

Seasonal Development of *Aphaenogaster sinensis* in the South Primor'e: New Type of Seasonal Cycle in Ants*

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Ants overwinter with eggs and larvae of all three instars. Individual development is very slow: about 90 days from egg to pupa at 25° C. Therefore larvae emerging from eggs cannot complete development in the same summer and hibernate, i. e., there is no rapid brooding. Not all overwintered larvae pupate during the summer even at 25° C; up to 30% of them hibernate a second winter. A short day and temperatures of 17-20° C increase the percentage of larvae that hibernate a second winter. Pupation ceases in mid-August as a result of a spontaneous endogenous process of developmental potential exhaustion proceeding during the summer and the effect of the short day. All pupae complete development by September and do not hibernate. The lower temperatures in September supports larval diapause. There is no reproductive diapause in queens, and they lay eggs until the onset of cold weather. The end of the winter diapause is conditioned by cold-weather reactivation.

The seasonal developmental cycles of ants have only relatively recently attracted the attention of workers (Brian, 1977; Kipyatkov, 1981). There are few studies devoted to their phenomenological and, especially, experimental study. But they have already made particular conclusions regarding the structure, regulation and evolution of seasonal cycles within a family (Kipyatkov, 1987), possible indicating there is great promise in this field of study.

Seasonal development of ants in the genus *Aphaenogaster* has not been studied to date. There are 11 species of this genus in the USSR (Arnol'di, 1976). The range of *A. sinensis* Wheeler includes the central and northern regions of China, southern Primor'e (Maritime Territory) and Kuril' Islands (Arnol'di, 1976; Kupyanskaya, 1981). This species is spottily distributed in Primor'e and is probably a relict from the Tertiary (Kupyanskaya, 1981).

Our goal was an experimental study of the regulation of the seasonal cycle of *A. sinensis* and to collect materials on the seasonal development of this species in southern Primor'e. The authors consider it their obligation to thank A. N. Kupyanskaya of the Institute of Soil Biology, Far East Branch, USSR Academy of Sciences (DVO AN SSSR), T. G. Roman'kovaya of the Lazovskiy Reserve and V. I. Podugin, director of the Kedrovaya pad' Reserve for their help in conducting field studies.

Field work was carried out in August-September 1984 and at the end of 1985 at the Kedrovaya pad' Reserve, DVO AN SSSR, and Lazovskiy Reserve. The collected ants were kept in plastic laboratory formicaries and provided with an abundant food solution of sugar and honey and

*Originally published in Zoologicheskii Zhurnal, No. 7, 1990, pp. 69-78.

crushed *Nauphoeta cinerea* cockroaches raised in the laboratory. The experiments were performed in photothermostats with a long (17 h) and short (10-12 h) day (LD and SD, respectively) at 17°, 20° and 25° C. We briefly inactivated the ants with carbon dioxide to remove them from the nest and count eggs, prepupae, and pupae. We simulated hibernation at 0-5° C for 6 months. In all, in the experiments we used 62 groups of ants, each of which consisted of a single queen, 50-300 workers, and the brood. Statistical treatment of the results followed generally accepted methods, the significance of the differences between means was determined using Student's *t*-test, of the percentages by the ϕ -method with calculation of a Fisher test for independence (Plokhinskiy, 1970).

BRIEF DESCRIPTION OF ONTOGENESIS

Eggs are rounded, 0.5 × 0.38 mm. Three larval instars are identified. First instar larvae are completely lacking hairs with the exception of some setae on the head. Head not wider than the thorax. Mandibles are clear. Second instar larvae have clear short hairs on the head and first six segments; on each segment there are several tens of hairs uniformly distributed across the surface; on the other segments there are no hairs. Mandibles are clear. The entire body of third instar larvae is densely covered with golden red setae with hooklike bends at the tips; mandibles are brown.

The head of 2nd and 3rd instar larvae are somewhat wider than the three successive thoracic segments which form the "neck" that allows the larva to move the head to all sides and turn it into the abdomen. Abdominal segments widen gradually from the segments I to VII. Segment VIII narrows slightly. Thus, the larval body is pyriform.

First and, as a rule, second instar larvae are found together with eggs on which, most likely, they can feed. Each third instar larva is in the nest separately. Ants feed them from the mouth and also place them on pieces of prey; as a result of head mobility they gradually consume the soft tissues.

At 25° C, egg development lasts 21-23 days, 1st and 2nd instar (combined) 38-42 days, 3rd instar 28-31 days; in all, development to pupation last 85-90 days.

FIELD DATA

In excavations of nests at the Kedrovaya pad' Reserve 8-9 August 1984, we found eggs, larvae of all instars, separate prepupae, and numerous, mostly unpigmented pupae of workers and the winged forms. By 18-19 August there were virtually no prepupae; all winged forms and most workers had emerged from pupae. In excavations at the Lazovskiy Reserve 1-2 September we found in the nests eggs and larvae of all instars, a few pigmented pupae, and a small number of winged forms; only in one nest were there several prepupae. Thus, in southern Primor'e larvae cease pupation in mid-August or in the second half; thus, in the the nest prepupae disappear and then larvae. The flight of the winged forms apparently occurs at the end of August-beginning of September.

Nest excavations at the Kedrovaya pad' Reserve 24-27 April 1985 demonstrated that the ants at this time become active after hibernation. Workers, with a small number of the brood, warm up during the daytime in surface chambers under rocks, forming clusters on their bottom side; most of the brood and the queens are still in chambers at a depth of 20-30 cm where they hibernated. Soil temperature did not exceed 10° C there and the ants spent the time in a state of numbness; only those in the upper chambers and on the rocks moved slowly. The brood consisted of eggs and larvae of all instars, but the 3rd instar larvae were only small and average-sized. Since the tempera-

ture conditions ruled out oviposition by the queens at this time, we may conclude that the eggs overwintered with the larvae. When the springtime ants were kept in the laboratory, the overwintered eggs developed entirely normally.

In all nest excavations, we were able to find only one fecund queen, which points to the strict monogyny of *A. sinensis*. Winged ♀s and ♂s, which were established with all ants in the laboratory formicaries, mated, after which the ♀s shed their wings and begin to lay eggs. These eggs were fertilized since workers subsequently developed from them. In mid-August ants with winged forms, but without queens, were established in 44 nests kept at room temperature. By mid-October in 37 of them there were wingless ♀s; in 31 of them ♀s laid eggs. In another four nests ♀s remained winged or had not yet shed all wings, but in two nests they had deposited eggs. Only in three nests had all winged ♀s died. It is an interesting fact that the ants always left only one fertilized ♀ that had shed her wings in the nest and killed the rest, thus maintaining a strict monogyny.

Thus, in *A. sinensis* replacement of a disappeared queen by a young winged ♀ which the ♂s fertilized directly in the nest is possible. Ledoux (1976) observed such replacement in *A. senilis* and it most likely is typical of all *Aphaenogaster* species.

EXPERIMENTAL STUDY OF INDUCING DIAPAUSE AND REACTIVATION

Ants collected in the fall were established in formicaries and at the beginning of November were placed in a refrigerator with a temperature of 0-5° C to hibernate. At the end of May the temperature was gradually increased to 25° C; at this temperature and with a LD the ants were kept to the end of June. Eggs and larvae that successfully overwintered began to develop; queens began oviposition, the first prepupae appeared by 9 June. Beginning 30 June an experiment was begun: four nests were kept at 23° C and with a LD, five at 23° C and with a SH. Every 7-10 days prepupae and pupae in the nests were counted and other reproductive categories were recorded.

The number of prepupae and pupae during the experiment declined, but more rapidly with the SD than LD; by the 45th day pupation with a SD ceased while with a LD pupae continued to be found in the nests although in lesser amounts than at the start of the experiment (Fig. 1). Thus, the SD clearly enhances cessation of development and induces diapause in 3rd instar larvae. At the same time, with a LD the number of prepupae and pupae in the nests decreases significantly with time, although the number of larvae in them even increased because they continued to develop from eggs. Thus, with a LD the percentage of pupating larvae gradually decreases and many of them temporarily or permanently enter diapause.

We now examine the effect of temperature. After day 80 the experiment was continued with the same nests. The temperature in two nests with a SD was increased to 25° C; this caused pupation to restart (Fig. 2a). After another 5 weeks the temperature was decreased in these nests to 22° C, which resulted in a gradual decrease in the number of prepupae and complete cessation of pupation after 4-5 weeks (Fig. 2a). Thus, increasing the temperature to 25° C may interrupt diapause of some larvae with a SD and at 22-23° C diapause is rather stable.

The temperature of two nests with a LD was dropped to 20° C, this resulted in a decrease in the number of prepupae and pupae in them and complete end to pupation after 6-7 weeks, after which an increase in temperature to 22° C caused only some pupae to appear in the next 12 weeks (Fig. 2b). On the other hand, increasing temperature in two other nests with LD to 25° C caused a rapid and significant increase in the number of pupating larvae after only two weeks (Fig. 2c). A subsequent drop in temperature to 22° C led to a decrease in the rate of pupation, but later in these

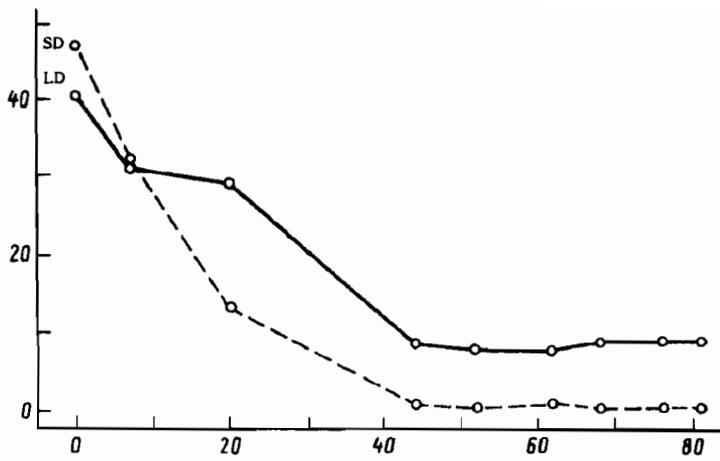


Fig. 1. Effect of photoperiod on larval pupation at 23° C: ordinate) mean number of prepupae and pupae per nest (calculated from data for 4 nests with a long day, LD, and 5 nests with a short SD); abscissa) days of experiment (started 30 June).

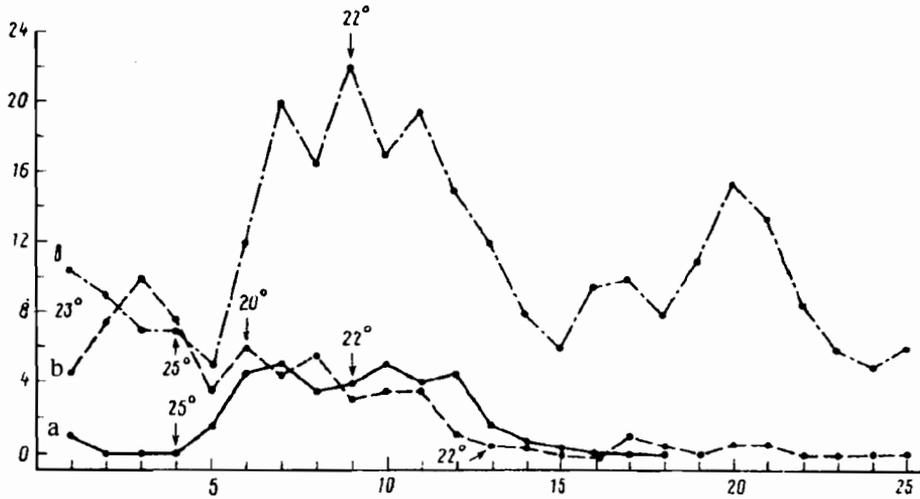


Fig. 2. Effect of temperature on larval pupation with short (a) and long (b, c) day. In each version data were averaged for two nests. Initial temperature was 23° C. Arrows indicate temperature changes during the experiment (started 31 August). Ordinate) mean number of prepupae and pupae per nests; abscissa) weeks of the experiment.

subsequent drop in temperature to 22° C led to a decrease in the rate of pupation, but later in these nests nonetheless significantly more larvae pupated (Fig. 2c) than in the two nests just described (Fig. 2b) that were at the same temperature. Most likely with a LD, a 20° C temperature creates a sufficiently strong developmental force that cannot be upset by increasing temperature by only 2°; at the same time, a 25° C temperature to a significant degree stimulates larval development, and the larvae then continue to pupate at 22° C as well.

In the following experiment the group of ants taken in the spring in nature with a queen but without brood was kept at 25° C with a LD from 21 May to 14 October and then with a LD at 22°

C for another 6 months. From eggs deposited by the queen larvae appeared that began pupation only at the start of September. Thus, larvae from eggs in theory could complete development in the same summer, but under natural conditions this is hardly observed since pupation ceases by mid-August. Thus, in *A. sinensis* in southern Primor'e there is no so-called "quick brood" (i.e., nonhibernating larvae) which, above all, results from very slow individual development.

Pupation of larvae in the experiment described continued a little more than a month and no more than 20-30 individuals pupated. In mid-October prepupae, and pupae, disappeared from the nest by the end of October. For the next 3+ months there were only eggs and larvae of all instars in the nests. But at the beginning of February prepupae again appeared; the rate of pupation rapidly increased and by the end of March there were 45-50 prepupae and pupae in the nest simultaneously. At the end of April the experiment was stopped because not enough ants survived.

The results of this experiment suggest that when ants are kept under constant conditions allowing development without diapause (LD, 22° C), from the beginning cessation of pupation is observed and then its spontaneous resumption. Similar endogenous developmental rhythms have already been described in many species of ants (Kipyatkov, 1987). In particular, in *A. subterranea* maintenance of an annual seasonal behavioral rhythm was observed under constant conditions without external time sensors: In a nest with a temperature gradient ants selected zones with a different temperature where they aggregated with the queen and brood in various periods of the year. In fact, there were two thermopreferenda: a high summer and low winter (Bruniquel, 1978). Unfortunately, data are lacking in that study on the development of the brood in the experimental family of ants.

Results of the experiment reflected in Fig. 1 also agree with the conclusion that an endogenous rhythm is present in *A. sinensis* that regulates development: with the LD there is a gradual decrease in the rate of pupation, i.e., there is a reduction in the tendency toward development without diapause. Thus, cessation of development at the end of summer in *A. sinensis* as in many other ants (Kipyatkov, 1987) is caused on the one hand by spontaneously proceeding endogenous physiological process of decreasing potential for development without diapause, and, on the other hand, the exogenous effect of a contracting day (photoperiod reaction). Since August is the warmest summer month in south Primor'e, cessation of pupation in mid-August cannot even partially be caused by a drop in temperature. However, the temperature reactions identified above may participate in maintaining the stability of diapause in larvae in the fall when there is cooling.

In all the experiments described above the queens continuously laid eggs, and thus in the nests there were always eggs and larvae of all instars. The absence of diapause in the queens is confirmed also by the results of a fall experiment conducted in 1984. Ants collected in nature in August to mid-October were kept at room temperature and then under six experimental conditions: 25°, 20°, and 17° C with a SD or LD. The eggs deposited by the queens were removed and counted weekly. Under all conditions the queens laid eggs during the entire experiment, and while the rate of egg-laying underwent considerable fluctuation, there was no distinct tendency toward reduction (Fig. 3). On average for the entire period of the experiment, productivity of the queens was very similar under all conditions and was independent of photoperiod and temperature (Table 1).

Thus, in *A. sinensis* queens, there is no winter reproductive diapauses and oviposition does not cease even at 17° C and with a short day. Most likely, the queens cease laying eggs only when the temperature drops below a threshold. It is just for this reason that in the nests there are always eggs and larvae of all instars and that all these stages hibernate.

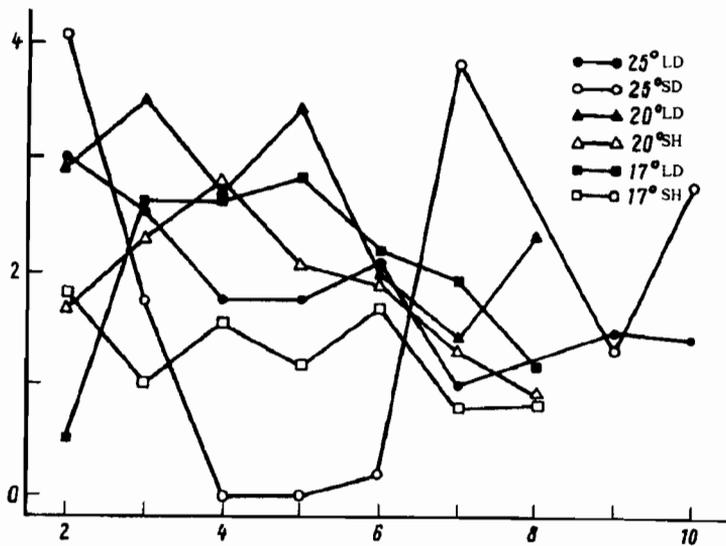


Fig. 3. Dynamic of productivity of queens in the fall with a long day (LD) and short day (SD) and at various temperatures (experiment begun 19 October). Ordinate) mean number of eggs per queen per 24 h; abscissa) weeks of the experiment.

The low productivity (on average, on the order of two eggs per day) of the queens recorded in the fall experiment is also very interesting. Perhaps this is partially explained by an insufficient number of workers to ensure abundant feeding of larges queens in the experimental nests. More likely, however, the productivity of the queens by fall is reduced by a spontaneous drop in the potential for active development. Unfortunately, we were unable to determine queen productivity in summer.

In the same fall 1984 experiment, we recorded the condition of the larvae. At 17° C, diapause in 3rd instar larvae was entirely stable: Only slight growth was observed and there was not a single cause of pupation. At 25° C many larvae grew and pupated. In so doing, a distinct photoperiod effect was demonstrated: in 8 weeks with a LD in 5 nests on average 11.4 larvae pupated per nests, with the SD in 4 nests only 2.0 per nest and the majority of them pupated in the first 10 days of the experiment; after this, pupation practically ceased. At 20° C an intermediate situation was observed: With a SD there was no pupation, with the LD in 5 nests only 1.6 larvae per nest pupated.

Thus, diapause in 3rd instar larvae of *A. sinensis* is quite stable, but in some of the individuals it may be disrupted by elevated temperature and, in particular, the effect of a long photoperiod. This conclusion is confirmed by the results of the experiment described above (Fig. 2). It should be noted that photoperiodic reactivation in *A. sinensis* is expressed to a considerably lesser degree than in *Myrmica rubra* in which with a LD and at 25° C all diapausing fall larvae pupate over the course of several weeks (Kipyatkov, 1977).

Diapausing 3rd instar larvae even with a short day at 17° C continue to feed. We constantly observed workers feeding them pieces of prey. In addition, when neutral red vital dye was introduced into the food of the ants, the staining was soon visible in the nephrocytes of the fat body of many 2nd and 3rd instar larvae. However, diapausing larvae grow very slowly, especially at reduced temperatures. Growth of diapausing larvae is well studied in *Myrmica* ants (Brian, 1968).

Table 1

Mean total productivity of queens in the fall with long (17 h) and short (10 h) day at different temperatures

Productivity	25° C			20° C			17° C		
	LD	SD	Σ	LD	SD	Σ	LD	SD	Σ
	Number of queens								
	2	2	4	3	6	9	3	2	5
\bar{x}	1.68	1.59	1.64	2.73*	1.89	2.17	2.02	1.31*	1.74
$\pm\sigma$	0.89	0.92	0.74	0.15	1.31	1.12	0.60	0.11	0.58
$\pm m$	0.63	0.65	0.37	0.09	0.53	0.37	0.34	0.07	0.26

Note: Duration of experiment: at 25° C, 84 days ; at 20° C and 17° C, 56 days. Asterisk indicates significantly different ($P>0.95$) means. Productivity expressed as number eggs per queen per day.

DEVELOPMENT OF OVERWINTERED LARVAE

Ants and brood were collected in six natural nests at the end of April, when hibernation is completed. From this material 14 experimental groups were formed, each consisting of 250-300 workers and about 300 3rd instar larvae of all sizes; there were no queens in the group. To 21 June, the ants were kept at 17° C, and were then distributed among six regimes: LD and SD at 17°, 20°, 25° C (Table 2). The formicaries were examined once weekly and all pupae and prepupae that appeared were removed. The experiment continued for 3 months until new pupae ceased to appear.

The rate of development of overwintered larvae was determined on the basis of the first prepupae appearing in the nests. The rate showed the usual linear dependence on temperature with lower developmental limit around 6.5° C (Fig. 4). Photoperiod had no effect on the rate of development. Thus, if in fall disruption of larval diapause is possible only when temperatures are sufficiently high and with a LD, then in spring larvae develop and pupate under any conditions, even at 17° C and with a SD. Thus, during hibernation of ants there occurs a cold-weather reactivation that changes their normal reaction to temperature and photoperiod.

If at the start of the experiment larvae developed and pupated under all regimes, then later their development became dependent on temperature and photoperiod. The summed data showed that during the entire period of the experiment (Table 2) the number of pupated larvae (as a percentage of those surviving) with a LD was about 70% and was not temperature dependent. With a SD there was a clear relation between pupation and temperature; a drop in temperature reduced the percentage of pupated larvae. At 17° and 20° C and with the SD the percentage of pupated larvae dropped significantly. At 25° C the dependence on photoperiod was inverse; this is perhaps explained by chance and related to the high mortality of larvae at 25° C with a SD.

Thus, the effect of the SD and reduced temperature does not allow many overwintered larvae to complete development and pupate. Even at 25° C not all larva pupate. The appearance of new pupae in the experimental nests at 25° and 20° C ceased as early as the beginning, and at 17° C in middle, of August. This closely matches the cessation of development periods in nature. Thus, it is possible to assert that under natural conditions during a summer not all overwintered larvae may

Table 2

Effect of photoperiod and temperature on development of overwintered larvae (results of experiment conducted between 21 May and 23 August 1985)

Temperature, °C	Photo-period	Number of replications	Overall number of surviving larvae	Total pupated				Percentage of winged forms among pupated larvae
				number	%	including winged forms		
						♀s	♂s	
25	LD	3	339	239	70.5a	4	54	24.3
	SD	3	37	34	91.9a,d	13	1	41.2
	Σ	6	376	273	72.6*	17	55	26.4*
20	LD	2	49	34	69.4b	2	0	5.9
	SD	2	382	167	43.7b,d	0	16	9.6
	Σ	4	431	201	46.6	2	16	9.0
17	LD	2	227	158	69.6c	5	1	3.8
	SD	2	345	99	28.7c,d	0	6	6.1
	Σ	4	572	257	44.9	5	7	4.7

Note: Percentages marked with identical letters differ significantly ($P>0.99$) from one another. Asterisk indicates percentages differ significantly ($P>0.99$) from overall percentages for the remaining temperatures.

pupate, and part of them diapauses and hibernates again. It is not now possible to assess the number of repeat overwintering larvae. But it is clear that the number changes as a function of actual summer weather conditions and is affected as well by temperature conditions in the ant nests.

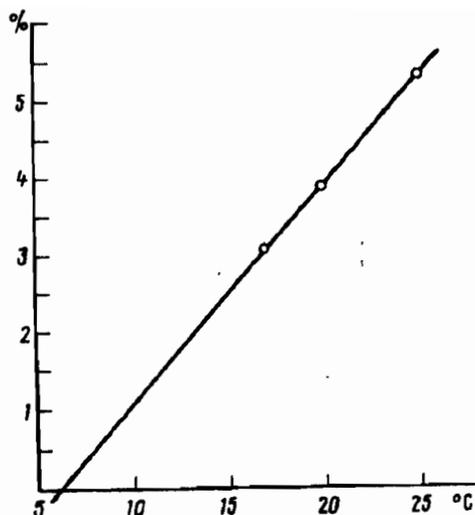
Almost in all nests in this experiment ants raised winged ♂s and ♀s. In a number of cases in so doing they concentrated their attention on a few winged larvae and did not care for the remaining brood. Clearly, this mostly explains the increased mortality of the larvae observed in certain experimental variants (Table 2). Raising winged forms from overwintered larvae is typical of the majority of ants in moderate climates (Brain, 1977; Kipyatkov, 1981).

Photoperiod conditions did not have a marked effect on raising winged forms, while the drop in temperature significantly reduced their percentage among pupated larvae (Table 2). Probably, to feed large larvae of winged ♀s, ants need a rather high temperature; the ♂ larvae, perhaps, die in large numbers at low temperatures. It is interesting that in *M. rubra* temperature does not affect raising winged forms in the spring (Kipyatkov, 1979).

Ants occurring in moderate and cold climates usually overwinter with larvae or without a brood at all (Eidmann, 1943). It is therefore proposed that in ants two types of seasonal cycles be identified: a *Myrmica* type and *Formica* type, respectively (Kipyatkov, 1987). Data we obtained do not make it possible to relate the seasonal cycle of *A. sinensis* to either of these types; it deserves a third, *Aphaenogaster* type, most likely typical of all species in the genus occurring in moderate climates. Our preliminary field and experimental investigations of *A. gibbosa chroassanica* K. Arnold, in western Kopet-Dag demonstrated that this species has exactly the same developmental cycle as *A. sinensis*.

The *Aphaenogaster* seasonal cycle type is characterized by hibernation of ants with eggs larvae of all instars, which was previously unknown in other species. There is no reproductive dia-

Fig. 4. Effect of temperature on rate of development (% per day) of overwintered larvae.



pause in queens, and they lay their eggs right up to the onset of cold weather. Therefore, the eggs and young larvae hibernate. At the same time, development of 3rd instar larvae at the end of summer is interrupted by diapause, and, therefore, all pupae complete their development before the onset of cold weather and do not overwinter.

The very slow individual development of *A. sinensis* compared to other species of ants distributed in moderate climates deserves attention. For example, in *M. rubra* occurring beneath the cover of oak woods, i. e., under conditions very close to the *A. sinensis* habitat, development from egg to pupa at 25° C is 30-35 days (Kipyatkov, 1974), which is almost 3 times less than for the latter. Here, however, it should be noted that the constant temperatures at which we conducted our experiments may extend development to some extent. In nature the ant brood experiences daily temperature fluctuations that may be amplified when the workers carry them along a temperature gradient during the day into warmer zones and at night deep into the nest. If such a daily thermorhythm is physiologically more beneficial for developing larvae, then constant temperatures will retard their development. This question is still open and deserves special study.

Because of slow individual development, *A. sinensis* larvae emerging from eggs deposited by queens at the beginning of summer are unable to complete development that same summer and overwinter, i. e., there is no rapid brooding. In exactly the same way, many overwintered larvae are unable to reach the pupal stage and they overwinter again. It may be assumed that such slow individual development is one of the factors inhibiting movement of *Aphaenogaster* ants to more northern regions. It is understandable, too, why *A. sinensis*, a relict species for Primor'e, establishes itself exclusively on the warmer southern slopes (Kupyanskaya, 1981).

Regulation of the seasonal cycle in *A. sinensis* is based, as in the majority of ants (Kipyatkov, 1987) on a combination of endogenous and exogenous mechanisms. During the summer there is a gradual decrease in developmental potential and an increase in the tendency toward diapause (a spontaneous endogenous process). In addition, the effect of the short day at the end of summer also induces diapause in larvae. As a result of the combination of these processes in mid-August pupation ceases, and after this all 3rd instar larvae diapause. The drop in temperature in September helps maintain diapause in the larvae.

During hibernation there is a cold-weather reactivation, and as a result the potential for development without diapause is restored. Therefore, growth and development of overwintered larvae begins in spring as soon as nest temperatures exceed the low temperature threshold.

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