

## **Regulation of annual cycle of development in ants of the subgenus *Serviformica* (Hymenoptera, Formicidae)**

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**Abstract** - Colonies of *Formica cinerea*, *F. clara*, *F. fusca*, *F. japonica* and *F. lemani* were collected in nature and maintained in plastic laboratory nests in photothermostats at constant temperatures of 17, 20, 23, 25, and 28 °C or at 12-hours thermoperiod of 15/25, 16/30 and 20/30 °C under long (18 h) or short (10 h) days. Ant groups were inspected every week (or every day in the studies on the developmental rates) with the census of the brood stages. The temperature adjustment of brood development and the developmental times for eggs and larvae at different temperatures were quite similar in all species. *F. cinerea* development is the most temperature dependant. Constant temperature of 28 ° is unfavourable for development. The lower temperature thresholds of development for eggs and larvae are almost identical in all species and have the values between 14 and 15 °C. The queens have an obligate diapause, their oviposition cycle is highly independent of the exogenous factors, such as temperature and photoperiod, and is regulated mainly by the endogenous physiological rhythms. The species-specific length of this cycle might be genetically determined and correspond in the best way to the mean duration of the year warm period suitable for development in a region where this population lives. The photoperiodic regulation of *Serviformica* species is absent. The temperature fall in the end of summer could hasten to some extent the cessation of queen oviposition in some species, e.g. in *F. cinerea*. For the full restoration of the ability for normal development and oviposition the ants should experience a long exposition at low positive temperatures (cold reactivation). In *F. fusca* a chilling period of no less than 4-5 months is needed. Daily thermoperiods are the most favourable temperature regimes unless their daytime (i.d. the higher) temperature exceeds the upper limit of the optimal zone. Thermoperiods accelerate significantly the rate of brood development and prolong the queen oviposition period in some species.

**Keywords:** *Formica*, seasonality, temperature, thermoperiod, photoperiod, diapause, induction, termination, developmental rates, regulation, cold reactivation.

## Introduction

The ants of the genus *Formica* are well known to hibernate without a brood (Eidmann, 1943; Otto, 1962; Dlussky, 1967). This type of annual cycle has been found only in a few other ant genera and is characterized by the reproductive queen diapause that begins in summer long before the end of the warm season favourable for development; therefore, all eggs and larvae, even the latest ones, manage to finish their development, all imagoes emerge from the pupae before the autumn cold weather and the ants hibernate without a brood (Kipyatkov, 1993). Thus, the duration of the active period of the annual cycle when ants rear their brood is determined by the dates of the beginning and cessation of queen oviposition.

In our earlier works the endogenous regulation of seasonal development has been shown to prevail in red wood ants of the *Formica rufa* group (Kipyatkov and Shenderova, 1989, 1990, 1991) and in species of the subgenus *Serviformica* (Lopatina and Kipyatkov, 1990b; Kipyatkov, 1994). The cessation of oviposition in these ants is mainly controlled by the endogenous process of unknown physiological nature (so-called "sand-glass device") going on during the summer. This is why the annual cycle of *Formica* ants is ascribed to the endogenously heterodynamous group (for more details see Kipyatkov, 1993). Temperature and other external factors could also regulate to some extent the seasonal development of these ants and play a modifying role adjusting the date of diapause arising to the climatic characteristics of a given year.

The aim of this work was to study more thoroughly the exogenous regulation of seasonal development in ants of the subgenus *Serviformica*.

## Materials and Methods

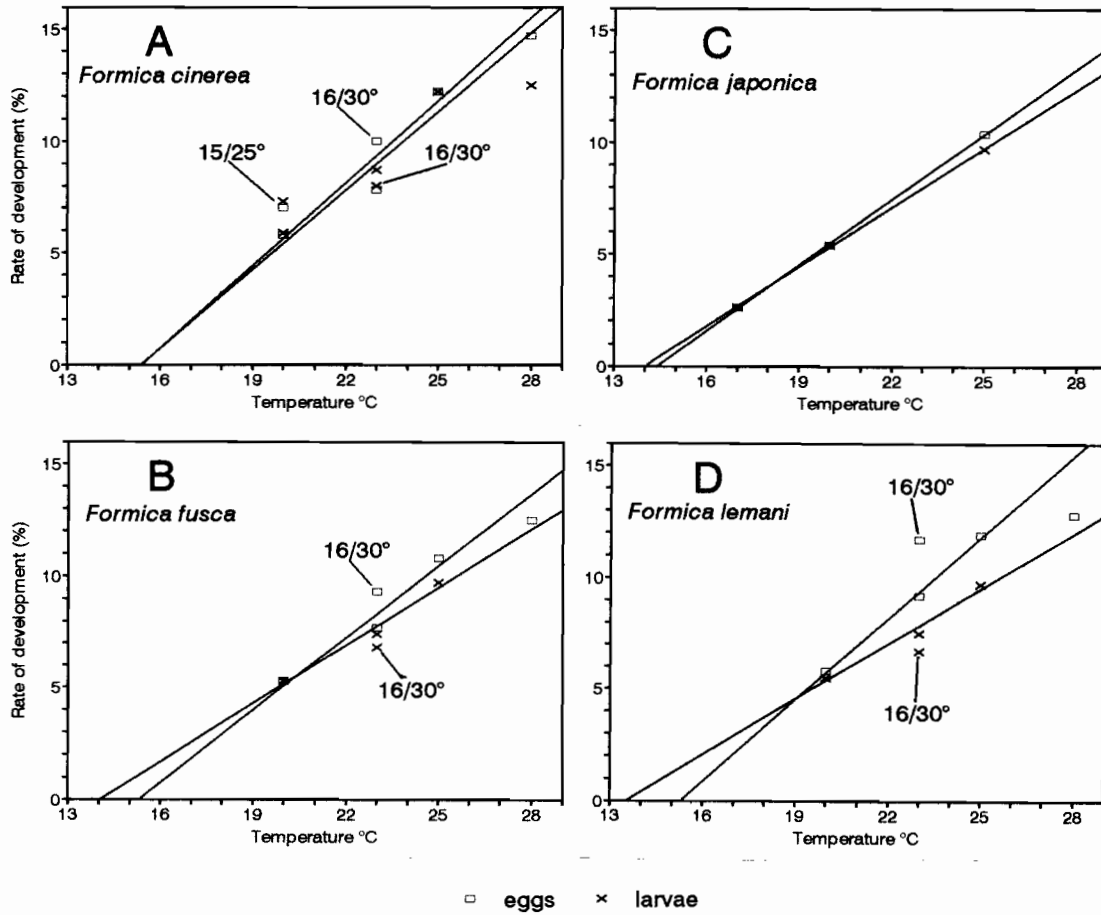
Ants were collected from natural habitats mainly in spring and were maintained in plastic laboratory nests in photothermostats. As a rule colony fragments (more rarely whole natural colonies) consisting of a queen (or some queens), workers and brood were used as experimental groups. Ants were fed twice a week with crushed cockroaches and 10% sugar solution. The experimental regimes were the combinations of a constant temperature of 17, 20, 23, 25 and 28 °C or a 12-hours thermoperiod of 15/25, 16/30 and 20/30 °C with a long-day (18 hours per day) or a short-day (10 h) photoperiod. Experimental groups were inspected every week (or every day in the studies on the developmental rates temperature dependence) with the census of the brood stages. For the artificial overwintering ant colonies were placed into a refrigerator and maintained under 3-5 °C for some months.

Five ant species were used in experiments: *Formica japonica* Montsch. collected in 1986 in the "Kedrovaya Pad'" Reserve not far from Vladivostok (Southern Primorie), *F. clara* Forel collected in 1988 near Kara-Kala (Turkmenistan, West Kopetdag), *F. cinerea* Mayr, *F. fusca* L. and *F. lemani* Bondroit collected in 1989 in the Carpathians (West Ukraine) near Kolochava.

## Results and Discussion

### Temperature impact on the developmental rates

The dependence of brood development on temperature and the developmental times of eggs at different temperatures (Tab. 1, Fig. 1, 2) appeared to be quite similar and did not differ significantly in all species of *Serviformica* and in two red wood ants species studied by V. E. Kipyatkov and S. S. Shenderova (unpublished results). As regards to the larval developmental time this parameter was also found to be nearly the same in all *Serviformica* species except *F. cinerea*. In the latter species the mean larval developmental times at 23 and 25 °C proved to be significantly shorter in than in other species (Tab. 1). Moreover, the development of *F. cinerea* larvae was also somewhat more temperature dependant (Fig. 1A).



**Figure 1.** Regression of the developmental rates of eggs and larvae in four species of *Formica* (*Serviformica*) ants.

**Table 1.** Developmental times (in days) of eggs and larvae of six *Formica* species at different constant temperatures and thermoperiods

Species, Year, Brood stages		Temperature °C						LTT °C	
		17	20	23	25	28	15/25		16/30
<b><i>F. (Serviformica) cinerea</i>, 1990-1991</b>									
eggs	n	-	9	6	3	2	9	5	15.4
	mean	-	17.2 <sup>a</sup>	12.7 <sup>b</sup>	8.2	6.8	14.2 <sup>a</sup>	10.0 <sup>b</sup>	
	s.d.	-	2.10	1.03	0.29	1.77	2.40	0.71	
acceleration of development at thermoperiods (%)							17.4	21.3	
larvae	n	-	4	6	3	2	7	3	15.4*
	mean	-	16.8 <sup>a</sup>	11.5 <sup>1</sup>	8.2 <sup>234</sup>	8.0	13.7 <sup>a</sup>	12.5	
	s.d.	-	1.50	0.84	0.29	0.00	0.95	2.50	
acceleration of development at thermoperiods (%)							18.2	-8.0**	
<b><i>F. (Serviformica) fusca</i>, 1990-1991</b>									
eggs	n	-	3	4	3	3	-	4	15.3*
	mean	-	19.0	13.0 <sup>a</sup>	9.3	8.0	-	10.8 <sup>a</sup>	
	s.d.	-	1.00	0.00	0.58	1.00	-	0.50	
acceleration of development at thermoperiods (%)							-	17.3	
larvae	n	-	3	4	3	-	-	4	14.0
	mean	-	19.0	13.5 <sup>1</sup>	10.3 <sup>2</sup>	-	-	14.8	
	s.d.	-	1.00	1.00	0.58	-	-	1.50	
acceleration of development at thermoperiods (%)							-	-9.0**	
<b><i>F. (Serviformica) lemni</i>, 1990-1991</b>									
eggs	n	-	4	4	4	2	-	2	15.3*
	mean	-	17.1	10.9 <sup>a</sup>	8.4	7.8	-	8.5 <sup>a</sup>	
	s.d.	-	0.85	1.03	0.48	0.35	-	0.71	
acceleration of development at thermoperiods (%)							-	22.0	
larvae	n	-	4	3	4	-	-	1	13.5
	mean	-	18.3	13.3	10.3 <sup>3</sup>	-	-	15.0	
	s.d.	-	2.06	2.31	0.96	-	-	-	
acceleration of development at thermoperiods (%)							-	-12.0**	
<b><i>F. (Serviformica) japonica</i>, 1986</b>									
eggs	n	6	7	-	9	-	-	-	14.4
	mean	38.4	18.4	-	9.6	-	-	-	
	s.d.	8.75	2.46	-	1.13	-	-	-	
larvae	n	3	7	-	9	-	-	-	14.0
	mean	38.8	18.6	-	10.3 <sup>4</sup>	-	-	-	
	s.d.	3.18	2.37	-	1.56	-	-	-	

Species, Year, Brood stages	Temperature °C							LTT °C	
	17	20	23	25	28	15/25	16/30		
<i>F. (Formica) aquilonia</i> , 1976-1980***									
eggs	n	2	9	-	50	-	-	-	14.7
	mean	39.0	17.4	-	8.8	-	-	-	
	s.d.	2.12	4.57	-	2.82	-	-	-	
<i>F. (Formica) polyctena</i> , 1976-1980***									
eggs	n	20	24	-	64	-	-	-	14.7
	mean	38.8	18.5	-	9.1	-	-	-	
	s.d.	4.88	2.82	-	1.67	-	-	-	

The identical letters in the same line denote the means that differ significantly ( $P \geq 0.95$ ) from each other; The identical exponents denote the same in the columns; LTT - Lower temperature threshold;

\* - calculated with the use of the data for 20, 23 and 25 °C (the developmental rate at non-optimal temperature of 28 °C excluded); \*\* - negative values reflect the decrease of larval developmental rates at thermoperiod 16/30 °C; \*\*\* - based on experimental data of V. E. Kipyatkov and S. S. Shenderova.

It was found that the constant temperature of 28 °C is rather unfavourable for brood rearing in *F. fusca* and *F. lemni*; it slows the development of eggs and causes the death of almost all larvae (Tab. 1, Fig. 1B, 1D). In *F. cinerea* at 28 °C the eggs develop successfully but the larval development is somewhat delayed (Tab. 1, Fig. 1A). Thus, the latter species is slightly more thermophilic.

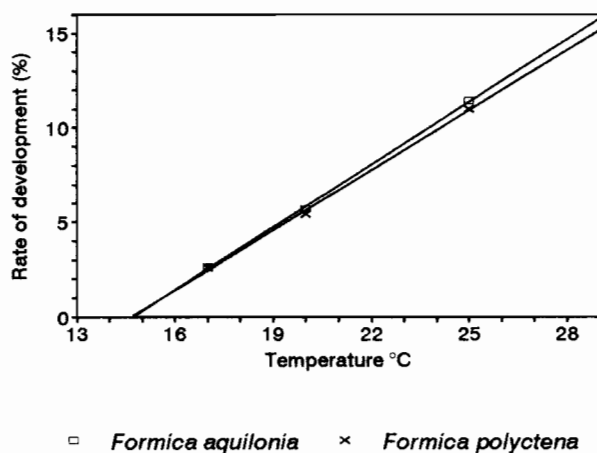


Figure 2. Regression of the developmental rates of eggs on temperature in two species of red wood ants

The lower temperature thresholds (i.d. theoretical minimums) of development for eggs and larvae turned out to be almost identical in all *Formica* species and have the values between 14 and 15 °C (Tab. 1, Fig. 1 and 2). It is noteworthy that these ants have the most elevated temperature thresholds and the highest developmental rates among all other species occurring in the Northern Palaearctic (for more details see Kipyatkov, 1993).

Daily temperature rhythms (thermoperiods) are known to be of great significance for the development of ants, often being more favourable and accelerating the brood development in comparison with the corresponding constant temperatures (Buschinger, 1973; Elmes and Wardlaw, 1983; Lopatina and Kipyatkov, 1990a,b, 1993). In our experiments with *Serviformica* species the thermoperiod 16/30 °C (mean daily temperature 23 °C) accelerated the development of eggs in three *Serviformica* species by 17-22% comparing with the constant temperatures equal to the mean

daily temperatures of thermoperiods, these differences being significant in all cases (Tab. 1, Fig. 1A, B, D).

Thermoperiod 15/25 °C (mean daily temperature 20 °C) was found to quicken significantly the development of not only the eggs but also the larvae in *F. cinerea* (for other species the data at these regime have not been obtained) in comparison with constant 20 °C (Tab. 1, Fig. 1A). On the contrary thermoperiod 16/30 °C slowed the larval development in all three species studied by 8-12% (Tab. 1, Fig. 1A, B, D). Obviously such an adverse influence of this thermoperiod is completely explained by the fact discussed above that constant temperature of 30 °C (i.d. the day temperature of this thermoperiod) is too high and unfavourable the ant larvae.

### Queen diapause control

All *Formica* species have an obligate queen diapause arising after a certain oviposition period in any circumstances; the external factors could not prevent this endogenous induction of diapause but they can alter the date of its beginning to some extent (Kipyatkov, 1993). We have carried out some experiments to study the effects of photoperiod and temperature upon the duration of queen oviposition period in *Serviformica* ants.

During several years we studied the influence of constant temperatures and photoperiods upon the oviposition period duration of *Serviformica* species. Ant colonies just after their artificial hibernation were allocated between different temperature regimes and then maintained there until the queen ceased laying and the eggs disappeared.

**Table 2.** Durations of the eggs presence period (in weeks) in the annual cycle of *Formica japonica* colonies at two constant temperatures and photoperiods (1985-1986)

Temperature °C	20		25	
Day length, h	18	10	18	10
n	4	5	18	6
min	8	8	9	8
max	13	13	13	14
mean	10.5	9.8	10.1	10.7
s.d.	2.08	1.92	1.30	2.42

In the first experiment colonies of *F. japonica* just after the artificial hibernation were maintained under long or short days at 20 or 25 °C (in total four regimes). The queens began to oviposit soon after the temperature had been raised and continued to lay for about two months. The duration of eggs presence in groups, which nearly corresponds to the period of oviposition, turned out to be on average exactly the same at all four experimental regimes (Tab. 2). Thus, neither photoperiod, nor temperature had affected the spontaneous diapause induction in queens. The absence of the photoperiodic regulation of seasonal development has been proved for red wood ants (Kipyatkov and Shenderova, 1989). Our other experi-

ments on the species of the subgenus *Serviformica* described below also confirmed this conclusion. Therefore, in the following experiments carried out during 1986-1993 to determine the duration of oviposition period in the annual cycle of *F. cinerea*, *F. fusca* and *F. japonica* colonies we used only long days regimes.

The results of these experiments are summarized in Table 3. Before their analysis, however, it should be noted that the last eggs laid by the red wood ants queens just before the end of oviposition have been shown to perish and not yield larvae because they are usually cannibalized by young larvae and by workers (Kipyatkov and Shenderova, 1989). We have observed this phenomenon also in *Serviformica* species. Taking into account the destruction of the last egg portions laid by the queens one can conclude that the duration of the eggs presence observed in our experimental nests does not differ significantly from the oviposition period. In fact these two parameters almost coincide.

Obviously the temperatures within an interval between 20 and 28 °C do not exert clear effects upon the duration of egg presence periods and, therefore, upon the diapause induction in queens: all slight differences detected appeared to be insignificant (Tab. 3). Simultaneously the thermoperiods caused a significant prolongation of the mean oviposition period in *F. cinerea* and *F. fusca* by 16-35% in comparison with the same species colonies maintained under constant temperatures equal to the mean daily temperatures of the thermoperiods.

**Table 3.** Durations of the eggs presence period (in weeks) in the colony annual cycle at different constant temperatures and thermoperiods in four *Serviformica* species

Temperature °C		20	23	25	28	15/25	16/30	20/30
<i>F. cinerea</i> 1990-1993	n	5	10	7	2	9	10	-
	min	13	8	14	14	16	13	-
	max	16	16	16	18	21	21	-
	mean	14.4 <sup>a1</sup>	12.2 <sup>bc</sup>	15.3 <sup>d3</sup>	16.0 <sup>e</sup>	19.3 <sup>abdef</sup>	16.5 <sup>cf</sup>	-
	s.d.	1.14	2.74	0.95	2.82	1.87	2.72	-
<i>F. fusca</i> 1991-1993	n	4	4	3	-	3	4	-
	min	13	12	12	-	15	13	-
	max	15	13	15	-	17	17	-
	mean	14.0 <sup>a2</sup>	12.5 <sup>bc</sup>	14.0 <sup>4</sup>	-	16.3 <sup>ac</sup>	15.6 <sup>b</sup>	-
	s.d.	0.82	0.58	1.73	-	1.15	1.89	-
<i>F. lemami</i> 1990	n		2				1	
	min		8				-	
	max		15				-	
	mean		11.5				13.0	
	s.d.		4.95				-	
<i>F. japonica</i> 1986-1987	n	9	-	24	-	-	-	12
	min	8	-	8	-	-	-	9
	max	13	-	13	-	-	-	12
	mean	10.1 <sup>12</sup>	-	10.2 <sup>34</sup>	-	-	-	10.9
	s.d.	1.90	-	1.61	-	-	-	1.38

The identical letters in the same line denote the means that differ significantly ( $P \geq 0.95$ ) from each other; The identical exponents denote the same in the columns.

The influence of thermoperiods was most substantial in *F. cinerea*, which possibly could be connected with the greater thermolability of this species development described above. In this species the most considerable effects were induced by the thermoperiod 15/25 °C whereas the second one had a smaller impact, which is obviously explained by an inhibitory influence of too high temperature of 30 °C used in this thermoperiod.

It is notable that the thermoperiod 20/30 °C caused no effect on the duration of oviposition in *F. japonica* (Tab. 3). This species differs from the others by a very short oviposition period averaging only 10-11 weeks and showing no dependence on temperature at all (Tab. 3). According to our data on *F. clara* the oviposition period in this species lasts in the laboratory at 25 °C for 13-15 weeks. This value

coincides well with the data for *F. cinerea* and *F. fusca* (Tab. 3). Thus, the species-specific differences in the duration of oviposition period could exist in *Formica* ants.

In another series of experiments we studied the role of the temperature and photoperiod changes in the regulation of the ant annual cycle. It might be supposed that nearer the end of the active phase of the annual cycle the fall of temperature of the short days could hasten the cessation of oviposition and the induction of diapause in queens.

The groups of *F. cinerea*, *F. fusca* and *F. lemni* collected from natural colonies on 10-16 June 1989 when the eggs were already present in them were maintained at 25 °C and the long days for about three weeks. On 7 July the eggs were removed from the nests and the ant groups were allocated between eight regimes: 17, 20, 25 °C and thermoperiod 15/25 °C under long or short days. After that the eggs laid in all groups were removed weekly to determine the duration of the oviposition period.

The queens ceased laying in a short period after the beginning of eggs censuses. Apparently the photoperiods did not affect the diapause arising (Tab. 4). Therefore, the data for long and short days under each temperature regime were combined to reveal the effects of temperature (Tab. 5). The Table 5 also contains the results of another experiment carried out on the colonies of *F. clara* and *F. japonica* with the use of the same methods except that the colonies used were not taken from the field but had experienced the artificial hibernation in the laboratory.

**Table 4.** Influence of temperature and photoperiod upon the queen diapause arising in three *Formica* species. Times in weeks elapsed from the change of experimental regime until the cessation of oviposition are given.

Temperature °C	17		20		25		15/25		
Day length, h	18	10	18	10	18*	10	18	10	
<i>F. cinerea</i> 1989	n	4	4	5	4	4	3	4	4
	min	0	1	2	1	1	2	1	1
	max	0	2	4	1	5	3	3	2
	mean	0.0	1.3	2.6	1.0	3.0	2.7	2.0	1.8
	s.d.	0.00	0.50	0.89	0.00	1.83	0.58	0.82	0.50
<i>F. fusca</i> 1989	n	2	2	2	2	2	2	-	-
	min	2	1	2	2	2	3	-	-
	max	2	2	3	4	2	4	-	-
	mean	2.0	1.5	2.5	3.0	2.0	3.5	-	-
	s.d.	0.00	0.71	0.71	1.41	0.00	0.71	-	-
<i>F. lemni</i> 1989	n	-	-	1	2	1	2	-	-
	min	-	-	-	2	-	2	-	-
	max	-	-	-	3	-	2	-	-
	mean	-	-	4.0	2.5	2.0	2.0	-	-
	s.d.	-	-	-	0.71	-	0.00	-	-

\* - Base regime (25 °C, 18 h); ant colonies were being maintained under these conditions after their collection in the field for about three weeks and then had been allocated between all regimes; afterwards the eggs laid in colonies were being removed weekly to determine the time of the queen diapause arising.



Evidently the changes of temperature from 25 °C to thermoperiods, to constant 20 °C and even to 17 °C (in *F. japonica*) did not affect significantly the dates of the diapause arising in queens of four species. However in *F. cinerea* the temperature fall from 25 to 20 and to 17 °C resulted in slightly earlier diapause induction, these differences being significant only for 17 °C.

**Table 5.** Influence of temperature upon the queen diapause arising in five *Serviformica* species. Times in weeks elapsed from the change of temperature until the cessation of oviposition are given

Temperature °C		17	20	25*	15/25	20/30
<u><i>F. cinerea</i></u> 1989	n	8	9	7	8	5
	min	0	1	1	1	1
	max	2	4	5	3	4
	mean	0.6 <sup>ab</sup>	1.9 <sup>a</sup>	2.9 <sup>b</sup>	1.9	2.6
	s.d.	0.74	1.05	1.35	0.64	1.14
<u><i>F. fusca</i></u> 1989	n	4	4	4	-	-
	min	1	2	2	-	-
	max	2	4	4	-	-
	mean	1.8	2.8	2.8	-	-
	s.d.	0.50	0.96	0.96	-	-
<u><i>F. lemni</i></u> 1989	n	-	3	3	-	-
	min	-	2	2	-	-
	max	-	4	2	-	-
	mean	-	3.0	2.0	-	-
	s.d.	-	1.00	0.00	-	-
<u><i>F. japonica</i></u> 1987	n	2	3	3	-	-
	min	5	5	5	-	-
	max	5	7	7	-	-
	mean	5.0	5.7	6.3	-	-
	s.d.	0.00	1.15	1.15	-	-
<u><i>F. clara</i></u> 1988	n	-	2	1	-	-
	min	-	9	-	-	-
	max	-	9	-	-	-
	mean	-	9.0	8.0	-	-
	s.d.	-	0.00	-	-	-

\* - Base regime (25 °C); ant colonies were being maintained under this temperature for a while and then had been allocated between all regimes; afterwards the eggs laid in colonies were being removed weekly to determine the time of the queen diapause arising; *The identical letters* in the same line denote the means that differ significantly ( $P \geq 0.95$ ) from each other; The data for three first species are the same as in Tab. 4 (see the text).

In an analogous experiment on *F. cinerea* and *F. fusca* the ant colonies were moved from 25 °C to 20 °C (both temperatures under long days) but we did not remove the eggs from these nests and so determined only the duration of their presence in ant groups. The results showed only a slight and

insignificant decrease of this parameter at 20 °C comparing with the control colonies remaining at 25 °C (Tab. 6).

Temperature °C		20	25*
<i>F. cinerea</i> 1993	n	4	4
	min	3	5
	max	7	7
	mean	4.8	6.3
	s.d.	2.06	0.96
<i>F. fusca</i> 1993	n	5	3
	min	3	3
	max	6	6
	mean	4.6	5.0
	s.d.	1.14	1.73

**Table 6.** Influence of temperature change on the queen diapause arising in *Formica cinerea* and *Formica fusca*.

Times in weeks elapsed from the change of temperature until the cessation of oviposition are given.

\* - Base regime (25 °C); ant colonies were being maintained under this temperature for a while and then a half of them had been moved to 20 °C.

#### Diapause termination

It has been shown that the termination of diapause in ant larvae and queens might have both endogenous (i.d. spontaneous) and exogenous origin. The spontaneous resumption of the queen oviposition in the ant colonies, maintaining after the end of queen reproductive cycle for a long time under the same conditions at which the diapause had arose, has been repeatedly observed in various ants including *Formica* species (Kipyatkov and Shenderova, 1990; Kipyatkov, 1993, 1994). We also observed this phenomenon in our experiments.

The diapause is, however, quite stable in *Formica* queens and could end at optimal temperature only in several weeks or even in some months. We have realized some experiments in which the ant colonies maintained at 17 or 20 °C were moved to 28 or even 30 °C just after the cessation of their queens' oviposition. We have never observed the renewal of oviposition in response to temperature rising.

In northernmost distributed ant species, as in other temperate climate insects, the full restoration of the ability for normal development and oviposition is impossible without the long exposition at low positive temperatures during the hibernation, i.d. cold reactivation (Kipyatkov, 1993). We have experimentally studied this process in *F. fusca*.

Eighteen ant colonies after the cessation of their queen oviposition when the brood in their nest completely disappeared were placed into a refrigerator and kept at 3-5 °C for different periods. After 4, 6, 8, 10, 12, 15, 20, 24 and 28 weeks a set of two colonies was moved from the refrigerator to a thermostat with a temperature of 20-21 °C. The colonies were maintained at this temperature until the beginning of oviposition.

The time elapsed from the moment of temperature rising (i.d. from the end of the artificial hibernation) to the queen oviposition renewal was found to be clearly dependent upon the duration of the hibernation period and decreased from 13-15 weeks to a few days (Tab. 7). It is believed that in the experimental sets with shorter hibernation periods the reactivation was mainly of endogenous nature but after the longer expositions at low temperatures it was apparently a result of cold reactivation.

It should be concluded that for the full reactivation of *F. fusca* queens the exposition at low temperature for no less than 4-5 months is needed.

**Table 7.** Cold reactivation in *Formica fusca*

Set N	Duration of exposition at 3-5°C (weeks)	Time elapsed until the oviposition resumption at 20-21°C (weeks)
1	4	13-14
2	6	8-10
3	8	7-8
4	10	5-6
5	12	3-5
6	15	3-4
7	20	3
8	24	1
9	28	3-5 days

Two ant colonies with diapausing queens had been used in each set. After a certain exposition at 3-5°C each set had been transferred to 20-21°C and ants were being maintained there until the queens began to lay eggs.

### Concluding Remarks

The most important conclusion of this study is that the queen oviposition cycle in *Serviformica* ants is highly independent of the exogenous factors, such as temperature and photoperiod, and is regulated mainly by the endogenous physiological rhythms. These ants are also characterized by the absence of the photoperiodic regulation of seasonal development. However, in the end of summer period the decreasing temperature could accelerate the cessation of oviposition and the diapause arising in queens at least in some species. Just the same has been proved formerly for the red wood ants queens (Kipyatkov and Shenderova, 1989, 1990, 1991).

It might be also supposed that each species and most likely each population has its own length of the queen oviposition period that is genetically determined and corresponds in the best way to the mean duration of the year warm period suitable for development in a region where this population lives.

Our data clearly confirm this assumption. According to the field observations, in the natural colonies of *F. japonica* the first eggs appear in the end of April or the beginning of May and the oviposition stops in the middle of July, so that in the beginning of August only pupae are present in the nests. Thus, the total duration of oviposition in nature is no more than 10-12 weeks that is the same as in our laboratory experiments. In natural *F. cinerea* colonies the queens lay the first eggs in May; the last pupae were found in nests in the middle of September. Thus, it may be concluded that the queens of this species in the region of our study have the duration of oviposition period about 15 weeks, i.d. as in the laboratory. It would be very interesting to study from this point of view some more *Formica* species and populations inhabiting different regions from the North to the South.

In addition our results have proved ones more that the daily temperature rhythms play an important role in the temperate climate ants development. In fact, we have shown that the constant temperature is less adequate for normal development of *Formica* brood comparing with the daily rhythms of temperature. The constant temperatures somewhat inhibit the development of the ant eggs and larvae and shorten the queen oviposition period.

## References

- Buschinger, A. 1973. The role of daily temperature rhythms in brood development of ants of the Tribe Leptothoracini (Hymenoptera; Formicidae). In: *Effects of Temperature on Ectothermic Organisms* Ed.), Springer Verlag, Berlin, pp. 229-232.
- Dlussky, G.M. 1967. *Ants of the Genus Formica (Hymenoptera, Formicidae, G. Formica). Biology, Practical Importance and Use, Keys for the Species Founded in the USSR. [In Russian]*. Nauka, Moscow, 236 pp.
- Eidmann, H. 1931. Ueberwinterung der Ameisen. *Z. Morphol. Ökol. Tiere*, 39: 217-275.
- Elmes, G.W. and J.C. Wardlaw. 1983. A comparison of the effect of temperature on the development of large hibernated larvae of four species of *Myrmica* (Hymenoptera: Formicidae). *Insectes Soc.*, 30: 106-118.
- Kipyatkov, V.E. 1990. Comparative study of seasonal development cycles in ants. [In Russian with Engl. summary]. Proc. I Coll., Sect. Study Soc. Ins., All-Union Ent. Soc., Leningrad, 1990, pp. 114-122.
- Kipyatkov, V.E. 1993. Annual cycles of development in ants: diversity, evolution, regulation. pp. 25-48 in this volume.
- Kipyatkov, V.E. 1994. The role of endogenous rhythms in the regulation of annual cycles of development in ants (Hymenoptera, Formicidae). [In Russian with Engl. summary]. *Entomol. Obozr.*, 73 (in press).
- Kipyatkov, V.E. and S.S. Shenderova. 1991. Effects of temperature and photoperiod on egg laying and productivity of queens of ants (Hymenoptera, Formicidae, *Formica rufa* L. group). *Entomol. Rev.*, 70: 13-24.
- Kipyatkov, V.E. and S.S. Shenderova. 1989. Influence of temperature and photoperiod on the beginning and termination of queen diapause in red wood ants (*Formica rufa* group). [In Russian with Engl. summary]. *Vestn. Leningr. Univ., Biol.*, N 10 (2): 7-16.
- Kipyatkov, V.E. and S.S. Shenderova. 1990. Endogenous rhythm of reproductive activity of red wood ant queens (*Formica rufa* group). *Entomol. Rev.*, 69: 137-149.
- Lopatina, E.B. and V.E. Kipyatkov. 1990a. Influence of daily temperature rhythms on the development of ants. 1. Rate of development. [In Russian with Engl. summary]. Proc. I Coll., Sect. Study Soc. Ins., All-Union Ent. Soc., Leningrad, 1990, pp. 146-152.
- Lopatina, E.B. and V.E. Kipyatkov. 1990b. Influence of daily temperature rhythms on the development of ants. 2. Possibility for development and duration of the active period of seasonal cycle. [In Russian with Engl. summary]. Proc. I Coll., Sect. Study Soc. Ins., All-Union Ent. Soc., Leningrad, 1990, pp. 153-159.
- Lopatina, E.B. and V.E. Kipyatkov. 1993. The influence of temperature on brood development in the incipient colonies of the ants *Camponotus herculeanus* (L.) and *Camponotus xerxes* Forel (Hymenoptera, Formicidae). pp. 61-74 in this volume.
- Otto, D. 1962. *Die roten Waldameisen*. A. Ziemsen Verlag, Wittenberg, Lutherstadt, 151 pp.