Entomological Review, Vol. 79, No. 9, 1999, pp. 1138–1144. Translated from Entomologicheskoe Obozrenie, Vol. 78, No. 4, 1999, pp. 804–813.

Social Regulation of Larval Diapause by Workers in Three Species of the Ant Genus *Myrmica* Latreille (Hymenoptera, Formicidae)

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Received February 23, 1998

Abstract—Larvae were experimentally exchanged between the ant colonies collected in nature in spring just after hibernation, and the laboratory colonies which had been in diapause. Three experimental variants were used: (1) overwintered workers with overwintered larvae; (2) overwintered workers with diapausing larvae; (3) diapausing workers with overwintered larvae. The experiment was performed for 2–3 months, until the process of pupation was completed. In variant 1, all surviving larvae of *M. rubra* and *M. ruginodis* and 84% of *M. lobicornis* larvae pupated. However, not all spring larvae pupated when fed by diapausing workers (variant 3); the percentage of pupated larvae was significantly higher in *M. rubra* (on the average, 67.1% of survivors) than in *M. ruginodis* (31.7%). Therefore, workers in the autumn physiological state were able to prevent pupation and induce repeated diapause in some larvae (25–70% of survivors). The development of spring larvae in *M. lobicornis* depended on the state of workers to about the same extent as in *M. ruginodis*: only 27.8% of the surviving larvae pupated. The diapausing autumn larvae of *M. rubra* and *M. ruginodis*, fed by workers in the spring physiological state (variant 2), pupated in considerable quantity (36–100% of survivors); the percentage of pupating larvae was on the average higher in *M. rubra* (70.3%) than *M. ruginodis* (57.1%), even though these differences were insignificant. At the same time, only 3 of 300 *M. lobicornis* larvae pupated in this variant; therefore, overwintered workers of this species had almost no ability of terminating the diapause and stimulating development in autumn larvae. Of special interest is the fact that the two closely related species, *M. rubra* and *M. ruginodis*, proved to be rather similar also in the mechanisms of social control over induction and termination of the larval diapause, whereas *M. lobicornis*, a species belonging to a different taxonomic group, differed considerably from them in this respect.

The ant colony is a socially organized group of individuals, which can substantially affect the behavior, development, and physiological state of all its members. This social regulation, or social control, affects almost all aspects of the insect biology and plays the central role in the colony organization (Wilson, 1971; Brian, 1983; Passera, 1984; Hölldobler and Wilson, 1990). Social factors are also very essential in the regulation of reproduction and development in an ant colony.

Until recently, investigations of the social regulation of reproduction and development of ants have followed 2 main directions: (1) study of the influence of workers and the queen on the development and differentiation of individuals of different castes and the sex ratio in the reproductive offspring (Wilson, 1971; Brian, 1983); and (2) study of the regulation of oviposition and the queen's productivity by larval workers (Brian, 1983; Tschinkel, 1988). At the same time, the social control over the induction and termination of diapause in relation to the control over the seasonal development of ants has attracted almost no attention of entomologists (Brian, 1977, 1983), so that these aspects remained rather obscure before the beginning of our work (Kipyatkov, 1981).

First investigations in this field were conducted by Brian (1955) on *Myrmica rubra*. For his experiments, Brian used the diapausing autumn III instar larvae of varied size, looked after by workers in one of the two physiological states: (1) spring ants, which had just been reactivated after a long hibernation in a refrigerator, or (2) autumn individuals, which had passed the complete cycle of brood development for 3 or more months after hibernation, at optimal temperatures. In these conditions, the spring workers stimulated rapid growth and induced pupation in many autumn larvae. At 25°C, small larvae grew very rapidly, and the entire group pupated within 4 weeks; at 20°C, the majority of small larvae pupated, whereas a few of them grew but remained in diapause.

Among medium-sized and large larvae, no more than half of the group pupated at 25°C, and only few individuals did so at 20°C. Thus, the diapause of large larvae is much deeper and more stable than in small ones; this phenomenon will be specially discussed below.

At the same time, at 20°C the diapausing larvae only grew and almost never pupated when fed by workers in the autumn physiological state. Some large and medium-sized larvae and almost all small ones (whose diapause is not very deep) pupated only at 25°C; as shown by Brian, this temperature is considerably higher than the development optimum (21–22°C) and, therefore, stimulates the resumption of development.

Thus, workers in the spring physiological state proved to be capable of terminating the diapause in about half of the large autumn larvae and in almost all small ones. It is interesting, however, that only worker pupae were produced in this case; i.e., the autumn larvae stimulated by spring ants never developed into alate females. Wintering is necessary for the larvae to acquire such an ability. The corresponding physiological process was termed vernalization (Brian, 1955).

A similar phenomenon was observed in other ant species as well. In particular, Wesson (1940) was the first to show experimentally that alate females of *Leptothorax longispinosus* and *L. curvispinosus* can develop only from overwintered larvae. Later, the same was demonstrated for *L. nylanderi* (Chauvin, 1947; Plateaux, 1971) and *L. acervorum* (Buschinger, 1973). Hibernation of an ant colony is necessary for the larvae to develop into alate females also in *Tetramorium caespitum* (Poldi, 1961, 1963) and *Plagiolepis pygmaea* (Passera, 1969).

In experiments with separate chilling of *M. rubra* larvae and workers Brian revealed that vernalization takes place at the larval stage, because the individuals which had not overwintered never developed into alate females, even when fed by spring workers. The results obtained by this author were confirmed by Weir's experiments (1959) with the same ant species. Weir additionally demonstrated that shortly after emergence young workers resemble the autumn individuals in their physiological state, being also unable to stimulate pupation in diapausing larvae.

In similar experiments with *L. nylanderi*, Plateaux (1971) found that spring workers of this species can stimulate development and pupation of autumn larvae, which, however, develop only into workers and never into alate females. When pupation was spontaneously resumed in a colony of this ant, the larvae always developed into workers; however, spring larvae placed in such a colony became alate females (Plateaux, 1971). Therefore, vernalization in *L. nylanderi* also occurs at the larval stage.

Thus, the social mechanisms (in this case, the physiological state of the workers) control not only the induction and termination of diapause, but also the production of alate reproductives in ants. The same was revealed in experiments with *Cataglyphis cursor*. Workers of this species were able to rear alates only during the first weeks following the hibernation. The physiological state of the workers proved to be an essential factor in this case: spring workers were able to rear alate reproductives from both the very first spring eggs and from those laid in a later period, which normally develop into workers (Cagniant, 1981, 1988).

The discovery of photoperiodic reactions in ants of the genus *Myrmica* (Kipyatkov, 1972, 1974a) allowed us to develop an essentially different design of experiments for studying the social regulation of the induction and termination of diapause. The physiological state of the workers can be easily changed by the action of alternate photoperiods: the ants enter diapause at short day (less than 15 h), but the subsequent 2-week exposure to long day at 25°C results in a quick photoperiodic reactivation (Kipyatkov, 1977). Later, it was experimentally proved that the larvae of *M. rubra* do not perceive the photoperiod independently, and that their development is entirely controlled by the nursing workers. The long-day (physiologically active) workers stimulate rapid growth and pupation in both the developing summer larvae and autumn ones. The short-day (physiologically inactive, diapausing) workers cannot stimulate growth and pupation in larvae, including the summer ones, which enter diapause in this case (Kipyatkov, 1974b, 1976). Thus, short-day workers induce the larval diapause, while long-day workers terminate it, i.e., reactivate the larvae.

All these facts led to a conclusion (Kipyatkov, 1976), that larvae of *M. rubra* do not perceive the photoperiod independently; their development in summer and autumn is rather flexible and, except in some (usually the largest) individuals with stable diapause, is completely controlled by the workers, which can either stimulate development and pupation in the larvae, or induce the larval diapause.

When studying the mechanisms of social regulation, we widely used the experimental scheme introduced by Brian (1955), which was extended by including the overwintered (i.e., subjected to cold reactivation) larvae and queens. This approach is in fact based on the artificial misphasing of the annual development cycles of experimental colonies, allowing one to simultaneously work with ants in the spring physiological state, i.e., ready to begin the next development cycle, and with the autumn colonies which had already completed development and entered diapause. In this case, one can perform experiments with controlled transfer (exchange between colonies) of diapausing or developing larvae, or diapausing or ovipositing queens, to/from other colonies with reactivated (spring) or diapausing (autumn) ants. Thus, the regulatory influence of workers on larvae and queens, inducing diapause or, contrariwise, resumption of development and oviposition, can be discovered and investigated. Other forms of social regulation, including the effect of queens on the development of larvae or the (hypothetically possible) influence of larvae on the workers and queens, can be revealed as well.

First experiments using this technique were conducted by Kipyatkov (1979) with *M. rubra*. They generally confirmed the results of Brian's pioneer work: small spring larvae do not pupate after the normal cold reactivation when nursed by diapausing autumn workers; whereas workers in the spring physiological state induce pupation in 85–90% of the surviving small larvae, both reactivated (spring) and diapausing (autumn). These and the preceding investigations led to the conclusion that the development of *M. rubra* larvae is extremely flexible and completely dependent on the physiological state of the workers (Kipyatkov, 1979).

The subsequent researches were carried out with two ant species of another genus: *Camponotus herculeanus* and *C. japonicus* (Kipyatkov and Lopatina, 1994, 1996). These species revealed the absolute control over induction and termination of larval diapause by workers. Workers in the spring physiological state can stimulate rapid growth and pupation in all or almost all diapausing autumn larvae, whereas autumn diapausing workers completely block the development of any larvae, including the overwintered ones, which only grow but never pupate under such conditions.

However, similar experiments conducted later with *Lasius niger* and *Leptothorax acervorum*, produced somewhat unexpected results. The social control of larval development and diapause proved to be much more restricted in these two species as compared to those studied previously. Even though overwintered (i.e., subjected to cold reactivation) workers of *L. niger* can terminate diapause in a substantial part of autumn larvae, no more than 85% of small larvae and only 30–40% of large ones (of the surviving larvae) pupate. Some, not only large but also small, spring larvae of this species develop and pupate even when fed by autumn diapausing workers; therefore, pupation of some larvae (up to 17%) is induced solely by the cold reactivation. Thus, the larval development in *L. niger* is on the whole less flexible, and not completely controlled by the workers' influence, inducing or terminating the diapause (Kipyatkov *et al.*, 1996). In *L. acervorum*, the development of larvae is even more independent, because the workers have practically no influence on the induction or termination of the diapause (Kipyatkov *et al.*, 1997).

The purpose of this work was to reveal the possible variability limits of the mechanisms of social control over the diapause within a single ant genus. For this purpose, we experimentally estimated the nature and degree of the workers' influence on the induction and termination of the diapause in 3 species of the genus *Myrmica*: *M. lobicornis* Nyl., *M. rubra* (L.), and *M. ruginodis* Nyl.

MATERIALS AND METHODS

The material for the experiments was collected in the environs of St.-Petersburg (Vyritsa settl., Gatchina District), in the summer of 1995. The ant colonies, which completed their development in autumn, were placed in a refrigerator for artificial wintering at 3–5°C. Four months later, after the cold reactivation was complete, the colonies were transferred to conditions favorable for development (22.5°C, day length 20 h), thus initiating the normal seasonal cycle of development. After 1–1.5 months, the colonies were transferred to short-day conditions (day length 12 h) at the same temperature, which resulted in a diapause 1.5–2 months later, i.e., by May 1996. At this time, colonies of the same ant species, ready for development after natural wintering, were collected in nature.

We then exchanged the larvae between natural ant colonies, which had just completed hibernation, and laboratory colonies, which had been in diapause.

The experiments included three variants of the combination of workers and larvae: (1) overwintered workers and overwintered larvae, (2) overwintered workers and diapausing larvae, and (3) diapausing workers and overwintered larvae (below, the variants are designated by their numbers). The fourth possible variant (diapausing workers and diapausing larvae) was not used, because the results of all previous investigations unambiguously indicate that larvae never pupate in this variant.

Larvae of different size (from small to the largest) were selected for experiments in approximately equal number from overwintered and diapausing colonies. Groups of 50–100 workers with 1–2 queens were used, and 20–60 larvae were placed in each group. The experiment with *M. lobicornis* included only 3 monogynous colonies with 200–250 workers each, and 300 larvae were placed in each colony. A more detailed information on the experimental groups is presented in the table.

The ants were kept at short day (12 h) and 22.5°C and fed twice a week with *Nauphoeta cinerea* cockroaches, cut in pieces, and 15% solution of honey or sugar. The number of pupated and non-pupated larvae was roughly determined during the weekly inspection of the nests with a binocular microscope. For precisely counting the brood, the ants were anesthetized with carbon dioxide for a short time. This procedure was conducted several times during the experiment; all pupae were removed and counted; eggs laid by the queens and the I instar larvae hatched from them were also removed, so as not to confuse them with the larvae which had been placed in the nests in the beginning of the experiment. The experiments were performed for 2–3 months, until the pupation of the introduced larvae ceased completely in all groups. All non-pupated larvae remaining in the groups were counted in the end of the experiments.

The percentage values were calculated from the total data, and the significance of percentage difference was evaluated using the Fisher criterion (Plokhinskii, 1970).

RESULTS AND DISCUSSION

The results of all the experiments we conducted are summarized in the table. The survival rate of larvae in most groups was above 60%. The smallest percentage of surviving larvae of *M. rubra* and *M. ruginodis* was observed in variant 2 (although the differences were not always significant), where overwintered workers stimulated the development of diapausing larvae, as usually observed in similar experiments (Kipyatkov *et al.*, 1996, 1997; Kipyatkov, 1979). The stimulating effect of the workers, aimed at diapause termination, probably creates the conditions incompatible with the physiological state of the diapausing larvae, thus causing the increased mortality. It becomes clear in this connection why the survival rate of *M. lobicornis* larvae was not lower in variant 2 than in other variants: overwintered workers of this species cannot stimulate pupation in the diapausing larvae (see below) and therefore do not reduce the survival rate.

All surviving overwintered larvae of *M. rubra* and *M. ruginodis* pupated in variant 1, where they were nursed by overwintered workers. In *M. lobicornis*, a large part of surviving larvae (84%), though not all of them, pupated. The incomplete pupation is probably related to the fact that in the experimental colonies of this species, the larvae : workers ratio was somewhat higher than in groups of *M. rubra* and *M. ruginodis*, so that not all larvae could get the sufficient amount of food; this situation is often observed in spring in natural colonies of *Myrmica* (Brian, 1978, 1983).

At the same time, pupation was far from complete in spring larvae tended by diapausing workers (variant 3). Therefore, workers in the autumn physiological state can prevent the resumption of development in a part of overwintered larvae and induce a repeated diapause in them. However, the development of many spring larvae is quite autonomous, so that they pupate in spite of the effect of diapausing workers. It is very interesting that such larvae were significantly more numerous in *M. rubra* (on the average, 67.1% of the survivors) than in *M. ruginodis* (31.7%). The development of the spring larvae of *M. lobicornis* showed approximately the same degree of dependence on workers as that observed in the larvae of *M. ruginodis*: only 27.8% of the surviving larvae pupated when nursed by diapausing workers.

Differences of quite different nature were observed between the three species regarding the influence of overwintered workers on diapausing autumn larvae (variant 2). The pupated larvae comprised a considerable percentage (from 36 to 100%) of the surviving

Experiments with exchange of larvae in ants of the genus *Myrmica*

Variants of the experiment		Group no.	Total number of larvae	Surviving larvae		Pupated larvae			Not pupated larvae		
				number	% of the total number	number	% of the total number	% of survivors	number	% of the total number	% of survivors
				Myrmica ruginodis							
Overwintered workers	Overwintered larvae	4	20	15	75	15	75	100	0	0	0
		5	20	13	65	13	65	100	0	0	0
		Total	40	28	70ab	28	70ab	100a	0	0ae	0ae
	Diapausing larvae	1	25	11	44	4	16	36.4	7	28	63.6
		2	25	11	44	6	24	54.5	5	20	45.5
		3	20	6	30	6	30	100	0	0	0
		Total	70	28	40af	16	22.9af	57.1ag	12	17.1ag	42.9ag
Diapausing workers	Overwintered larvae	6A	40	21	52.5	7	17.5	33.3	14	35	66.7
		6B	40	24	60	7	17.5	29.2	17	42.5	70.8
		8	40	12	30	4	10	33.3	8	20	66.7
		10	10	25	62.5	8	20	32	17	42.5	68
		Total	160	82	51.3bg	26	16.3bg	31.7aei	56	35ai	68.3ai
				Myrmica rubra							
Overwintered workers	Overwintered larvae	4	60	54	90	54	90	100	0	0	0
		5	60	34	56.7	34	56.7	100	0	0	0
		Total	120	88	73.3h	88	73.3cd	100.0bcf	0	0bcf	0bcf
	Diapausing larvae	1	45	38	84.4	27	60	71.1	11	24.4	28.9
		2	45	28	62.2	21	46.7	75	7	15.6	25
		3	45	25	55.6	16	35.6	64	9	20	36
		Total	135	91	67.4cf	64	47.4cf	70.3bh	27	20bh	29.7bh
Diapausing workers	Overwintered larvae	13	60	53	88.3	41	68.3	77.4	12	20	22.6
		2A	60	42	70	23	38.3	54.8	19	31.7	45.2
		8B	60	51	85	34	56.7	66.7	17	28.3	33.3
		Total	180	146	81.1cg	98	54.4dgh	67.1cij	48	26.7cj	32.9cij
				Myrmica lobicornis							
Overwintered workers	Overwintered larvae	2	300	250	83.3dh	210	70	84def	40	13.3def	16def
	Diapausing larvae	1	300	240	80ef	3	1ef	1.3dgh	237	79dgh	98.8dgh
Diapausing workers	Overwintered larvae	3	300	194	64.7deg	54	18eh	27.8dj	140	46.7dij	72.2dj

Note: The statistical evaluation of the percentage difference was performed with respect to the total number of larvae in all groups for each variant of the experiment; the significance of differences was determined between all the variants for each species and between the analogous variants for different species. The significantly different values (in most cases $P \leq 0.01$–0.001) in each column are marked with identical letters.

brood in *M. rubra* and *M. ruginodis*; the average value was higher in *M. rubra* than in *M. ruginodis* (70.3 and 57.1%, respectively), even though the difference was insignificant. At the same time, only 3 of 300 larvae of *M. lobicornis* pupated in this variant, indicating that the overwintered workers of this species have almost no ability to terminate diapause and stimulate development in the autumn larvae.

Thus, the results obtained generally confirm the previously made conclusion (Kipyatkov, 1979) that the larval development of *M. rubra* is rather flexible and controlled by workers, which can stimulate pupation or induce diapause in larvae, both during the photoperiodic control over the seasonal cycle and after the cold reactivation in spring. *M. rubra* and *M. ruginodis* proved to be rather similar in this respect. At the same time, the possibilities of social control over larval development by workers of *M. lobicornis* are much more restricted.

However, the social control over larval development by workers is by no means absolute. For example, even though the physiologically active spring workers of *M. rubra* and *M. ruginodis* can induce pupation in the majority of diapausing larvae, the diapause is not terminated in 10–15% of small larvae (Kipyatkov, 1979) and in up to 30–40% of larger ones (see above). Exactly the same situation is observed in the case of photoperiodic reactivation (Kipyatkov, 1974b, 1976): not all diapausing larvae of *M. rubra* pupate under the influence of the long-day workers, and up to 25% of them remain in diapause; these are mainly large larvae whose diapause is more stable.

Similarly, the diapausing autumn workers induce diapause only in 90–95%, but not all, of developing summer larvae (Kipyatkov, 1974b, 1976), and cannot prevent pupation in a major part (30–65%) of overwintered larvae. The latter have a high potential for development after cold reactivation and pupate even when fed by the autumn workers.

Therefore, part of larger larvae of *M. rubra* and *M. ruginodis* are practically independent of workers in their development: in autumn, their diapause is so deep that it cannot be terminated by physiologically active workers; whereas after the cold reactivation, these larvae are capable of rapid development and pupation, regardless of the physiological state of the nursing workers.

It is very interesting that the two very closely related species, *M. rubra* and *M. ruginodis*, proved to be quite similar also in the mechanisms of social control over larval diapause. At the same time, *M. lobicornis*, belonging to a different taxonomic group (Radchenko, 1994), differs essentially from them in these biological aspects. More detailed comparative investigations of the social regulation in *Myrmica* species are necessary to explain the observed differences to be proposed. However, it has become clear that the mechanisms of social control over the induction and termination of diapause in an ant colony may differ considerably even within a single genus, not to mention higher taxa.

The aforesaid leads to a very important conclusion (Kipyatkov and Lopatina, 1996) that the systems of social control over the induction and termination of diapause in ants are much more diverse than it was assumed only several years ago. The potential for control over larval development and diapause by the workers varies from almost complete, when the fate of the larvae is unambiguously determined by the physiological state of the nursing workers (diapausing workers induce diapause in larvae, while physiologically active workers terminate diapause and stimulate development and pupation),—to rather weak, when diapausing workers cannot prevent pupation in the majority of the larvae, reactivated during hibernation, whereas the overwintered spring workers induce development and pupation only in a small portion of diapausing autumn larvae. It is obvious that some intermediate variants of developmental control can also be realized in many species.

ACKNOWLEDGMENTS

The work was financially supported by the Russian Foundation for Basic Research, grant no. 94-04-12183, and INTAS, grant no. 94-2072.

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