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Influence of the Queen and Worker Ants on Onset and Termination of the Larval Diapause in *Lasius niger* (L.) (Hymenoptera, Formicidae)

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Abstract—Social control of the larval diapause, executed by workers, has been investigated in *Lasius niger*. Experimental ant colonies in the autumn diapause state were placed in a refrigerator for cold reactivation at 3–5°C. Three months later half of colonies were moved to conditions suitable for development (23°C, 20 h day length), whereas other colonies remained in a state of prolonged dormancy. A complete cycle of development took 3–4 months and ended with a diapause in all the warmed colonies. Then colonies in the spring state were removed from the refrigerator, and immediately after that larvae of spring and dormant colonies were interchanged. Four basic experimental sets were studied: (1) overwintered workers with overwintered larvae; (2) overwintered workers with diapausing larvae; (3) diapausing workers with overwintered larvae; (4) diapausing workers with diapausing larvae. The experiment was finished after 2.5–3 months, when pupation terminated. All or almost all larvae in set (1) pupated in a way similar to pupation in outdoor spring colonies. Larvae did not pupate in set (4), since larval diapause is very stable in autumn. Wintered workers in set (2) provoked development and pupation in a considerable part (up to 75% of survived larvae) of diapausing larvae; however, part of these larvae (15–72.5%) stayed dormant. In set (3), where diapausing workers cared for wintered larvae, 3.6 to 17.2% (average 10.4%) of survived larvae pupated. Thus, the workers are able to induce and terminate the larval diapause, depending on their physiological state. However, in *L. niger*, larvae are not so plastic and the control of workers is not so absolute, as in other previously investigated species. It is shown, that the presence of a queen in a colony increases rates of survival and pupation in larvae.

A colony of ants or other evolutionary advanced social insects is an organized group of individuals capable of influencing considerably the behavior, development, and physiological state of all the members of the colony. This mutual influence (or, put otherwise, social regulation or social control) affects practically all aspects of vital activity in the social insects and plays the central role in the structure of a colony (Wilson, 1971; Brian, 1983; Passera, 1984; Hölldobler and Wilson, 1990). The role of social factors is also particularly great in regulation of development processes. The attention of investigators dealing with this problem has been concentrated on the following two main directions: (Kipyatkov, 1981): (1) influence of the queen and workers on development and differentiation of individuals of different castes, and on the sex ratio in reproductive descendants (Wilson, 1971; Brian,1983); (2) social regulation of oviposition and productivity of the queen by workers and larvae (Brian, 1983; Tschinkel, 1988).

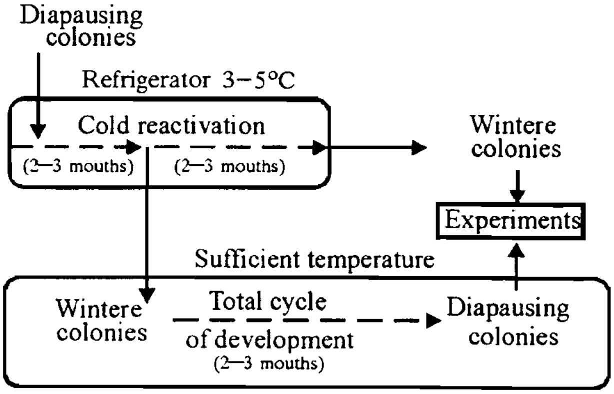
At the same time, not so much is known about the social control of development and diapause in the context of regulation of annual cycles in ants; nearly all the available data have been obtained on a single ant species, *Myrmica rubra* L. Brian (1955) was the first to conduct investigations in this area. His experiments used diapausing autumn third (last) instar larvae of various size, cared by worker ants in two physiological states: either spring workers, immediately following the resumption of their activity after prolonged hibernation in refrigerator, or autumn workers, which performed a complete cycle of raising breed at optimum temperatures for three months after hibernation. It turned out, that the spring workers stimulate rapid growth and pupation of larvae both at 25°C and at 20°C. Even the largest larvae, which possess a significantly deeper diapause, pupate mostly at 25°C and in part at 20°C. However, similar diapausing larvae do not develop at all, when fed by autumn workers; only part of the smallest larvae pupate at 25°C, which, as shown by Brian, is essentially higher than the developmental optimum of 21 to 22°C. Therefore, this temperature provokes pupation in small larvae whose diapause is not so deep.

Thus, workers in the spring physiological state are able to interrupt the larval diapause. It is interesting, however, that only workers' pupae are formed in this case; larvae stimulated by spring workers will never develop into winged females. To acquire ability to develop into reproductive individuals, larvae have to winter at low positive temperatures; the occurring physiological process was called "vernalisation" by Brian (1955). In experiments with separate cooling of worker ants larvae, he also established, that it is larvae that undergo vernalization, because unwintered larvae never developed into winged females. The results of Brian were confirmed by Weir's (1959) experiments on the same species who revealed in addition that young workers recently emerged from pupae were similar in their physiological state to the autumn ones, being also unable to stimulate pupation of diapausing larvae.

In subsequent experiments Brian revealed one more highly interesting variety of social control over the diapause: the stimulating effect of the queen's presence, manifested as 4 to 5-fold increase in the percentage of pupating larvae in the presence of the queen, in comparison with ant groups without queens (Brian 1963, 1968).

Later, Kipyatkov (1979) repeated experiments with *M. rubra* according to the scheme by Brian and Weir, including in the experiments naturally wintered larvae also. It was found that spring larvae, which were normally reactivated by cold, do not pupate under care of the autumn workers, whereas the spring workers provoke pupation in the majority of both reactivated spring larvae and diapausing autumn larvae.

Discovery of photoperiodic regulation of the annual cycle in *M. rubra* (Kipyatkov, 1972, 1974a) allowed V. E. Kipyatkov to realize another experimental scheme in studying the social regulation of development and diapause. It appeared rather easy to change the physiological state of workers by photoperiodic influences: under short (less than 15 h) day conditions a diapause started in ants; however, the subsequent two week exposition at long day and optimum temperature conditions resulted in photoperiodic reactivation and resumption of the physiological activity (Kipyatkov, 1977). The conducted experiments showed that larvae did not perceive the photoperiod without assistance; their development was totally controlled by workers in care. At the same time, long-day (i.e. maintained under long day and, hence, physiologically active) workers stimulated rapid growth and pupation in both developing summer and diapausing autumn larvae. Short-day (i.e. exposed to rather long influence of short day photoperiods and, hence, physiologically inactive) workers were unable to stimulate growth and pupation of larvae, including the summer larvae, which start to diapause in this case (Kipyatkov, 1974b, 1976). Thus, the short-day workers induce larval diapause, whereas the long-day workers interrupt it, i.e. reactivate the larvae.



The scheme of manipulations used during preparation of experimental ant colonies to disturb artificially their annual developmental cycles.

It seems natural to pose a question: whether similar social mechanisms of development and diapause regulation occur in other ant species, and to what extent do they differ from the scheme of regulation revealed in *Myrmica rubra*? To answer this question we started extensive comparative investigations of different ant species by the methods tested previously on *M. rubra* (Kipyatkov and Lopatina, 1994). The first results obtained by us on ants of the genera *Camponotus* and *Tetramorium* were closely similar to those for *M. rubra*, with the exception of photoperiodical regulation of diapause, which is lacking in the majority of ants (Kipyatkov, 1993). Similar to *Myrmica*, wintered workers of *C. herculeanus*, *C. japonicus*, and several species of the genus *Tetramorium* are able to stimulate rapid growth and pupation in diapausing autumn larvae; at the same time, overwintered, i.e. reactivated by cold, larvae neither develop nor pupate, when fed by diapausing autumn workers.

The present work studies the social regulatory mechanisms of development and diapause in one of the common palaearctic ant species, *Lasius niger* (L.). The main methodological approach used in our investigations is based on artificial disturbance of annual cycles in experimental colonies and makes it possible to obtain simultaneously colonies in the spring physiological state, i.e. ready to start their regular annual cycle, and autumn colonies which had terminated their development and passed into the diapause state. Such a situation allows one to perform experiments with controlled displacement (exchange between colonies) of diapausing or developing larvae and diapausing or ovipositing queens into other nests with reactivated (spring) or diapausing (autumn) ants, correspondingly. As a result, regulatory influences can be revealed of workers on larvae or queens, provoking a diapause or, on the contrary, causing recommencement of development and oviposition. Another forms of social regulation can also be revealed, e.g. influence of queens on larval development, or a hypothetically possible influence of larvae on workers and queens. Preparation for such experiments is laborious and time consuming. For this purpose ant colonies that have terminated their development in autumn are placed into a fridge for artificial overwintering at temperatures from 3 to 5°C. After 3 or 4 months, when cold reactivation has terminated, all the material is divided into two parts; some nests are placed in conditions optimum for development, while the other are left in a situation of artificially prolonged winter in the fridge. In ant colonies transported into optimal conditions, the normal full annual cycle occurs, ending after 3 to 4 months with the diapause. After that, colonies of ants that were stored in refrigerator (and now are ready for spring development) are also placed in optimum conditions. Immediately after that experiments are started with exchange of larvae and or queens between ant colonies that have just terminated wintering and are in the state of diapause.

MATERIAL AND METHODS

Finding the only queen in the ground nest of the monogynous species *L. niger* during excavation, and preserving it alive is a very complicated task; therefore, it was practically impossible to gather complete, i.e. including the queen, colonies in amount necessary for the experiments. In this connection, founder females gathered on the ground surface at the beginning of August 1994 in St. Petersburg were used for creating experimental groups. These females were placed in laboratory nests (formicaria), made of plastic Petri dishes. Three females were placed in each formicarium; after that several hundred of pupae, collected from outdoor nests of *L. niger* in the environs of St. Petersburg were added. Workers emerged little by little from these pupae, being loyal to females and starting to feed their offspring. In this way artificial colonies were formed; after some time most of them became monogynous, i.e. only one female-queen was left (superfluos females were eliminated by workers). After the appearance of a sufficient number of larvae that had developed from queen's eggs in experimental groups of ants conditions of maintenance were changed (temperature 17–18°C, day length 12 h) in order to advance the onset of the diapause. After pupation and oviposition ceased in the middle of November, ants were placed in a refrigerator for wintering at temperatures 3–5°C.

Further, all the material was divided into two parts (figure): some nests were taken from the fridge at the end of February and placed in conditions favorable for development (23°C, day length 20 h); other nests were left in the fridge. It is known, that *L. niger* belongs to the group of endogenous and heterodynamous ant species, i.e., its annual cycle of development is limited obligatorily, and diapause starts independently of conditions of maintenance (Kipyatkov, 1993). Therefore, after 3 to 4 months development in experimental groups stopped and eggs and pupae disappeared, i.e. diapause started in larvae, workers, and the queen. Larvae of *L. niger* overwinter in all the three instars, with larvae of the third instar being usually small (Peakin, 1985).

At the end of July 1995, the nests that had been staying in refrigerator were also placed in warmth; immediately after that interchange was performed between these groups of ants, which had just terminated wintering, and those colonies whose annual developmental cycle has ended with a diapause. Thus, four basic variants were used in the experiment: (1) wintered workers with also wintered larvae; (2) wintered workers with diapausing larvae; (3) diapausing workers with wintered larvae; (4) diapausing workers with diapausing larvae. All wintered larvae were small (body length shorter than 2 mm), whereas diapausing larvae included larger individuals (longer than 3 mm). For this reason, the diapausing larvae were divided into two categories: "large" (longer than 2 mm) and "small-median" (shorter than 2 mm). Larvae of both sizes were used separately in variant (2). Additionally, each basic variant included ant groups with and without a queen. So, the total number of variants reached 10; 29 groups of ants were used in them, with 17 groups having a queen, and 12 groups without it. The majority of groups included 200–300 workers. The number of larvae placed in experimental groups is indicated in the table.

Ants were maintained at a temperature of 23°C and 20 h day length, and fed twice a week with *Nauphoeta cinerea* coacroaches cut into pieces, and a 15% solution of honey or sugar. The number of pupated and not

Results of experiments with *Lasius niger* (L.)

Type of data			Physiological state									
			wintered workers						diapausing workers			
			wintered larvae		diapausing larvae				wintered larvae		diapausing larvae	
Experimental variant no			1		2				3		4	
Size of larvae			small-medium		large		small-medium		small-medium		small-medium	
Presence of a queen in the group			present	lacking	present	lacking	present	lacking	present	lacking	present	lacking
Number of groups			2	1	2	2	6	3	5	5	2	1
Number of larvae in a single group			200		120	120	250	200	250	250	250	
			300					250			550	
								300				
total			500	100	240	240	1500	750	1250	1250	800	250
Number of survived larvae	Number	min	–	–	88	30	67	–	98	89	–	–
		max	–	–	109	70	207	–	169	198	–	–
		average	–	–	98.5	50	157.8	–	130.8	136.6	–	–
		± σ	–	–	–	–	49.69	–	26.68	41.00	–	–
		Σ	468	79	197	100	947	443	654	683	752	199
	Share in total number, %	min	91.0	–	73.3	25.0	26.8	34.3	39.2	35.6	92.4	–
		max	97.5	–	90.3	58.3	82.8	78.5	67.6	79.2	94.7	–
		average	94.3	–	81.8	41.7	63.1	62.0	50.3	54.6	93.6	–
		± σ	–	–	–	–	19.88	24.13	11.29	16.40	–	–
		Σ	**93.6^{a}**	**79.0^{c}**	**82.1^{ab}**	**41.7^{cd}**	63.1^{ab}	59.1^{cd}	52.3^{ab}	65.6^{cd}	**94.0^{b}**	**79.6^{d}**
Number of pupated larvae	Number	min	–	–	29	30	19	10	5	0	–	–
		max	–	–	46	45	165	99	23	1	–	–
		average	–	–	37.5	37.5	115.5	40.7	13.6	0.4	–	–
		± σ	–	–	–	–	54.28	50.54	7.13	0.55	–	–
		Σ	451	79	75	75	693	122	68	2	1	0
	Share in total number, %	min	89.0	–	24.2	25.0	7.6	3.3	2	0	0	–
		max	91.0	–	38.3	37.5	66.0	39.6	9.2	0.4	0.4	–
		average	90.0	–	31.3	31.3	46.2^{a}	16.5^{b}	**5.4^{a}**	**0.2^{b}**	0.2	–
		± σ	–	–	–	–	21.71	20.10	2.85	0.22	–	–
		Σ	**90.2^{a}**	**79.0^{bc}**	31.3^{a}	31.3^{bc}	**46.2^{a}**	**16.3^{bc}**	**5.4^{a}**	**0.2^{b}**	0.1^{a}	0^{c}
	Share in survived larvae, %	min	91.3	–	33.0	64.3	28.4	8.2	3.6	0	0	–
		max	100	–	42.2	100	86.7	54.1	17.2	0.9	0.4	–
		average	95.7	–	37.6	82.2	**68.0^{a}**	**24.0**	**10.4^{a}**	**0.3**	0.2	–
		± σ	–	–	–	–	20.53	26.08	4.87	0.44	–	–
		Σ	**96.4^{a}**	**100^{bc}**	**38.1^{a}**	**75.0^{bc}**	**73.2^{a}**	**27.5^{bc}**	**10.4^{a}**	**0.3^{b}**	0.1^{a}	0^{c}
Number of un-pupated larvae	Number	min	–	–	59	0	25	84	89	89	–	–
		max	–	–	63	25	50	144	151	198	–	–
		average	–	–	61	12.5	42.3	107	117.2	136.2	–	–
		± σ	–	–	–	–	8.96	32.36	24.78	41.05	–	–
		Σ	17	0	122	25	254	321	586	681	751	199
	Share in total number, %	min	0	–	49.2	0	10	31.0	35.6	35.6	92.0	–
		max	8.5	–	52.5	20.8	20	72.0	60.4	79.2	94.7	–
		average	4.3	–	50.9	10.4	16.9^{a}	45.5	46.9^{a}	54.5	93.4	–
		± σ	–	–	–	–	3.58	22.96	9.91	16.42	–	–
		Σ	**3.4^{ab}**	**0^{c}**	**50.8^{a}**	**10.4^{c}**	**16.9^{ab}**	**42.8^{c}**	**46.9^{b}**	**54.5^{c}**	**93.8^{ab}**	79.6^{c}

Table. (Contd.)

Type of data			Physiological state									
			wintered workers						diapausing workers			
			wintered larvae		diapausing larvae				wintered larvae		diapausing larvae	
Experimental variant no			1		2				3		4	
Size of larvae			small-medium		large		small-medium		small-medium		small-medium	
Presence of a queen in the group			present	lacking	present	lacking	present	lacking	present	lacking	present	lacking
Number of groups			2	1	2	2	6	3	5	5	2	1
	Share in	min	0	–	57.7	0	13.3	45.9	82.8	99.1	99.6	–
	survived	max	8.7	–	67.0	35.7	71.6	91.7	96.4	100	100	–
	larvae,	average	4.4	–	62.4	17.9	**32.0**^{a}	**76.0**	**89.6**^{a}	**99.7**	99.8	–
	%	± σ	–	–	–	–	20.53	26.05	4.87	0.44	–	–
		Σ	**3.6**^{a}	**0**^{bc}	**61.9**^{a}	**25.0**^{bc}	**26.8**^{a}	**72.5**^{bc}	**89.6**^{a}	**99.7**^{b}	99.9^{a}	100^{c}

Statistic comparison of the significance of differences was performed as follows: (1) separately in groups with and without queens, between all experimental sets; in this case similar letters (a–d) in the same row denote values significantly (P ≥ 95%, or P ≤ 99%) differing according to Student's criterion (for mean values), or to Fisher's criterion (for percentage); (2) between colonies with and without queens within the limits of each experimental set (significantly differing numbers are printed in semibold type). Designations: (min) minimum; (max) maximum; Σ total.

pupated larvae was determined approximately with the help of a binocular light microscope during weekly examination of nests. To calculate the offspring exactly, ants were put to a short sleep with the help of carbon dioxide. This procedure was performed 2–3 times in every experiment, with all the emerged pupae removed and counted. Eggs laid by the queen and first-instar larvae emerged from these eggs were also removed in order not to be confused with larvae placed in nests at the beginning of experiment. The experiment was terminated after 3 months, when pupation of larvae placed in the nests totally ceased in all ant groups. At the end of experiment all larvae left unpupated in the groups, were counted.

The results were processed with the use of the conventional methods of variation statistics, including calculation of arithmetic mean and mean square deviation (in cases when number of repetitions was two and more). The significance of the difference of means was estimated with the help of Student's criterion and that of the difference of fractions (percentage), calculated from the overall data, was determined by the ϕ method with the use of Fischer's criterion (Plokhinskii, 1970). The data obtained are summarized in the table.

RESULTS AND DISCUSSION

The survival of larvae was higher than 50% in the majority of variants; moreover, being noticeably and significantly higher in groups with queens, than analogous variants without queens in 3 cases out of 5, and practically the same in one case. In those situations, when noticeable pupation of larvae occurred (i.e. in all the variants, except the groups with diapausing workers and larvae), the percentage of pupated larvae was reliably higher in 3 cases out of 4 in groups with queens, and the same in case. These results can be easily explained by the well known from the literature effect of stimulating influence of the queen on development of larvae, performed through the mediation of worker ants; worker's care for larvae is pronouncedly more zealous and efficacious in the presence of a queen (Brian, 1983; Hölldobler and Wilson, 1990). Hence, this effect was well manifested in our experiments, too. However, because the average number of survived larvae was lower in groups without queens, calculating the number of pupated larvae as percentage of survived larvae gave contradictory results in two cases, i.e. the fraction of pupated larvae appeared to be larger in groups without queens (see the table).

Moreover, the conformity (or nonconformity) of the physiological state of workers to that of larvae, which they fed, pronouncedly influenced the survival. In those cases when this conformity took place, i.e. the combination of workers and larvae was natural, possible in outdoor conditions (overwintered workers and overwintered larvae, or dormant workers and dormant larvae), survival was essentially and significantly higher, in comparison with cases without such conformity, i.e. combination of workers and larvae was unnatural (wintered workers and diapausing larvae, or diapausing workers and wintered larvae). This effect manifested itself identically in both groups with and without queens.

Let us examine now the pupation of larvae in basic variants of our experiment. In all the three groups with diapausing larvae cared for by also diapausing workers [set (4)], only one larva pupated (from nearly a thousand survived larvae). In fact, this variant is the control one, demonstrating the stability of diapause in autumn ant colonies.

In the same manner we can take as control set (1), where both workers and larvae were wintered: here the overwhelming majority of survived larvae (from 91.3 to 100%) pupated, as it occurs in the wild in spring ant colonies.

The results of two other variants of experiment are of particular interest. Wintered workers initiated pupation in a considerable part (up to 75% of survived individuals) of diapausing larvae [set (2)]; however, still not in all of them with a noticeable part of larvae (25 to 72.5%) remaining dormant. Thus, wintered workers could not stimulate pupation in all dormant larvae. The above stimulating effect of the presence of a queen manifested itself here noticeably. The influence of the size of larvae was indeterminate: in groups with queens an essentially larger number of small larvae pupated in comparison with large larvae; and, for some reason or other, a reverse situation was observed in groups without queens: larger number of large larvae pupated.

In set (3), where diapausing workers cared for wintered larvae, a small number of pupae emerged, particularly in groups without queens, where only two pupae had pupated. However, in groups with queens 3.6 to 17.2% (10.4 on average) of survived larvae did pupate. Hence, dormant workers could not prevent pupation in a small part of wintered larvae.

Thus, social control of larval development and diapause by worker ants of *L. niger* is not as complete, as in species studied by us earlier. Recall that in *C. herculeanus*, *C. japonicus*, *M. rubra*, and species of the genus *Tetramorium* wintered workers are able to stimulate development and pupation practically in all dormant larvae, whereas dormant workers totally block development of wintered, i.e., spring, larvae; none of them pupates in such conditions (Kipyatkov, 1979; Kipyatkov and Lopatina, 1994, 1995). In the same manner short-day workers of *M. rubra* induce a diapause in all the larvae, whereas long-day workers initiate termination of diapause and pupation practically in all the larvae (Kipyatkov, 1974b, 1975). The larval development in all these species is, therefore, very flexible and totally controlled by workers who induce the diapause or initiate its termination. In these species, it looks like only workers, but not larvae, pass through a cold reactivation during wintering. Surely, this statement is not quite correct, and the larval physiological state also changes during wintering; however, examination of this question is beyond the scope of the present work.

At the same time, as shown above, some spring larvae of *L. niger* do develop and pupate, even being fed by dormant autumn workers; this means that cold reactivation is enough for these larvae to pupate. Wintered, i.e. subjected to cold reactivation, workers of *L. niger* are able to interrupt the diapause and stimulate growth and pupation in a considerable part of autumn larvae; however, still not in all of them. Hence, larval development in *L. niger* is not so flexible, and cannot be totally controlled by workers which induce or terminate the diapause.

In the light of our data, the necessity for further similarly directed studies of other species and genera of ants becomes particularly clear. It will reveal greater diversity and, probably, distinguish fundamentally different schemes of social control over development and diapause in the family Formicidae.

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