

## Social Regulation of Development and Diapause in the Ant *Leptothorax acervorum* (Hymenoptera, Formicidae)

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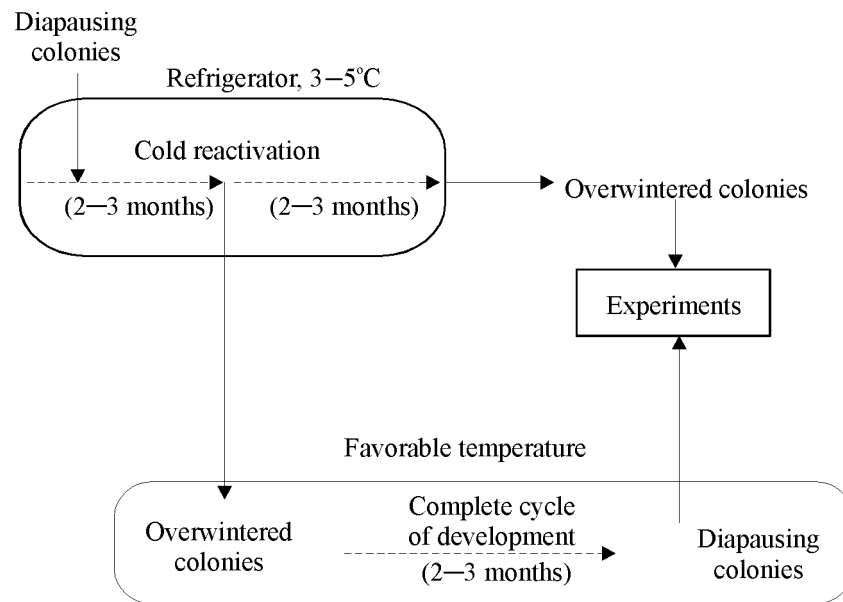
**Abstract**—An exchange of larvae between overwintered (*O*) and diapausing (*D*) colonies was performed. Four experimental sets were used: (s–1) *O* workers with *O* larvae; (s–2) *O* workers with *D* larvae; (s–3) *D* workers with *O* larvae; (s–4) *D* workers with *D* larvae. In s–1, the majority of larvae (90.4–98.3% of survived larvae) pupated, as it usually occurs in natural ant colonies in spring. In s–4, less than 2% of larvae pupated, demonstrating stability of the diapause at fall. In s–2, workers provoked pupation only in an insignificant part of *D* larvae (3.6 to 40.1% of survived larvae) while the majority of larvae (59.9 to 94.6%) remained in a diapause. A significantly larger number of small larvae (average 32.1%) pupated in comparison with the larger ones (average 13.4%), testifying to more stable diapause of the latter. In s–3, no workers could prevent rapid growing and development of *O* larvae; practically most of them (90.7–100% of survived larvae) pupated. Moreover, *O* larvae provoked termination of the diapause in queens which began to lay eggs and, probably, in workers which were able not only to rear these larvae, but also part of the rapid breed. Thus, *L. acervorum* workers possess rather limited abilities to control the beginning and termination of larval diapause in comparison with other ant species studied.

A colony of ants (and other evolutionarily advanced social insects) is an organized group of individuals which are able to influence the behavior, development, and physiological state of all members of the colony. This mutual influence, in other words social regulation or social control, affects practically all life aspects of social insects and plays a main role in the organization of a colony (Kipyatkov, 1971; Wilson, 1971; Brian, 1983; Passera, 1984; Hölldobler and Wilson, 1990). Attention of investigators who worked on the problem of the role of social factors in the regulation of developmental processes was focused mainly on two aspects (Kipyatkov, 1981): (1) influence of workers and a queen on processes of development and differentiation of individuals from various castes and on the sex ratio in reproductive posterity (Wilson, 1971; Brian, 1983); and (2) social regulation of oviposition and productivity of a queen affected by workers and larvae (Brian, 1983; Tschinkel, 1988). At the same time, less is known about the social control of development and diapause in the context of regulation of annual cycles in ants; all the available data were obtained on *Myrmica rubra* L.

Brian (1955) was the first to perform investigations in this field. Diapausing autumn larvae of third (last) instar differing in size were used in his experiments. They were cared by worker ants in two physiological states: either spring workers which had just been re-

tivated after overwintering in a refrigerator, or autumn workers which had passed the whole cycle of breed growing at optimum temperatures during three months after wintering. It was found that spring workers stimulate rapid growth and provoke pupation of larvae both at 25°C and 20°C. Even the largest larvae with a deeper diapause pupate mostly at 25°C and partly at 20°C. However, no similar diapausing larvae develop when being fed by autumn workers. Only the smallest pupate at 25°C. This temperature is significantly higher than that needed for optimum development (21–23°C), as it has been shown by Brian, and, therefore, provokes pupation of small larvae with less strong diapause.

Thus, workers in the spring physiological state are able to interrupt the larval diapause. However, it is interesting that pupae of workers are always formed in this case, and no larvae stimulated by spring workers develop into winged females. Wintering at low positive temperatures is essential for larvae to acquire an ability to develop into reproductive individuals; an accompanying physiological process was called vernalisation by Brian (1955). In experiments with cooling of isolated larvae and workers, he had also established that vernalisation occurs just in larvae, because no larvae developed into winged females without wintering. Brian's results were confirmed by Weir (1959) who, in addition, found that young workers



Scheme of manipulations necessary for artificial destaging of annual cycles in experimental ant colonies, used during preparation of experiments

newly emerged from pupae are similar in their physiological state to the autumn ones, because they also cannot stimulate pupation of diapausing larvae.

In his subsequent experiments, Brian found one more interesting form of social control over the diapause in *M. rubra*: the stimulating effect of queen's presence which provoked a 4–5 times increase in the amount (percentage) of pupating larvae in comparison with ant groups without queens (Brian, 1963, 1968).

The fact of a photoperiodic regulation of seasonal development was revealed in *M. rubra* (Kipyatkov, 1972, 1974) allowed realization of another scheme of experiments for studying the social regulation of both the development and diapause. The physiological state of workers can be readily changed by photoperiodic influences: at a short (less than 15 h) day period, a diapause started in ants; however, a subsequent two-week exposition at a long day and optimum temperatures caused photoperiodic reactivation and resumption of physiological activity (Kipyatkov, 1977). The experiments showed that larvae do not perceive the photoperiod on their own; their development is totally controlled by caring workers. Long-day (i. e., maintained at a long day for a long time) and, hence, physiologically active workers stimulate rapid growth and pupation in both developing summer and diapausing autumn larvae. Short-day (i. e., maintained for long enough time at short-day photoperiods) and, hence, physiologically inactive (diapausing) workers

are unable to stimulate growth and pupation of larvae, including summer ones, which in this case start to diapause (Kipyatkov, 1974a, 1976). Thus, short-day workers provoke a diapause in larvae, while long-day workers interrupt it, i. e., reactivate the larvae.

It is natural to ask a question: do any similar social regulatory mechanisms of development and diapause occur in other ant species and to what extent they differ from the scheme of regulation established for *Myrmica rubra*? In order to answer this question, we started a series of extensive comparative investigations of various ant species by methods tested earlier on *M. rubra* (Kipyatkov and Lopatina, 1994). The first results were obtained by us on representatives of the genera *Camponotus* and *Tetramorium* (Kipyatkov and Lopatina, 1995) and appeared to be similar to the data available for *M. rubra*, excluding photoperiodic regulation of the diapause which is not observed in most of experimental ants (Kipyatkov, 1993). Overwintered individuals of *Camponotus herculeanus*, *C. japonicus*, and several species of the genus *Tetramorium* are able to stimulate rapid growth and pupation of diapausing autumn larvae in the same way as *Myrmica*; at the same time, no wintered (i. e., reactivated by cold) larvae develop and pupate when being fed by diapausing autumn workers.

The present work is concerned with the social regulating mechanisms of diapause beginning and termination in one of the most common Palearctic spe-

cies, *Leptothorax acervorum* (Fabr.). The method used in our investigations is based on an artificial destaging of annual developmental cycles in experimental colonies. It allows a researcher to possess simultaneously colonies in a spring physiological state, i. e., ready to start their next developmental cycle, and autumn ones that have finished their development and stay in diapause. In this case, experiments with controlled transition (exchange between colonies) of diapausing or developing larvae, diapausing or ovipositing queens into other nests with reactivated (spring) or diapausing (autumn) ants become possible. As a result, regulatory influences of worker ants on larvae or queens, provoking a diapause or, on the contrary, renewing development and oviposition, can be distinguished and studied. Other forms of social regulation may also be revealed, e. g., influence of queens on larval development or hypothetical possible influence of larvae on workers and ants.

Preparation of such experiments is very laborious and time-consuming. Ant colonies that have finished their development in autumn are placed in a refrigerator for artificial wintering at 3–5°C. After 3–4 months, when cold reactivation has already finished, the whole material is divided into two parts: some nests are placed in optimum conditions for development, others are left in refrigerator, in a situation of artificially prolonged wintering. A normal full annual developmental cycle, which finishes after 3–4 months with a diapause, occurs in colonies transported into optimum conditions. After that, the ant colonies which stay in refrigerator, being ready for spring development, are also placed in optimum conditions; experiments with exchanges of larvae and (or) queens between colonies (just overwintered and diapausing) start immediately.

#### MATERIALS AND METHODS

Ants used in the experiments were collected in August 1994 in dead wood on forest glades in environs of settl. Vyritsa, Gatchina district, Leningrad Region. They were maintained in laboratory nests (formicaria) made of plastic Petri dishes, under “autumn” conditions, i. e., at a 12 h day length and 20°C temperature. After pupation of larvae and oviposition by queens in the beginning of October, ants were placed in refrigerator for wintering at a temperature 3–5°C.

Then the material was divided into two parts (figure): some nests were placed in conditions favor-

able for development conditions (23°C and 20 h day length) in the beginning of January, 1995; others stayed in refrigerator. It is known that *L. acervorum* belongs to a group of endogenous-heterodynamic species, i. e., its annual developmental cycle is obligatorily limited and diapause begins independently of the maintenance conditions (Kipyatkov, 1993). Therefore, development in experimental colonies stopped after 3–3.5 months, larvae and pupae disappeared, i. e. a diapause began in larvae, queens, and workers. *L. acervorum* larvae winter mainly as two last (III and IV) instars; larvae of IV instar vary from small to very large. Large larvae develop in spring into winged males and females, and smaller larvae into workers (Buschinger, 1973, 1987).

In the middle of April, 1995, the nests which were left in refrigerator were also placed in warmth, and, immediately after that, an exchange of larvae between these newly overwintered groups of ants and those colonies whose annual developmental cycle had terminated with a diapause was performed. Thus, there were four main experimental variants: (1) overwintered workers with overwintered larvae; (2) overwintered workers with diapausing larvae; (3) diapausing workers with overwintered larvae; and (4) diapausing workers with diapausing ants.

Larvae were divided into two categories: “large” (with body longer than 2 mm) and “small” (shorter than 2 mm); both groups were used in the experiments separately, because differences in size are related to differences in their development and bias towards a caste. Rather small number of large larvae were found in overwintered ant colonies; therefore, they were used only in variant 3. Large diapausing larvae were more abundant and were used in both variants of experiments (nos. 2 and 4). Thus, 30 ant colonies and 7 experimental variants were used. The majority of colonies consisted of several dozens of workers and a fertile queen. Eighty to one hundred large larvae were placed in every colony. The initial number of small larvae was determined approximately, because of the impossibility to count them precisely, and in every experimental colony (see Table). In this connection, part of pupated small larvae could be determined only as percentage of individuals that survived during an experiment (this number was determined very accurately for all the sets).

Ants were fed with dissected cockroaches (*Nauphoeta cinerea*) and 15% sugar solution twice a week.

Results of experiments with *Leptothorax acervorum*

Data			Overwintered workers			Diapausing workers						
			overwintere- red larvae	diapausing larvae		overwintered larvae		diapausing larvae				
			No. of experimental set									
			1	2		3		4				
			Size of larvae									
			small- medium	large	small- medium	large	small- medium	large	small- medium			
			Number of groups									
			3	5	5	7	6	1	3			
			Number of larvae in a group									
			100–200	100	150–270	80	120–150		100–160			
			total									
			400–500	500	1000– 1100	560	600–700	100	350–400			
			Survived larvae	number	min	94	84	118	30	63	–	95
					max	180	98	262	71	117	–	156
aver.	148.3	91.6			190.0	58.4	96.8	–	120.7			
± σ	47.27	5.32			56.42	14.66	20.08	–	31.63			
Σ	445	458			950	409	581	99	362			
% of total number	number	min	–	84.0	–	37.5	–	–	–			
		max	–	98.0	–	88.8	–	–	–			
		± σ	–	91.6	–	73.1	–	–	–			
		Σ	–	5.32	–	18.34	–	–	–			
		–	–	91.6 <sup>a</sup>	–	73.0 <sup>a</sup>	–	99.0 <sup>a</sup>	–			
Pupated larvae	number	min	85	3	31	30	61	–	1			
		max	177	24	95	71	113	–	4			
		aver.	143.3	12.6	63.0	58.4	91.7	–	2.7			
		± σ	50.72	7.89	28.61	14.66	19.85	–	1.53			
		Σ	430	63	315	409	550	2	8			
	% of total number	number	min	–	3.0	–	37.5	–	–	–		
			max	–	24.0	–	88.8	–	–	–		
			aver.	–	12.6 <sup>a</sup>	–	73.1 <sup>a</sup>	–	–	–		
			± σ	–	7.89	–	18.34	–	–	–		
			Σ	–	12.6 <sup>a</sup>	–	73.0 <sup>a</sup>	–	2.0 <sup>0</sup>	–		
	% of survived	number	min	90.4	3.6	23.8	100	90.7	–	0.6		
			max	98.3	24.5	40.1	100	97.3	–	3.6		
			aver.	95.6 <sup>a</sup>	13.4 <sup>abc</sup>	32.1 <sup>abc</sup>	100 <sup>c</sup>	94.6 <sup>b</sup>	–	2.5 <sup>abc</sup>		
± σ			4.53	7.82	87	0	2.80	–	1.63			
Σ			96.6 <sup>ab</sup>	13.8 <sup>abc</sup>	167	100 <sup>bc</sup>	94.7 <sup>bc</sup>	2.0	2.2 <sup>ab</sup>			
Not pupated larvae	number	min	3	74		0	2	–	92			
		max	9	82		0	9	–	155			
		aver.	5.0	79.0	127.0	0	5.2	–	118.0			

The number of pupated and not pupated larvae was approximately determined with a binocular light microscope during weekly examination of nests. Ants were immobilized with carbon dioxide for a short time, in order to calculate the breed accurately. This procedure was performed 2–3 times during the experiment. All pupae were removed and counted, eggs laid by the queen and 1st instar larvae emerged from these eggs were also removed in order not to mix them with larvae placed in nests at the beginning of the experiment. The experiment finished after 2.5 months, when pupation of all larvae under study terminated. All not pupated larvae left in nests were counted at the close of the experiment.

Results were processed using common methods of analysis of variance, with the arithmetic mean and standard deviation calculated (in cases when number of replications exceeded 2). The significance of mean differences was estimated by Student's criterion, and significance of differences of fractions (percentage) calculated from the total numbers was determined by the  $\phi$  method and Fisher's criterion (Plokhinskii, 1970). The data obtained are summarized in the table.

## RESULTS AND DISCUSSION

Survival of larvae was high enough (no less than 84%) in variants with diapausing larvae. In set 3, overwintered larvae possessed a reliably lower mean level of survival (37.5–88.8%); this is, undoubtedly, explained by less favorable environmental conditions (no diapausing workers could provide sufficient feeding for larvae).

Now, let us examine larval pupation in the main experimental sets. In all the four groups with diapausing larvae cared by also diapausing workers (set 4), only several larvae (about 2%) pupated out of more than 450 survived. In fact, this variant is a control one and demonstrates a sufficient stability of the larval diapause in autumn ant colonies. In the same manner, set no. 1 with overwintered workers and larvae could be taken as a control: there, the overwhelming majority (from 90.4 to 98.3%) of survived larvae pupated, in the same manner as it happens in natural ant nests.

Results of two other experimental sets are especially interesting. Overwintered workers provoked pupation only in an insignificant part of diapausing larvae (less than 40% of survived specimens) (set no. 2) and most of them (59.9–96.4%) stayed diapausing. Thus, overwintered workers could stimulate pupation

only in some diapausing larvae, among which the number of small individuals markedly exceeded that of large ones (32.1 and 13.4% on the average, respectively; mean significant differences between arithmetic means; the table). This testifies to the stronger stability of large in comparison with small ones. Similar dependence of diapause stability on larval size was observed by Brian (1955, 1968) and Kipyatkov (1974a) in *Myrmica rubra*.

Entirely unexpected results were obtained in set no. 3: diapausing workers could not prevent rapid growth and development of overwintered larvae, most of which pupated (90.7–100% of survived individuals). This fact would be less surprising if mainly large larvae pupated. The point is that the main growth of larvae of reproductive individuals in the annual developmental cycle of ants of the genus *Leptothorax* occurs in the end of summer and in fall. During this time they slowly increase their weight, being already in the state of a diapause, and are large enough to finish their development and pupate in the beginning of wintering (Plateaux, 1970, 1971; Buschinger, 1973; original data). Therefore, they need practically no food and pupate already during first warm days.

We conducted a special experiment with 50 medium and large larvae, taken from refrigerated inactive *L. acervorum* colonies and placed in a Petri dish on a damp cotton without worker ants. Twenty of them died during the first three days at a temperature about 20°C; however, others significantly grew owing to absorbed water (larvae dehydrate during wintering, become smaller, their integument wrinkles up), their cuticle became smooth, i. e., they looked exactly like developing spring larvae. By the third day, two larvae defecated and turned into prepupae. After two next days, 11 and after a week 8 more prepupae added to them. Thus, 29 of 50 larvae maintained without workers died during 12 days and the rest successfully turned into prepupae. Surely, no pupation occurred, because this process needs an obligatory participation of workers, helping pupae to get rid of their larval integument. However, the largest overwintered *L. acervorum* larvae can evidently pupate without any care and additional feeding provided by workers.

Analysis of the results of the conducted experiment shows that it is no surprising that no diapausing workers are able to prevent pupation of large overwintered larvae. However, nearly all small larvae that stayed in nests together with autumn diapausing workers (90.7–

97.3%) pupated in our experiment. Evidently, no larvae could grow, develop, and pupate without sufficient feeding and caring by workers. Could diapausing workers have provided sufficient conditions for larvae if their physiological state was stable? Apparently, no. We assume that in this case it is overwintered larvae that in some way influenced the workers, leading to either partial restoration of the physiological activity of workers or even to full termination of the diapause. During our experiments, we obtained facts confirming this assumption.

In all colonies of set 4, queens staying with diapausing workers and larvae were diapausing and no eggs were laid. At the same time, in all colonies of set 3 with reactivated (not diapausing) larvae, all queens began to lay eggs and continued oviposition till the end of the experiment. It seems reasonable to assume that their diapause was terminated owing to the stimulating affect of overwintered larvae. Unfortunately, aims of the conducted experiment were somewhat different and, thus, our methods were insufficient to count exactly the eggs laid by the queen.

As mentioned above, during our experiment we removed eggs laid by a queen and emerged larvae from the nest. However, in nests with large overwintered larvae (experimental set no. 3) eggs were removed either not always or in some cases not at all, because large larvae pupated very rapidly and it was impossible to confuse them with larvae emerged from eggs. It is this "violation" of the method that allowed us to reveal one more interesting effect: larvae emerged from eggs grew rather rapidly and some of them even pupated. It is necessary to explain that larvae which develop from laid eggs and pupate in the same summer are usually called rapid breed (Brian, 1968, 1983). In *L. acervorum* colonies, the rapid breed is usually either absent or very small in number, and most of larvae emerged from eggs diapause and winter (Buschinger, 1973). In our experiments, we succeeded in obtaining a small amount of rapid breed in this species only at especially favorable conditions (temperature higher than 25°C or thermoperiod, sufficient amount of food and number of workers in nests). The appearance of the rapid breed at least in some experimental colonies of set no. 3 testifies to a sufficient activity of workers in relation to larval care.

We assume that overwintered larvae of *L. acervorum* can somehow stimulate queens and workers (neither source nor nature of these hypothetical stimuli

are known), provoking termination of diapause. Workers reactivated in this manner provide a sufficient care for both overwintered larvae and those emerged from eggs laid by the queen. Surely, this type of social regulation, found for the first time, will need future special investigations which will help to distinguish its mechanisms, role, and place in ant social organization.

It is also necessary to mention differences in number of reproductive specimens, winged males and females, which appeared in various experimental sets (Table). First of all, large overwintered larvae in set no. 3 developed mainly into males and females (85.7–98.5%). Small and medium larvae produced a significantly smaller number of reproductive individuals. Their fraction was noticeably and reliably higher (69.6% on the average) in set no. 1 (i. e., in the case when larvae were fed by overwintered workers) in comparison with set no. 3, where workers were diapausing (41.5% on the average). Winged individuals, which developed from overwintered larvae, included males and females (ratio 1:1) in all sets. All this agrees well with the available data on mechanisms of caste differentiation and raising of winged individuals in ants of the genus *Leptothorax* (Plateaux, 1970, 1971).

The fact that diapausing larvae fed by overwintered workers also developed into reproductive individuals (however, mainly into females; only two males developed) deserves a special attention. As much as 62.5% (25.4% on the average) of large and 20.98% (11.1% on the average) small pupated larvae turned into winged females; however, mean differences between large and small larvae were insignificant there owing to a great variability of this index. As is known, larvae of *Leptothorax* ants must pass through an obligatory diapause and wintering when developing into winged females; when reactivation is spontaneous, i. e., winter cooling is lacking, diapausing larvae always develop into workers (Plateaux, 1970, 1971). The same was established by Brian for *M. rubra* (see above). Only workers or males always developed in all our experiments with *Myrmica* when larvae were reactivated by either photoperiod or by workers. At the same time, overwintered *L. acervorum* workers were able to raise a significant number of winged females from diapausing larvae in our experiment. This interesting fact needs further careful study. It is also unclear why no males were raised in this set together with females?

Thus, *L. acervorum* workers possess very limited abilities to control the beginning and termination of the larval diapause in comparison with species investigated by us earlier. Indeed, control by workers is total in *C. herculeanus*, *C. japonicus*, and species of the genus *Tetramorium*.

Overwintered workers of these species are able to stimulate the development and pupation in practically all diapausing larvae, and diapausing workers stop development in all overwintered, i. e., spring larvae; no larvae pupate in these conditions (Kipyatkov, 1979; Kipyatkov and Lopatina, 1994, 1995). In the same manner short-day workers of *M. rubra* induce diapause in all larvae, and long-day workers provoke termination of diapause and pupation in practically all larvae (Kipyatkov, 1974a, 1976). Thus, the development of larvae in all these species is very variable and totally controlled by workers which induce a diapause or stop it. It looks like only workers, and not larvae of these ants are reactivated by cold during wintering. Of course, this statement is not entirely correct, and the physiological state of larvae also changes during wintering; however, this question is beyond the scope of the present work.

The development of *L. acervorum* larvae is not so variable, and workers cannot practically control the beginning and termination of diapause. Moreover, spring, i. e., reactivated by cold during wintering, *L. acervorum* larvae are able to both develop and pupate irrespective of the physiological state of workers and strong activating influence on queens and workers.

The necessity to conduct further studies of both *L. acervorum* and other ant species and genera is especially evident in the light of our results; apparently, it will lead to discovery of other schemes of control over development and diapause in the family Formicidae.

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