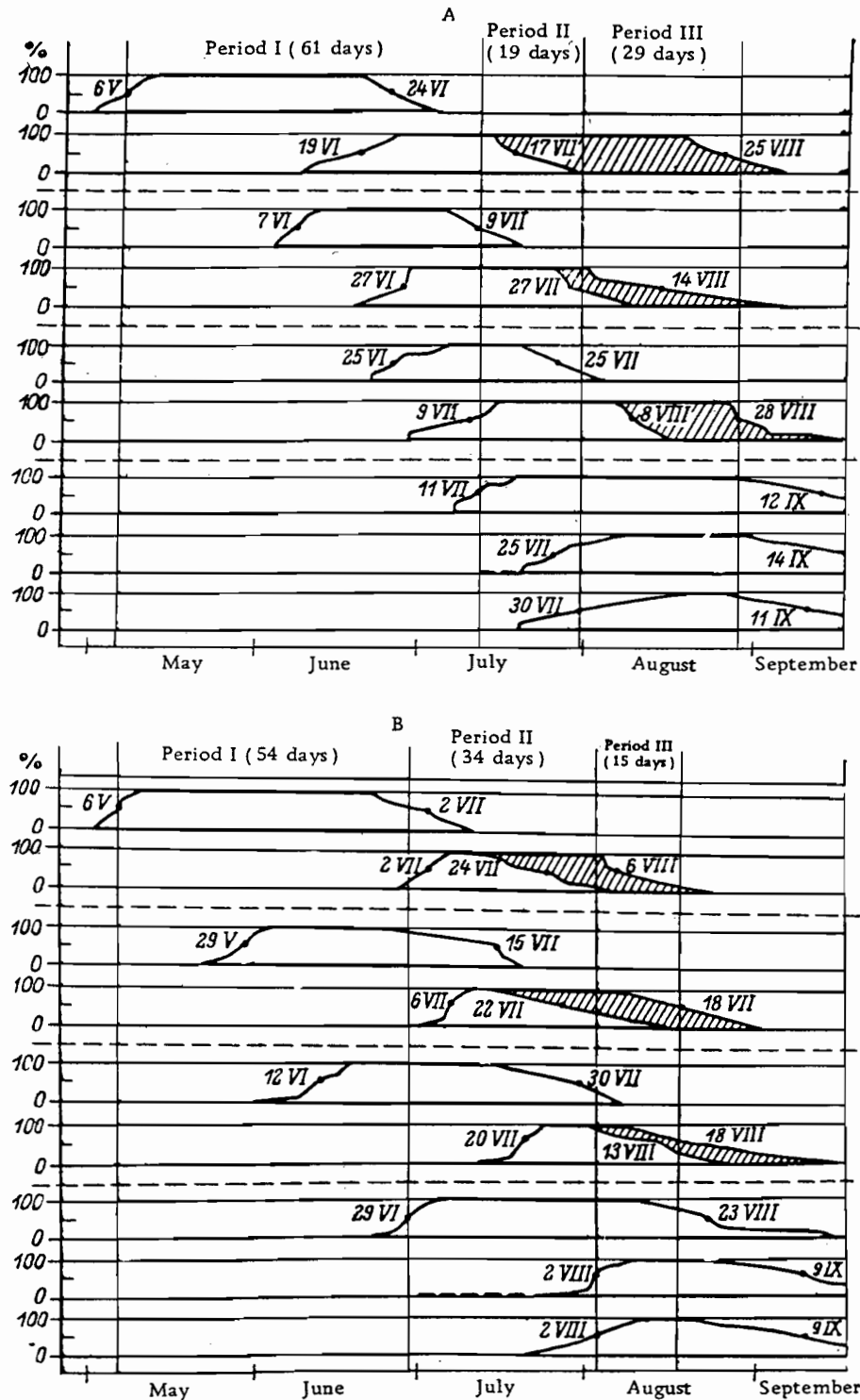


Fig. 3. Phenograms of the seasonal development of colonies of *Polistes gallicus* L.

A) pleometrotic colonies ($n = 9$) in cages in 1980; B) haplometrotic colonies ($n = 30$) in nature in 1980; C) haplometrotic colonies ($n = 48$) in nature in 1981; D) pleometrotic colonies ($n = 16$) in nature in 1981. Phenogram band breadth indicates the percentage of colonies in which the specific development stage is present. Dates are given for times the specific development stage was noted in 50% of colonies; hatching indicates the non-developing (moribund) brood; broken line indicates the premature appearance of reproductive individuals (males and females) in pleometrotic colonies in 1981 (D). Remaining explanations in text.

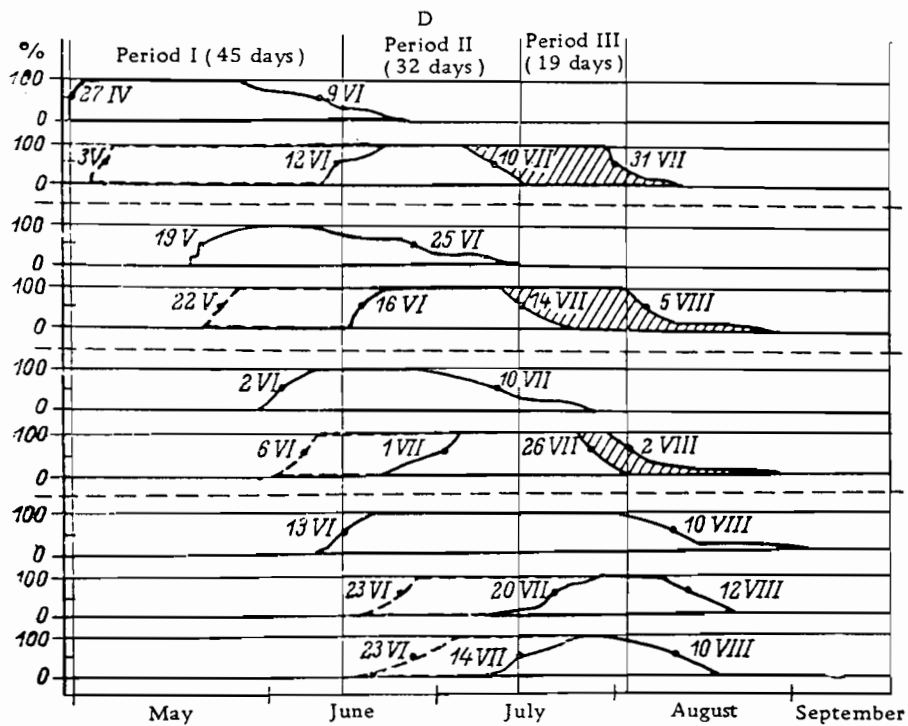
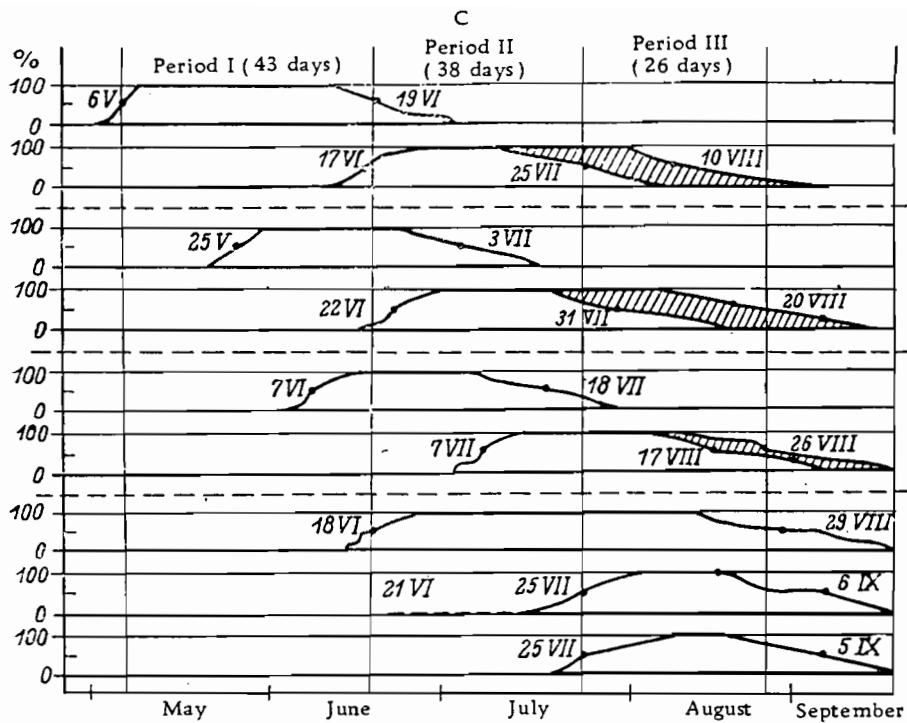


Fig. 3

colonies). The early reproductive individuals after 3-4 days usually left the nest independently or were expelled by the queens; after which the development of the colony proceeded normally. Transition to the rearing of reproductive individuals in the pleometrotic colonies also ensued after the appearance of the first workers, but earlier than in the haplometrotic colonies (Fig. 3,D). Therefore the large-

scale appearance of males and overwintering females in pleometrotic colonies was observed earlier, i.e., the duration of period II of the cycle was reliably shorter (Table 1). For the pleometrotic colonies in cages, no early single reproductive individuals were noted. In this case, however, large-scale rearing of males and overwintering females began long before the appearance of workers (Fig. 3,A), and therefore the duration of period II was much shorter (Table 1).

Curtailed of period II of the cycle in pleometrotic colonies, therefore, is engendered by earlier transition to the rearing of reproductive individuals. This is evidently connected with the better feeding conditions for the larvae in pleometrotic colonies, where workers appear earlier (Fig. 3) and where they are more numerous than in colonies with a single foundress. In the cages where the wasps received food in abundance and lost appreciably less energy in transporting it to the nest, transition to the rearing of reproductive individuals was observed even earlier. The appearance of early reproductive individuals in pleometrotic natural colonies is evidently brought about by the presence in them of supernumerary foundresses that fulfill the function of workers, which must greatly improve the trophic conditions of the larvae. This problem is closely connected with the problem of caste determination.

As has been indicated above, in the course of the summer a steadily increasing desynchronization occurs in the development of the individual colonies. This is also manifested in the fact that the degree of variability of the duration of the periods of the cycle increases appreciably from I to III, as can be determined from the increase in the coefficients of variation (Cr - Table 1): least variable was period I and most variable III. This points to the absence of any synchronization in the development of the colonies in nature and militates against the proposition as to the photoperiodic regulation of seasonal development in Polistine wasps. Our special experiments have made it possible to state that photoperiodic conditions in fact do not affect the development of wasp colonies.

In spite of the considerable variability (Cr up to 30-50%) of periods I and II, the duration of the whole cycle (periods I+II+III) varies much less: the coefficients of variation for it, as a rule, are even less than for period I, the most stable of the three. This makes it possible to postulate that the durations of all the periods of the cycle are interconnected by inverse correlations. In point of fact, the calculated coefficients of correlation in all cases except one were negative (Table 2). Consequently, the individual periods of the cycle mutually complement one another as it were so that the overall duration of the cycle is found to be very stable. In point of fact, this value differs considerably less in the different samples than the duration of the individual periods (Table 1).

All this has led us to conclude that the development cycle of the colony in Polistine wasps is regulated by various factors endogenous to it that create a correlation between the periods of the cycle such that its overall duration is a very constant value (about 100-110 days). The data we obtained enable us to formulate a number of propositions as to the nature of these factors.

In the first place the duration of the development cycle of the colony is determined by the physiological condition and activity of the queen. West-Eberhard (1969) suggests that the duration of the colony's existence is directly dependent on the presence of the queen, and that the colony disintegrates immediately after she is lost to it. This conclusion, however, was reached on the basis of observations of a single wasp colony only and therefore requires verification and investigation in detail.

According to our data, in 24% of the nests (12 out of 49) the queen disappeared more than 10 days before the end of the cycle. In these cases a clear positive correlation ($r = 0.7$) was noted between the times of her disappearance and the disintegration of the colony. In the remaining 76% of cases, the queen remained in the nest until completion of the cycle. Of these queens 40% (15 out of 37) ceased oviposition more than 10 days before the end of the cycle. At the same time, a positive correlation ($r = 0.7$) was also noted between the times for cessation of

Table 2

Coefficients of correlation between duration of the different periods of the development cycle in colonies of *Polistes gallicus* L.

Development periods	Samples studied				All colonies as a whole
	pleometrotic colonies in cages, 1980	natural haplometrotic, 1980	natural haplometrotic, 1981	natural pleometrotic, 1981	
I and II	-0.06	-0.01	-0.16	-0.5*	-0.4*
I and III	-0.8*	-0.1	-0.1	-0.4	-0.2
I and II+III	-0.8*	-0.1	-0.3*	-0.8*	-0.5*
II and III	+0.2	-0.02	-0.3*	-0.4*	-0.1

Note. Statistically reliable coefficients of correlation are indicated by an asterisk.

oviposition and the times for the disintegration of the colony. In 22 colonies (47% of the total number) the queens survived and laid eggs until the actual end of the cycle. These colonies on the average had a shorter duration of the cycle than the remainder (99.8 ± 3 days and 113.1 ± 3.5 days, respectively; $t_{st} = 3.6$). Evidently their disintegration occurred even before the loss of activity by the queen and was brought about by other causes.

Thus, the regular loss of activity and fecundity of the queen with age is one of the basic factors limiting the duration of the development cycle of the colony. The duration of the cycle, therefore, is sufficiently stable and is evidently the fundamental cause of the correlation between the duration of period I and periods II+III (Table 2). In actual fact, if workers are reared earlier (i.e., period I is shorter), then periods II and III will be longer since the overall duration of the cycle is constant. Furthermore, when workers emerge earlier, the queen becomes exhausted to a lesser extent and loses activity later, which results in prolongation of the cycle, i.e., extension of periods II and III. The shorter duration of the cycle in pleometrotic colonies (Table 1) may be connected with the more rapid aging of the queen as a result of enhanced oviposition intensity. It is also possible that the intensive domination exhausts the queen, as has been suggested for the bumble-bee (Röseler and Röseler, 1977).

The aging of the queen is not the only cause resulting in disintegration of the colony. In many cases cessation of oviposition due to the death of the queen or her loss of fecundity have been observed long before the end of the cycle (maximally after 45 days), but the colony continued to develop normally and only disintegrated after completion of the rearing of the last larvae.

Analysis of the data obtained indicates that the second most important factor determining the duration of the cycle are the age and physiological condition of the workers. Deleurance (1955), as indicated above, has already shown that old workers due to degeneration of the salivary glands lose the ability to feed the larvae normally. Since with the appearance of overwintering females emergence of new workers from the pupae ceases, with the lapse of time no functionally full-valued representatives of this caste remain in the colony. In most colonies this feature intervened even before the loss of fecundity by the queen, since eggs were still laid, but the brood perished (Fig. 3). In pleometrotic colonies the workers evidently age much earlier (in connection with early transition to the rearing of overwintering females), which may explain the relatively short cycle and the early death of these nests (Table 1). At the same time all the haplometrotic colonies are very close as regards the duration of the cycle (Table 1).

The times for colony disintegration are virtually unconnected with the time of the appearance of the first workers ($r = 0.1$), but are closely correlated with the times of emergence from the pupae of 50% of the workers ($r = 0.6$) and of the last

workers ($r = 0.7$). Consequently, the time for cessation of colony development depends to a great extent on the age and physiological condition of the workers and their ability to rear the brood. In this context, the existence of a slight negative correlation between the duration of periods II and III becomes comprehensively (Table 2). If in fact for any reasons period II was shorter, then on an average the workers would retain their activity longer in period III, and it would be somewhat longer.

It is well known that the death of the queen or her loss of fecundity in the early periods of the cycle do not result in the death of the colony since the foundress is rapidly replaced by one of the workers. This phenomenon has been very frequently noted by us (in 24% of the nests) in *P. gallicus*. Colonies with a replacement queen subsequently developed normally and were not inferior to normal ones as regards the duration of the cycle. Replacements, however, were not noted later than mid-July. Loss of the ability to replace the queen is undoubtedly the first sign of the aging of workers that still retained their other functions.

CONCLUSIONS

1. The nests of *P. gallicus* are established by overwintering females almost simultaneously (at the beginning of May). The times for the foundation of nests and the duration of period I of the development cycle (from the establishment of the nest to the appearance of workers) are determined primarily by temperature conditions.

2. In the course of the summer steadily increasing desynchronization of the development times takes place in the population; no synchronization whatsoever is noted in the development cycles of individual colonies at the end of the season. This is indicative of the absence of exogenous regulation of development (for example, photoperiodic regulation).

3. The transition from rearing workers to the rearing of males and overwintering females occurs earlier in pleometrotic (founded by several females) colonies; in them therefore the duration of period II of the cycle (from the emergence of the first workers to the appearance of the reproductive generation males and overwintering females) is on the average shorter than in haplometrotic colonies (founded by a single female). In pleometrotic colonies also premature rearing of males and overwintering females that already emerge in small numbers together with the first workers is observed.

4. Variability in the duration of all periods of the development cycle in the population increases in periods I to III, while the duration of the individual periods varies appreciably more markedly than the duration of the overall cycle as a whole. This is connected with the existence of negative correlations between the duration of the periods and postulates the presence of an endogenous regulation of colony development in Polistine wasps.

5. The basic factors that virtually to the same degree determine the duration of period III (from the time of the onset of the large-scale appearance of reproductive individuals to the disintegration of the colony) and of the overall cycle as a whole are: 1) the activity and fecundity of the queen; 2) the age and physiological condition of the workers. The life duration and the behavioral and reproductive activity of the queen as a whole determine the duration of the whole development cycle of the colony. At the same time, the workers with advancing age lose the ability for normal rearing of the brood, which limits the duration of the development cycle even in the presence of the ovipositing queen.

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