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Quantitative Study of the Behavior of the Ant *Myrmica rubra* L. (Hymenoptera, Formicidae), Relative to Photoperiodic Regulation of Larval Development*

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The seasonal developmental cycle in *Myrmica rubra* L. is regulated by a long-day photoperiodic reaction (Kipyatkov, 1972, 1974a, 1981). The reduction of day length at the end of summer leads to induction of diapause in adult ants and larvae of instar III (last). The capability of photoperiodic reactivation is well developed at the optimum temperature for development (20-25°C): long day (LD) causes resumption of oviposition and pupation within 1-2 weeks (Kipyatkov, 1977). It has been established that the larvae are photoperiodically neutral. Their development is totally controlled by the worker ants feeding them. The long-day (LD) workers (i.e., those maintained under LD) stimulate diapauseless development of larvae and quickly reactivate diapausing larvae even under short day (SD). The SD workers (i.e., those maintained under SD) induced diapause in larvae even under LD conditions (Kipyatkov, 1974b, 1976).

The study of mechanisms making it possible for the worker ants to regulate larval development is of great interest (Kipyatkov, 1981). The knowledge of these mechanisms requires quantitative study of behavior of ants during larval feeding, which we previously conducted (Kipyatkov and Lopatina, 1983). On the basis of our results, a lattice diagram of the main sequences of behavioral acts of the workers during larval feeding was constructed. It was established that feeding of ant larvae begins in most cases after palpation with antennae or licking of the anterior end of its body and mouth region by the tongue. Our results confirmed the conclusions of LeMasne (1953) that exchange of signals between worker and larva takes place before feeding. The larva reacts to the palpation of the worker, especially in the mouth region, by movement of mouth parts, head, or even by bending the entire body. Such movements are often used by hungry larvae also for "soliciting" food from the workers. Such movements are performed without stimulation by the workers or in response to chance palpation with them. Workers begin to feed the larva in response to these signal movements. Palpation and licking of the anterior end of the larval body and mouth are used not only to determine the preparedness of larvae to receive food but also for additional stimulation to feeding. Therefore, we have called these behavioral acts as "stimulating." Their frequency per unit of time or as percentage of all the observed behavioral acts serves as a good index of the level of stimulating activity of worker ants during larval feeding, and can be used in the study of behavioral mechanisms of regulation of larval development by the worker.

The present article is a quantitative study of ant behavior during larval feeding under different situations, such as different photoperiodic conditions, larval reactivation, and induction of diapause.

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Materials and methods. The study was conducted in 1980 and 1981 with ants collected in midsummer oak grove of the "Les na Vorskle" Reserve (Belgorod Province). The ants were maintained in plastic formicaries. Food consisted of 15-20% sugar solution or honey and pieces of insects, usually cockroaches from the laboratory culture. The formicaries were placed in photothermostats at 20°C and 18 h day length (LD) or 12 h day length (SD). The moist nesting area, where the ants kept their brood, was not shaded, so that the ants were adapted to light and did not change their behavior during observations.

Groups of 60-80 eggs and 10 instar III larvae were used in all observations. Diapausing larvae weighing 1.5-3.0 mg were taken from the base formicaries maintained under SD, in which pupation had stopped at least two weeks before the beginning of observations. The developing larvae originated from the groups maintained under LD from midsummer, and only small larvae weighing 0.5-1.0 mg were used, which had not reached the stage at which diapause is possible (Brain, 1968); i.e., they were definitely nondiapausing. The SD workers for observations originated from the groups maintained under SD for at least a month, and LD workers from the groups maintained under LD (summer), or (in autumn and winter) were obtained by 2-3 weeks of reactivation of SD workers under LD at 25°C.

Four treatments of conditions were used in the experiments.

1. **Long day**—groups of ants and developing larvae maintained under LD. Most larvae pupate under these conditions (Kipyatkov, 1974b, 1976).

2. **Short day**—groups of SD workers and diapausing larvae maintained under SD. The larvae do not pupate under these conditions when maintained in the laboratory for a few months (Kipyatkov, 1974a).

3. **Reactivation**—groups of LD workers obtained by photoperiodic reactivation (see above) and diapausing larvae maintained under LD. In this situation, the workers cause reactivation of larvae and resumption of pupation within 2-3 weeks (Kipyatkov, 1974b).

4. **Induction**—groups of SD workers and developing larvae maintained under SD. Under these conditions, if the larvae has still not passed the stage at which diapause induction is possible, their development stops and they do not pupate (Kipyatkov, 1974b).

Preliminary observations showed that the ants very rarely feed the larvae under SD conditions. Therefore, with a view to stimulate larval feeding and reduce the observation period, starved larvae were used in all treatments. Usually they were obtained by maintaining without workers for 12 h or taken from from the nests in which food was not given for one week.

The experiments were conducted as follows. The group of workers without larvae received food, and fed for one hour. Thereafter, 10 hungry larvae were added to the workers. After 0.5 h, when the workers calmed down, observations were started. The larvae were removed after one hour of observations. New larvae were used for regular observations, so that their physiological condition was standard in each treatment. Therefore, the results obtained characterized the behavior of ants in the first period of their interaction with larvae in a given physiological condition.

The observations were recorded in thermostatic premises at 20°C, which does not differ from the temperature of permanent maintenance of ants. The observations were recorded with the help of a binocular microscope. One of the larvae in a group was selected alternatively, and all the manipulations done by the ant with it as well as the reaction of the larva to the manipulations were recorded. This was followed by observations on the next larva, and so on, for 1 h. The behavioral acts were recorded on audio tape. This information was subsequently transferred to paper in the form of a chain of behavioral acts. The total duration of observations in different treatments was: LD 6 h, SD 11 h, reactivation 8 h, and induction 7 h. The data were analyzed statistically by the standard methods using Student's, Fisher's, and Kolmogorv-Smirnov's tests (Plokhinskiy, 1970).

RESULTS AND DISCUSSION

The number of behavioral acts recorded in each treatment was: LD 1294, SD 3035, reactivation 4732, and induction 1414, or 215.7, 275.8, 591.5, and 202.0 behavioral acts per hour, respectively (Table 3). Therefore, the behavioral activity was almost 3 times as much under reactivation as in the other treatments, where it was almost of the same order. The total number of interactions of workers with larvae in one hour was also much higher during reactivation (Table 1). By interaction, we mean the entire period of manipulation of a worker with the larva, from the first touch until changeover to actions not related to the larva. Larval feeding was observed only in a small part of interactions (interaction with feeding), and was not found in other cases (interactions without feeding).

Analysis of all the data leads to the conclusion that the frequency of behavioral acts and their relationship with each other are mainly determined by the combination of physiological condition of the workers and larvae. It is known that diapausing larvae of *Myrmica rubra* continue feeding (Brain, 1967) but consume much less food than developing ones. It is logical to assume that the diapausing larvae should react less to food offered by the workers than do the developing larvae. It is also reasonable to conclude that the more active LD workers should "try" to feed the larvae more frequently than do the less active SD workers (Kipyatkov, 1976). These conclusions explain the main peculiarities of interaction between the workers and larvae in different experimental treatments.

For instance, the number of interactions with feeding per hour and their frequency (%) is minimum under SD (Table 1); lower activity of SD workers is combined with "poor appetite" of diapausing larvae in this combination. Activity of SD workers is low under induction, but the developing larvae demand more food. As a result, the frequency of interactions with feeding is much higher than under SD (differences significant at $P > 0.99$). Under LD conditions, the developing larvae need much food, and the active LD workers offer them food much more frequently. Therefore, interactions involving feeding have a much higher percentage under LD (Table 1) than in other treatments (differences significant at $P > 0.99$). Reactivated ants were used in the treatment with reactivation (see Materials and Methods), which are much more active than the LD

Table 1

Frequency of interactions of workers with larvae per hour of observations

Type of interaction	Treatments							
	long day		short day		reactivation		induction	
	number	%	number	%	number	%	number	%
With feeding	16.3	23.2	4.5	5.5	23.3	16.5	10.9	15.3
Without feeding	54.0	76.8	77.8	94.5	117.6	83.5	60.1	84.7
Total	70.3	100.0	82.4	100.0	140.9	100.0	71.0	100.0

Table 2

Mean number ($\bar{x}$) of behavioral acts and feeding in one interaction of a worker ant with larva

Type of interaction	Treatment conditions	Total number of interactions (N)	$\bar{x}$	Standard error ($\pm m$)	Criterion of significance by Student's test		
					LD	SD	reactivation
		No. of behavioral acts					
Without feeding	LD	324	2.4	0.10	—	—	—
	SD	856	3.0	0.11	4.62 ***	—	—
	Reactivation	936	3.1	0.10	5.60 ***	0.62	—
	Induction	421	2.4	0.09	0	4.15 ***	5.14 ***
With feeding	LD	98	5.6	2.6	—	—	—
	SD	50	8.5	0.89	3.23 ***	—	—
	Reactivation	191	9.5	0.43	7.64 ***	0.94	—
	Induction	76	5.1	0.29	1.33	3.76 ***	8.41 ***
		No. of feedings					
With feeding	LD	98	1.4	0.09	—	—	—
	SD	50	2.2	0.27	2.81 **	—	—
—	Reactivation	191	2.4	0.12	6.54 ***	0.51	—
	Induction	76	1.3	0.06	1.70	3.47 ***	8.25 ***

Note. Differences of means significant at: $^{**}P > 0.99$, $^{***}P > 0.999$.

workers (Kipyatkov, 1976). Therefore, the total activity of ants (Table 3) and absolute number of interactions with feeding per hour (Table 1) were much higher in this treatment. However, the percentage of interactions with feeding out of total behavioral acts was significantly lower (P. 0.999) under reactivation than under LD (Table 1). This is easily explained by the fact that the diapausing larvae react more rarely to the food offered by the workers (see below regarding the larval response to the activity of workers).

Duration of interactions of the ants with larvae, measured through the number of behavioral acts in one interaction, also differs significantly in different treatments (Table 2). The mean duration of interactions with as well as without feeding was significantly longer under SD and reactivation than it was under LD and induction. The differences between SD and reactivation or between LD and induction are very small and are nonsignificant (Table 2). Similar results were obtained from a comparison of distributions of a number of interactions on the basis of their duration, with the help of the test of Kolmogorov—Smirnov. Therefore, the duration of interactions of ants with larvae, and mainly those accompanied by feeding, generally depends on the physiological conditions of larvae: the interactions with diapausing larvae were generally longer than those with active larvae. Possibly, the LD as well as SD workers require more effort to enter into close contact with a diapausing larva and induce reaction and feeding.

The physiological condition of workers has only very little effect on the duration of their interactions with larvae: the contacts of LD workers with larvae are generally slightly longer than those of SD workers (compare LD with induction and SD with reactivation in Table 2), but these differences are nonsignificant in their means (Table 2) as well as in the nature of distribution.

During a single continuous interaction with larva, an ant may give it food several times (LeMasne, 1953; Kipyatkov and Lopatina, 1983). The mean number of such "elementary" feedings in one interaction (Table 2) also depends mainly on the physiological conditions of larvae; it

Table 3

Frequency of different behavioral acts during interactions of workers with larvae (per hour of observations)

Behavioral acts	Frequency in different treatments							
	long day		short day		reactivation		induction	
	number	%	number	%	number	%	number	%
Palpation of body	45.5	21.1	80.7	29.3	112.3	19.0	54.9	27.3
Licking of body	38.2	17.7	41.3	15.0	61.9	10.5	37.4	18.6
Palpation of anterior end of body	40.5	18.8	58.8	21.3	153.8	26.0	33.7	16.7
Licking of anterior end of body	37.2	17.2	35.6	12.9	119.1	20.1	23.9	11.8
Palpation of posterior end of body	16.0	7.4	25.7	9.3	49.0	8.3	17.3	8.6
Licking of posterior end of body	11.7	5.4	20.7	7.5	36.8	6.2	15.0	7.4
Transportation of larva	3.0	1.4	2.7	1.0	1.8	0.3	5.3	2.6
Feeding with liquid food	23.3	10.8	10.1	3.7	56.5	9.6	13.7	6.8
Feeding with eggs	0	0	0	0	0.1		0	0
Feeding with insect pieces	0	0	0	0	0.1		0	0
Absorption of anal fluid	0.3	0.2	0	0	0.1		0.4	0.2
Total	215.7	100	275.8	100	591.5	100	202.0	100

is significantly higher in treatments with diapausing (SD and reactivation) than with developing larvae (LD and induction). This is possibly explained by the fact that the diapausing larvae swallow food unwillingly and that more "elementary feedings are required in their case, or by the fact that they prefer to eat food in smaller portions.

The physiological conditions of workers has very little effect on this parameter: the mean number of feedings per interaction is slightly higher in LD than in SD workers (compare LD with induction and SD with reactivation in Table 2), but these differences are nonsignificant.

The frequency of different behavioral acts during interaction of ants with larvae significantly varies in different treatments (Table 3). The number of larval feedings per hour differs in various treatments precisely as the number of feeding contacts (Table 1), and decreases in the following series: reactivation 56.5 ± 5.53 ($n = 8$); LD 23.3 ± 5.49 ($n = 6$); induction 13.7 ± 2.04 ($n = 7$); and SD 10.1 ± 4.13 ($n = 11$) (standard error of mean even taking into account variations between different hours of observations). Under reactivation, this value differs significantly $P > 0.999$) from the remaining treatments, differences among which are nonsignificant ($P < 0.95$), which is simply associated with small sample size. The differences in frequency of feedings in percentage (Table 3) are also analogous to the differences in frequency of feeding contacts (Table 1). These differences were explained above.

Of all behavioral acts constituting interactions of ants with larvae, the most interesting are the manipulations with the anterior end of its body, i.e., the stimulating behavioral acts. The differences in percentage of stimulating behavioral acts between various treatments out of the total number of behavioral acts are quite illustrative (Tables 4, 5, Fig. 1).

Table 4

Frequency of different behavioral acts during interactions of workers with larvae before first feeding

Behavioral acts	Frequency in different treatments							
	long day		short day		reactivation		induction	
	number	%	number	%	number	%	number	%
Palpation of body	23	13.0	9	9.6	60	11.8	15	10.6
Licking of body	16	9.0	4	4.3	27	5.3	9	6.4
Palpation of anterior end of body	92	52.0	54	57.4	248	48.7	79	56.0
Licking of anterior end of body	35	19.2	24	25.5	149	29.3	28	19.9
Palpation of posterior end of body	6	3.4	2	2.1	16	3.1	5	3.5
Licking of posterior end of body	4	2.3	1	1.1	9	1.8	3	2.1
Transportation of larva	2	1.1	0	0	0	0	2	1.4
Total	178	100	94	100	509	100	141	100

Table 5

Frequency of different behavioral acts during interactions of workers with larvae after last feeding

Behavioral acts	Frequency in different treatments							
	long day		short day		reactivation		induction	
	number	%	number	%	number	%	number	%
Palpation of body	34	18.9	23	18.5	52	12.0	24	18.5
Licking of body	40	22.2	9	7.3	23	5.3	27	20.8
Palpation of anterior end of body	21	11.7	46	37.1	155	35.7	23	17.7
Licking of anterior end of body	53	29.4	34	27.4	157	36.2	34	26.2
Palpation of posterior end of body	8	4.4	5	4.0	5	0.9	4	3.1
Licking of posterior end of body	4	2.2	3	2.4	2	0.5	1	0.8
Transportation of larvae*	20	11.1	4	3.2	41	9.4	17	13.1
Total	180	100	124	100	435	100	130	100

Note. *Interactions of workers with larva terminates immediately after the last feeding.

For instance, frequency of palpation and licking of the anterior end of the body (and particularly, these behavioral acts in totality) was almost always significantly higher in the treatments with diapusing larvae (SD and reactivation) than in those with developing larvae (LD and induction). This is undoubtedly explained by the fact that diapausing larvae require more stimulation to begin feeding. Most illustrative in this respect is the licking of the anterior end of the larval body, as such behavior most strongly stimulates the larvae to feeding (Kipyatkov and Lopatina, 1983). The frequency of licking of the anterior end before the first feeding (Table 4) is maximum particularly in SD and reactivation, and the first feeding mostly takes place after this act (Fig. 1); after last feeding, licking of the anterior end is observed most frequently under reactivation, while in the remaining treatment it had almost equal frequency (Table 5).

The physiological condition of workers also affects this parameter. For instance, the frequency of licking of the front body was higher under activation in the treatments with diapausing larvae than under SD, before (Table 4, Fig. 1) as well as after (Table 5) feeding. Similarly, the frequency of this behavioral act was higher under LD in treatments with developing larvae than under induction (Table 5; Fig. 1), or it was at least of the same order (Table 4).

Thus, diapausing larvae require greater stimulation from the workers for feeding and, therefore, increase the frequency of palpations, especially licking of the anterior body end. In contrast, the active LD workers are more inclined than SD workers to stimulate larvae for feeding and, therefore, demonstrate stimulating behavioral acts more frequently. The level of stimulating activity of workers is also expressed in the frequency of interactions with feeding and elementary feedings, which was discussed above (Tables 1, 3). It was highest under reactivation.

Thus, the level of stimulating activity of the ants observed is determined by the combination of two factors (physiological conditions of workers and larvae), and may have 4 grades: high—reactivation (LD workers and diapausing larvae); low—induction (SD workers and developing larvae); and two middle levels—LD and SD. it is most difficult to determine the differences in mean levels, as they are variable (Tables 3-5), but if we consider that stimulation of larvae to feeding is manifested most distinctly before its actual feeding, it must be recognized that the level of stimulating activity of workers is higher under SD than under LD (Table 4; Fig. 1). Although these differences are small, they are significant ($0.95 < P < 0.99$).

Signal improvements of larvae were also recorded in these experiments, but the only sufficiently noticeable reactions were body bending, raising of head, and movement of jaws, which

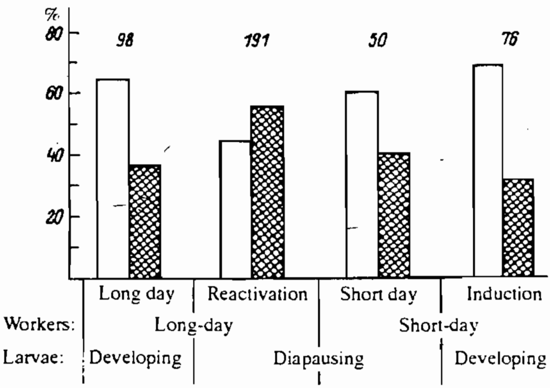

Fig. 1. Frequency of behavioral acts preceding larval feeding, by workers in different treatments. Frequency of palpation (blank columns) and licking (shaded columns) of the anterior body end of larva given as percentage of total number of behavioral acts recorded (shown by numbers), immediately after which the workers changed over to larval feeding.

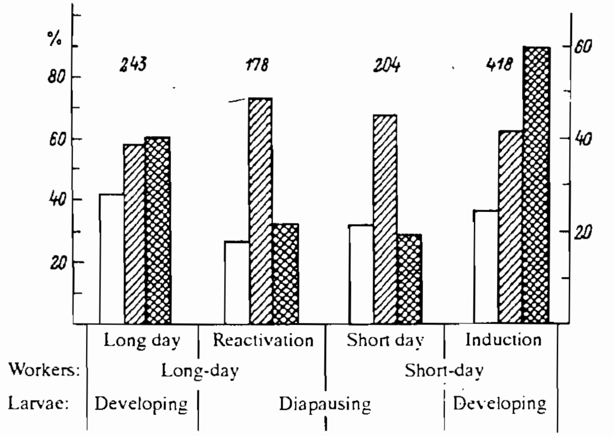

Fig. 2. Larval reactions to random and nonrandom actions of workers in different treatments. Frequency of larval reactions in response to random (blank columns) and directed (obliquely shaded columns) palpation of workers, given in percentage (left scale) of the total number of reactions recorded (indicated by numbers). Total number of reactions per hour of observations (right scale) indicated by darkly shaded columns. All differences in percentage significant at $P > 0.99$.

would be simply called reactions without precise characterization. The less noticeable reactions to the observer were not considered.

Larval reactions were observed during casual interactions of ants with them (usually random touching with larvae during movements over the nests) as well as during directed interactions with them. The percentage of reactions in response to random touch was significantly higher (Fig. 2) in the treatments with developing larvae (LD and induction). Therefore, the developing larvae react easily to any action of the workers, demanding food from them, as they are in much greater need of food than are the diapausing larvae. Higher reactivity of developing larvae is also confirmed by the fact that, on an average, the reactions per hour were more frequent in them than in diapausing larvae, in the total (Fig. 2) as well as directed actions of workers (Fig. 3). The highest frequency of reactions under induction is possibly explained by the fact that then the developing larvae receiving insufficient tactile stimulation from SD workers become more responsive.

The diapausing larvae are less reactive in comparison with the developing ones, but their reactions are more adequate; i.e., they often appear in response to the action of workers intending to feed the larvae than to other stimuli. this is confirmed by the fact that a significantly higher percentage of reactions is observed in the treatments with diapausing larvae (SD and reactivation), particularly during interactions associated with feeding (Fig. 3), and reactions in diapausing larvae (SD and reactivation) are observed much more frequently than in the developing ones (LD and induction) in response to palption or licking of the anterior body end by workers (Table 6), i.e., to the stimuli which are essential before feeding (Kipyatkov and Lopatina, 1983). Interestingly, the larval reactions are much less adequate when they are with SD workers than not with LD workers.

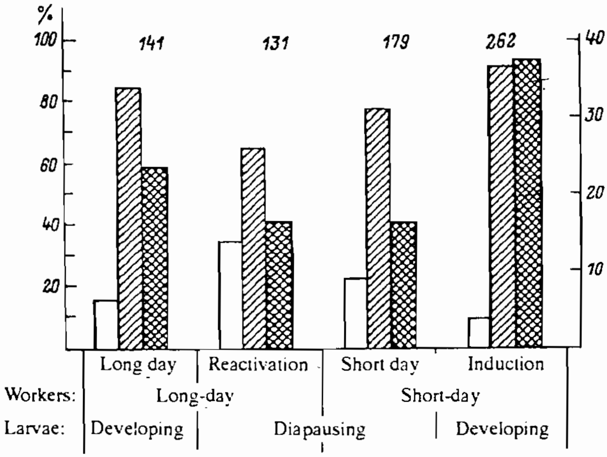

Fig. 3. Larval reactions to actions of workers under directed interactions with larvae in different treatments. Frequency of larval reactions to action of workers during interactions accompanied by feeding (blank columns) and without feeding (obliquely shaded columns) given in percentage (left scale) of total number of reactions (indicated by numbers), recorded during directed interactions of workers with larvae. Total number of such reactions per hour of observations (right scale) indicated by dark shaded columns. All differences in percentage significant at $P > 0.99$.

Table 6

Frequency of larval reactions in response to palpation or licking of their anterior or body end by workers

Type of interaction	Treatment conditions	No. of reactions recorded			Fisher's test of significance		
		total	after palpation or licking of the anterior body end		LD	SD	reactivation
			number	%			
With feeding	LD	22	11	50.0	—	—	—
	SD	39	24	61.5	0.76	—	—
	Reactivation	45	36	80.0	6.1 ***	3.52 **	—
	Induction	23	14	60.9	0.54	0.002	2.72 **
Without feeding	LD	119	58	48.7	—	—	—
	SD	140	101	72.1	15.1 ***	—	—
	Reactivation	86	67	77.9	19.1 ***	0.96	—
	Induction	239	80	33.5	7.7 ***	55.8 ***	54.6 ***
Total	LD	141	69	48.9	—	—	—
	SD	179	125	69.8	14.5 ***	—	—
	Reactivation	131	103	78.6	27.0 ***	3.1 ***	—
	Induction	262	94	35.9	6.4 ***	51.2 ***	70.1 ***

Note. Differences in percentage significant at: $^{**}P > 0.99$, $^{***}P > 0.999$.

Table 7

Probability of larval feeding after its reaction to the actions of workers

Type of interaction	Treatment conditions	No. of reactions recorded: total	with subsequent feeding: number	with subsequent feeding: %	Fisher's test of significance: LD	SD	reactivation
With feeding	LD	22	10	45.5	—	—	—
	SD	39	20	51.3	0.19	—	—
	Reactivation	45	29	64.4	2.2 *	1.5	—
	Induction	23	9	39.1	0.19	0.88	4.0 **
Without feeding	LD	141	10	7.0	—	—	—
	SD	179	20	11.2	1.68 **	—	—
	Reactivation	131	29	22.1	13.3 ***	6.7 ***	—
	Induction	262	9	3.4	2.5 ***	10.3 ***	32.3 ***

Note. Differences in percentage significant at: *$P > 0.95$; **$P > 0.99$; ***$P > 0.999$.

This aspect appears in the developing (compare induction with LD) as well as diapausing (compare SD with reactivation) larvae (Table 6). Possibly, as was mentioned above, increase in the reactivity, accompanied by reduction in adequacy of reactions, appears in the larvae as a consequence of insufficient tactile stimulation and, possibly, feeding by SD workers. This phenomenon, however, needs special study.

These results also show that the response of adult ants to the stimuli received from the larvae is to a great extent determined by physiological condition. For instance, LD workers more frequently respond to larval reactions by feeding than do SD workers in the treatments with diapausing (SD and reactivation) as well as developing (LD and induction) larvae (Table 7). Because the difference in the probability of larval feeding after reaction in the treatments with larvae in various physiological conditions is not at all clear, the LD workers (compare LD with reactivation) as well as SD workers (compare induction with SD) feed the developing larvae after reactions with almost half the frequency than they do the diapausing larvae (Table 7). Possibly, this is related to the fact that the developing larvae are more reactive (see above) and ants are found much more frequently with diapausing larvae, and therefore can respond to them less adequately. This question also requires special study.

CONCLUSIONS

1. The main quantitative parameters of ant behavior during interactions with larvae are determined by the physiological condition of workers and larvae.

2. The LD workers much more frequently try to feed the larvae and interact more intensively with them through tactile stimuli than do SD workers. The LD workers also respond better to the larval signals through feeding than do SD workers.

3. The developing larvae respond more frequently than those diapausing to the food offered by the workers. Diapausing larvae are less reactive, but their reactions are more adequate than those in the developing larvae; i.e., they are observed more frequently, particularly after specific stimuli of workers (palpation and licking of the anterior body end and the mouth region of larvae).

4. The intesity of tactile stimulation of larvae changes as a result of different combinations of physiological conditions of the workers and larvae. The intensity is maximum during photoperiodic reactivation of diapausing larvae by LD workers, minimum during induction of diapause in the developing larvae by SD workers, and medium with the reciprocal combinations of workfers and larval conditions (LD workers and developing larvae, or SD workers and diapausing larvae).

5. With an increase in the level of stimulating activity or workers, the mean duration of their interactions with larvae, mean number of feedings per interaction, and frequency of feeding and stimulating behavioral acts (especially licking of the mouth region of larvae) increase.

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