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Endogenous Rhythm in Reproductive Activity of Red Wood Ant Queens (*Formica rufa* group)*

V. E. KIPYATKOV and S. S. SHENDEROVA

Faculty of Soil Biology, Leningrad State University; Forestry Academy, Leningrad

The presence of an endogenous circumannual rhythm in the reproductive activity of queens is established. We observed alternation of periods of oviposition and absence of eggs when ants were kept under constant laboratory conditions (temperature 17, 20, 25 and 28-30°C, photoperiod 10-12 or 18-20 h) for 1-5 years. Oviposition ceases after a certain time and the queens enter diapause, which ceases spontaneously after several weeks or months (suspension of oogenesis and resorption of oocytes are confirmed by dissections). The duration of the rhythm and its phases (oviposition and diapause) are quite variable. Their mean durations are not temperature dependent within an optimal developmental range (20-25°), declining slightly when the temperature increases to 28-30°, and increasing when it drops to 17°. Constant photoperiods do not affect the parameters of the rhythm. At optimal temperatures the duration of the rhythm period varies between 90 and 525 (mean 212) days in *Formica aquilonia* and between 60 and 345 (mean 178.7) days in *F. polyctena.* The significance of the endogenous reproductive rhythm in regulating seasonal development of this group of ants is discussed.

The *Formica rufa* group of ants have been the object of numerous investigations summarized in a number of monographs (Otto, 1962; Dlusskiy, 1967; Sudd, 1967; Zakharov, 1972). The seasonal developmental cycle of these ants has been studied in rather great detail in the context of caste differentiation (Schmidt, 1974; Kipyatkov, 1981). It is known (Dlusskiy, 1967) that all *Formica* ants overwinter without reproducing. Queens that have overwintered begin laying eggs soon after hibernation and suspend oviposition during the second half of the summer. Therefore, all hatched larvae develop to imagoes before autumnal cold arrives. It follows that the duration of the active period of the seasonal cycle in which larvae are fed in the nest is determined by the beginning and end of oviposition by the queens. In the literature there are no data of any sort of the factors controlling these processes.

We previously established (Shenderova and Kipyatkov, 1979) that *F. aquilonia* queens possess a spontaneous reproductive rhythm. When ants are kept under constant laboratory conditions (temperature 25°, constant photoperiod of 18 and 12 h), after a certain time the queens suspend oviposition and enter diapause, which continues for several weeks or months, and then oviposition begins again. Such reproductive cycles alternate when the ants are kept in the laboratory for 2-3 years independent of the season outside the laboratory. This makes it possible to conclude that the phases are determined by some kind of endogenous processes. The object of this article is to report a detailed study of the endogenous reproductive rhythms in red wood ants in the context of the seasonal periodicity of their development.

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MATERIALS AND METHODS

Experiments were performed during 1976-1980 with *F. aquilonia* ants collected in Leningrad Province and *F. polyctena* ants from the "Les na Vorskle" Reserve in Belogorod Province. The ants were collected usually in April and May, more rarely in the summer and fall, from the inner cone and surface of mound nests and kept in plastic or plaster formicaries where they were provided with an abundance of sugar and honey solution and sliced cockroaches, *Nauphoeta cincera*. In each formicary there was one queen and 100-200 workers. The formicaries with the ants were placed in photothermostats where the temperatures were maintained at 17, 20, 25, and 28-30°); photoperiods were 18-20 h (long day) and 10-12 h (short day).

The nests were examined once each week. In so doing, the number of eggs, larvae, and pupae in the nest was counted. In this study devoted to the endogenous rhythmicity of oviposition, only the results from counting eggs were used; we have published other data separately. We did not use narcosis in the counts.

Experimental groups of ants were kept under constant conditions from 1 to 5 years. In cases when the number of workers declined in the groups in the formicaries, we added pupae taken from natural nests of the same population. Experiments usually ended after the death of the queen. In all, there were 72 *F. aquilonia* and 67 *F. polyctena* groups in the experiments. Of them 34 and 31 groups, respectively, were kept in the laboratory for more than 1 year (long experiments).

We dissected the queens after fixing them in 70% alcohol in water. All data were processed using generally accepted methods of biological statistics (Plokhinskiy, 1970).

RESULTS AND DISCUSSION

Reproductive Cycles of the Queens

In the long experiments the majority of the groups belonged to variants kept at 20-25°. The data obtained in experiments performed at 17 and 28-30° are less extensive because these temperatures are not optimal for red wood ants and caused viability and fecundity to decrease (confirmed by our experimental data published separately). In particular, mortality increased when ants were maintained at 28-30°. Under these conditions the majority of queens died during the first year and thus only 2 *F. aquilonia* and 6 *F. polyctena* groups survived longer than 1 year. It is known that *F. polyctena* queens prefer a temperature of 20-25° and rarely visit parts of the nest where the temperature exceeds 28° (Kipyatkov and Shenderova, 1986). This agrees with data provided on the nonoptimal nature of a temperature of 28-30° for queens (under constant conditions).

In all experimental groups of ants kept for more than 1 year, we observed the indicated spontaneous rhythms of oviposition: periods when eggs were present and when they were lacking in nests alternated (Figs. 1, 2). Two such periods together constitute the complete reproductive cycle of the queen, beginning when the queen begins oviposition. Fluctuations in the productivity of queens characterize the period of oviposition in red wood ants: Oviposition peaks alternate with periods of reduced productivity or virtual suspension of egg laying. During the entire period of oviposition, up to 6 such productive maxima were observed. But eggs are almost always present in the nests because the queens usually resume laying before the eggs deposited during the previous peak entirely disappear; only occasionally did we observe a brief (no more than 7-10 days) absences of eggs during the oviposition period (Figs. 1, 2).

The period of egg laying terminates with the onset of diapause in the queen. After this, eggs and developing larvae and pupae are still present in the nest for some time (Fig. 1). The reproduc-

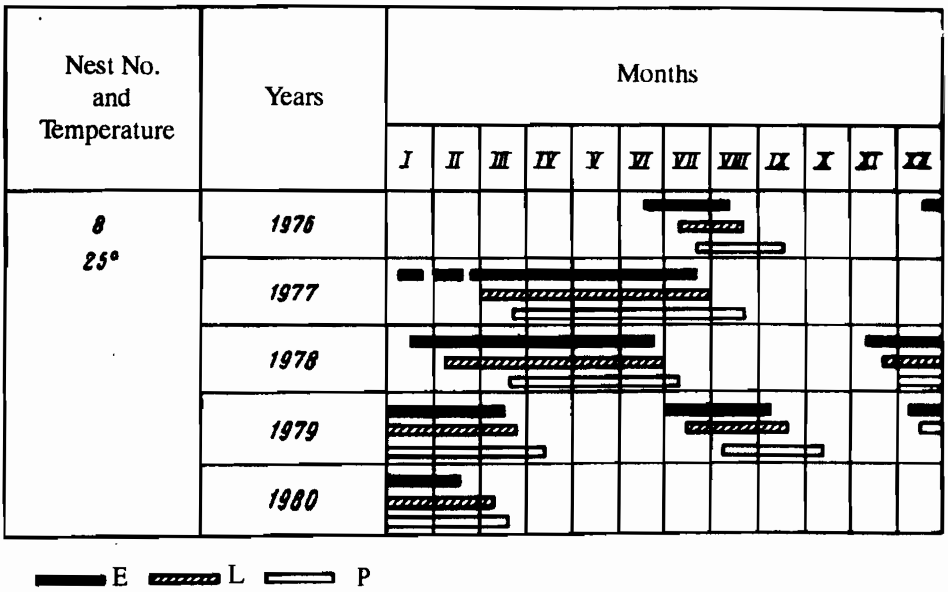

Fig. 1. Alternation of periods of reproduction and nonreproduction in an experimental *Formica aquilonia* group at 25° with short photoperiod: E) eggs; L) larvae, P) pupae.

tive cycle of the queens terminates with the end of diapause and resumption of oviposition. Thus, according to our data, the periods when eggs are present in the nests are somewhat longer than the periods of oviposition, and the periods when eggs are absent are shorter than periods of diapause. But the sum total of the periods when eggs are present and lacking are always equal to the sum total of the periods of oviposition and diapause, i.e., the overall duration of the reproductive cycle.

The duration of periods when eggs are present and lacking varied quite significantly: from 22 to 255 and from 22 to 337 days, respectively. However, when averaged, entirely distinct patterns emerged (Table 1). The durations of these periods, in particular, their sums, i.e., the durations of the reproductive cycles at 20 and 25° are almost identical, increase at 17° and decrease at 28-30°. Thus, within the optimal temperature range the mean duration of the reproductive cycle is virtually independent of temperature; temperatures above the optimum shorten the cycle and those below it prolong the cycle.

Sufficient data for statistical comparison of the effect of the photoperiod on the reproductive cycles of queens were obtained only at the optimal temperatures. The mean duration of periods when eggs were present and lacking and of the entire reproductive cycle with a long and short photoperiod are very close; the differences between them are insignificant (Table 2). Thus, constant photoperiods do not alter the parameters of the spontaneous rhythm of reproductive activity in queens.

Data from the same experiments were calculated in another way. The complete reproductive cycles were averaged. The values for mean duration of the reproductive cycle thus obtained (Table 3) were somewhat less than when calculated using the first method (Table 1). This is explained by the fact that many periods when eggs were present or lacking, primarily the longest, were not included in the averaging since they were not part of complete reproductive cycles. Because a sufficient number of complete reproductive cycles was lacking, calculations could not be performed for *F. aquilonia* in variants at 17 and 28-30°. Nonetheless the obtained results (Table 3) confirm the same pattern: At the optimal temperatures of 20-25°, duration of the reproductive cycle is indepen

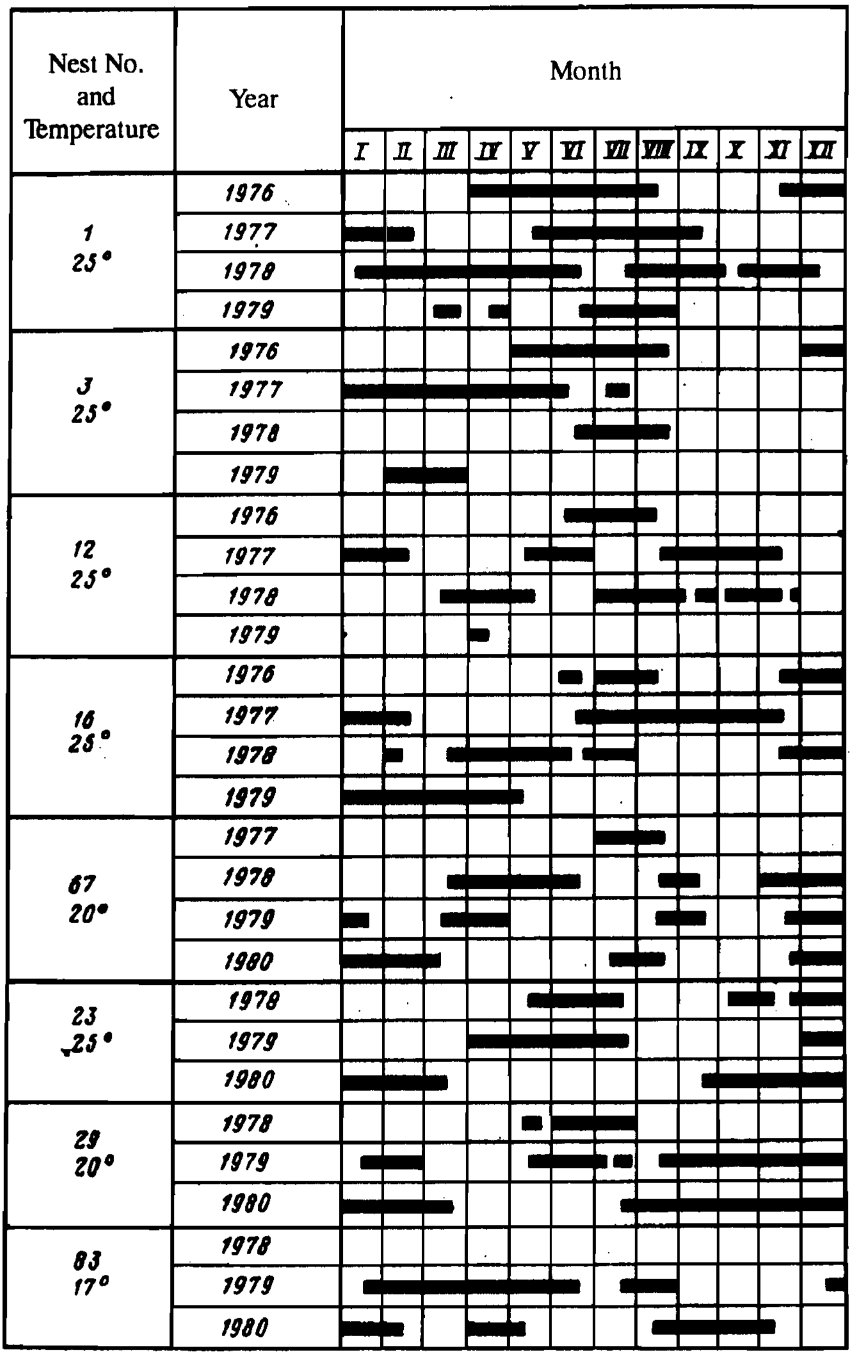

Fig. 2. Alternation of periods when eggs are present and lacking in experimental groups of *Formica aquilonia* (nests 1, 3, 12, 16, and 67) and *Formica polyctena* (nests 23, 29, and 83). Symbols as in Fig. 1.

Table 1

Duration of periods when eggs are present and lacking in experimental groups of ants at various temperatures (long experiments, 1976-1980)

Species	Temperature °C	Number of groups	Duration of periods, days										
			eggs present					eggs lacking					Sum of both periods
			N	range limits	$\bar{X}$	±δ	±m	N	range limits	$\bar{X}$	±δ	±m	
Formica aquilonia	28–30	2	2	75–83	78,8*	5,3	3,7	4	105–180	141,0	30,9	15,5	219,8
	25	22	54	45–255	115,5**	37,5	5,1	56	30–337	120,0**	44,7	6,0	235,5
	20	5	12	45–180	96,8	37,5	10,8	17	37–255	140,3	62,3	15,1	237,1
	17	5	7	90–113	102,0**	9,5	3,6	7	157–180	169,5**	9,5	3,6	271,5
Formica polyctena	28–30	6	16	37–113	68,3**	21,4	5,3	13	22–135	67,5*	34,1	9,5	135,8
	25	8	17	22–105	81,8	33,8	8,2	12	60–180	108,0	40,3	11,6	189,8
	20	12	28	30–225	85,5	49,9	9,5	26	22–300	105,0	65,6	12,9	190,5
	17	5	14	37–195	106,5**	39,8	10,6	12	37–165	108,8	37,7	10,9	215,2

Notes. Values of $\bar{X}$ marked with * differ significantly from the values of $\bar{X}$ for all other temperatures. Values of $\bar{X}$ marked with ** differ significantly among themselves (for each of the species).

Table 2

Effect of photoperiod on spontaneous rhythm of reproductive activity of queens at optimal temperatures (long experiments 1976-1980)

Species	Tem-peratures °C	Photo-period, h	Number of groups	Duration of periods, days										
				eggs present					eggs lacking					Sum of both periods
				N	range limits	$\bar{X}$	$\pm\delta$	$\pm m$	N	range limits	$\bar{X}$	$\pm\delta$	$\pm m$	
Formica aquilonis	25	18–20	9	22	45–202	116,3	37,0	7,9	27	45–225	107,3	40,7	7,9	223,6
		10–12	9	21	67–255	109,5	37,3	8,2	20	52–195	126,8	37,5	8,4	236,3
	20	18–20	2	4	60–135	90,0	36,8	18,4	8	68–232	150,8	60,8	21,5	240,8
		10–12	3	8	45–180	100,5	39,9	14,1	7	38–255	153,0	55,3	20,9	253,5
Formica polyctena	25	18–20	5	9	22–105	84,0	39,3	13,1	7	60–180	100,5	41,3	15,6	184,5
		10–12	3	8	22–105	79,5	28,9	10,2	5	68–173	118,5	40,9	18,3	198,0
	20	18–20	7	14	45–195	89,3	44,1	11,8	11	22–188	98,3	58,1	17,6	187,6
		10–12	5	14	30–225	81,0	56,6	15,1	13	22–202	90,0	46,2	12,8	171,0

dent of temperature; increasing temperature above the optimum shortens the cycle and decreasing it prolongs the cycle.

To test this pattern 2 other experiments were performed: one in 1979 with *F. aquilonia* and another in 1980 with *F. polyctena*. Ants were collected in the spring and kept at constant temperatures until the end of a complete reproductive cycle that lasted 171-256 days in *F. aquilonia* and 182-242 days in *F. polyctena*. The durations of periods when eggs were present and lacking as well as of the entire reproductive cycle varied significantly less than in the multiannual experiments, and after averaging the data the same pattern in general emerged: stability of mean duration of the cycle and its independence of temperature within an optimal range (Table 4). Mean duration of the period when eggs are present for both species is virtually independent of temperature. For *F. aquilonia* it was significantly shorter than for *F. polyctena*. This is basically explained by the fact that the experiment with *F. polyctena* was begun on 29 April, whereas that with *F. aquilonia* was started 16 May. Thus, the *F. aquilonia* queens spent a greater part of the oviposition period in natural nests than did the *F. polyctena* queens.

The mean duration of the period when eggs are lacking in *F. aquilonia* at temperatures of 20-30° was virtually the same, at 17°it was significantly greater, and in *F. polyctena* it was almost identical at 17-25°, but was significantly less at 30°. The overall duration of the reproductive cycle in *F. polyctena* declined significantly at 30° and increased at 17° as compared the value at the optimal temperatures. For *F. aquilonia* there was a significant increase in the mean duration of the reproductive cycle only at 17° as compared to the value at optimal temperatures (Table 4).

An interesting fact is that the mean duration of the reproductive cycle in all experiments was significantly greater in *F. aquilonia* than in *F. polyctena;* this is associated primarily with the greater duration of the period when eggs are lacking in *F. aquilonia* (Tables 1-4). Most likely, this is explained by the existence of some kind of physiological differences in the species.

In other experiments, the results of which have been published separately, it was demonstrated that the duration of the oviposition period is virtually independent of temperature in the 17-30° range. Using these results, one would expect the duration of the period when eggs are present in

Table 3

Duration of complete reproductive cycle of queens when ants are kept at various constant temperatures (long experiments 1976-1980)

Species	Temperature, °C	Number of groups	Duration of cycle, days				
			N	range limits	$\overline{X}$	±δ	±*m*
Formica aquilonia	25	18	41	98–525	212,0	81,8	12,8
	20	5	17	90–345	213,1	75,9	18,4
Formica polyctena	28–30	6	13	82–210	139,1*	41,9	11,6
	25	8	12	83–255	178,7	53,3	15,4
	20	11	24	60–345	178,7	80,7	16,5
	17	4	9	157–293	194,1	47,5	16,8

Note. Value of $\overline{X}$ marked with * differs significantly from values of $\overline{X}$ for other temperatures.

nests to increase significantly as temperature decreases as the duration of egg development increases (according to our data the duration of embryonal development in red wood ants when the temperature is decreased from 30 to 17° increases from 7-8 to 39-41 days). However, the experiments discussed above did not reveal a similar pattern. The duration of the period when eggs are present is either independent of temperature (Table 4) or is markedly temperature-dependent outside of the optimal temperature range (Table 1). An increase in the duration of the period when eggs are present at 17° and a decrease of 30° are thus not always observed and can only partially be associated with the effect of temperature on the rate of embryonal development. Thus, eggs disappear in the nests not only because the larvae emerge from them, but also for other reasons.

One such cause is undoubtedly use of the eggs as food by larvae of the first instar, a phenomenon very common among ants (Brian, 1951, 1957; Wilson, 1971) and which we observed in *Formica* species. Consumption of eggs by larvae may rapidly result in their complete disappearance from the nest. It may be assumed that this occurs with virtually identical speed at various temperatures, especially in the optimal range. It cannot be ruled out that worker ants also consume the final eggs and feed them to the larvae; nonoptimal temperatures may stimulate such consumption. This question requires special study.

STATE OF OVARIES OF QUEENS IN DIFFERENT PERIODS OF THE REPRODUCTIVE CYCLE

In all, 105 queens were dissected during the experiment. The main results from studying their ovaries are presented in Table 5. In springtime *F. polyctena* queens taken from nests before they warm up, many developing oocytes were found in the ovaries, but mature eggs were lacking. At the end of April, after the nests warmed up and oviposition had started, all dissected queens had mature eggs of normal size in the ovaries. In queens dissected at the end of August, when eggs had already disappeared in the nests, oocytes were found in various stages of degeneration and were small-sized; mature eggs were lacking.

Table

Duration of periods when eggs are present and lacking in experimental

Species	Temperature, °C	Duration of periods, days				
		eggs present				
		N	range limits	$\bar{X}$	±*m*	*N*
Formica aquilonia	30	11	53–70	59,7	1,9	10
	25	9	55–70	58,7	2,0	9
	20	9	49–65	56,7	1,3	7
(1979)	17	12	29–78	58,0	4,3	10
Formica polyctena	30	8	66–104	88,3	4,3	3
	25	10	59–106	82,3	11,5	5
	20	9	70–100	83,4	2,6	5
(1980)	17	9	73–115	90,9	4,5	5

Note. Values of $\bar{X}$ marked with * differ significantly from values of $\bar{X}$ for

All *F. aquilonia* and *F. polyctena* queens from the experimental laboratory nests that were dissected during the oviposition period had mature eggs and oocytes in various developmental stages in the ovaries (Fig. 3A). At 17°, there were few developing oocytes in the ovaries of queens; they were smaller compared to those in queens kept under various conditions (Table 5).

When queens were dissected during periods when there were no eggs in the experimental nests it was established that there were no mature eggs nor large differentiated oocytes in their ovaries (Table 5). As a rule, their ovarioles were empty or they contained individual degenerated, frequently irregularly formed oocytes. An example of such an ovary is presented in Fig. 3B. Thus, after suspension of egg laying at constant temperatures, true reproductive diapause begins that is accompanied by suspension of oogenesis and of the remaining oocytes in the ovarioles. After diapause ends, oogenesis resumes.

CONCLUSION

Results from all performed experiments indicate that under constant laboratory conditions, the cyclical alternation of reproductive activity and diapause characteristic of the natural annual cycle is maintained in red wood ant queens with the one difference that the overall duration of the cycle, in particular, the diapause period under laboratory conditions, is significantly shorter. The reproductive rhythm consists of 2 parts: oviposition and diapause phases. The length of a period of the rhythm as a fluctuating process corresponds to the duration of the complete reproductive cycle of the queens examined.

It should be emphasized that suspension of oviposition at optimal developmental temperatures is associated with formation of true imaginal diapause in queens (complete suspension of oogenesis and resorption of oocytes). Thus, under constant conditions, diapause spontaneously begins and also ends spontaneously.

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groups of ants at various temperatures (experiments performed 1979-1980)

eggs lacking			both periods together			
range limits	$\bar{X}$	±*m*	*N*	range limits	$\bar{X}$	±*m*
139–199	159,9	6,6	10	198–254	219,3	6,0
119–195	164,2	7,4	9	175–260	222,9	8,2
136–171	159,6	4,4	7	192–228	216,4	5,0
164–193	180,5*	3,0	10	241–250	243,5*	0,9
78–124	94,5	15,0	3	182–190	184,6*	2,6
91–145	123,6	9,6	5	197–239	208,2	7,9
113–134	128,6	3,8	5	204–218	212,5	2,5
109–152	128,3	7,6	5	209–242	223,1	8,0

all other temperatures.

The rhythm of reproductive activity in the queens is in no way associated with seasonal changes taking place outside the laboratory walls. It was observed that diapause came and went with identical frequency in all seasons (Figs. 1, 2). The absence of external synchronizing factors and the significant departure of the rhythm period from 12 months testify to the endogenous nature of the discovered rhythm (Ashoff, 1984; Gvinner, 1984a). The mean duration of the rhythm period is 140-215 days (5.5-7 months) for *F. polyctena* and 200-270 days (6.5-9 months) for *F. aquilonia.* Thus, these rhythms may be viewed as circumannual, i.e., having a periodicity of about 1 year (Gvinner, 1984a). Compared to other circumannual rhythms known for animals (Gvinner, 1984a), the rhythms of the red wood ants departs most significantly from an annual periodicity, and also differ in very great individual variability of phase duration and entire rhythm period as a whole: The lower and upper values may in some cases differ by almost an order of magnitude (Tables 1, 2).

The lack of dependence of mean duration of the rhythm period (the complete reproductive cycle of the queens) on temperature within an optimal range of developmental temperatures and the very weak dependence outside the optimal range are very interesting. Thermostability is one of the fundamental properties of circumannual and circadian rhythms (Gvinner, 1984a). The facts we discovered fit completely into this pattern.

Spontaneous developmental rhythms were discovered in a number of other ant species belonging to the genera *Aphaenogaster* (Bruniquel, 1978), *Camponotus* (Hölldobler, 1961; Kipyatkov, 1987). *Formica* (Kipyatkov, 1987), *Monomorium* (Petersen-Braun, 1975), *Leptothorax* (Plateaux, 1971), and *Myrmica* (Kipyatkov, 1987). Data we obtained on endogenous rhythms in the red wood ants are significantly more detailed and accurate than all those previously published. The wide distribution of endogenous developmental rhythms among ants makes it possible to view these rhythms as an important component in the seasonal developmental regulator system in insects (Kipyatkov, 1987).

The question concerning the ecological role of the endogenous rhythm of reproductive activity in red wood ants deserves special discussion. Above all, it is entirely clear that in nature such a rhythm cannot exist in the form in which it is observed in the laboratory. In nature, resumption of egg laying does not result from spontaneous suspension of diapause, but from a cold-weather reac-

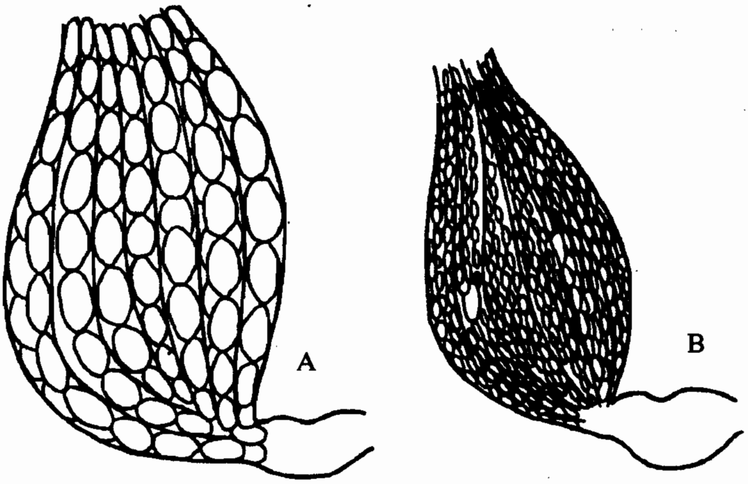

Fig. 3. Ovaries of queens from experimental nests when eggs are present (A) and lacking (B)

Table 5

Characteristics of overies in dissected queens

Origin of dissected queens	Characterization of variant	Eggs present in nests	Number of dissected queens	Mature eggs present	Maximal dimensions of dissected queens	Maximal number of differentiated oocytes per ovariole
From natural nests	9.IV.1980, before nests warm up	–	5	–	0,2×0,7	11
	21.IV.1980, after nests warm up	+	5	+	0,5×1,0	8
	23.VIII.1980, after oviposition is completed	–	11	–	0,3×0,6	4
From laboratory nests	30°	+	21	+	0,4×1,0	15
	25°	+	23	+	0,4×1,0	6
		–	7	–	< 0,1	0
		+	4	+	0,5×1,0	7
	20°	–	11	–	< 0,1	0
		+	8	+	0,3×0,8	4
	17°	–	10	–	<0,1	0

tivation taking place at low positive temperatures during hibernation. Results of our experiments published separately demonstrate that the effect on ants of temperatures around 5° over 1-2 months is enough to trigger rapid resumption of oviposition after the temperature rises to 20-25°; when ants are exposed to constant temperatures in the optimal range for development, oviposition is resumed only after 3-6 months. The cold-weather reactivation is a factor synchronizing the reproductive rhythms of individual queens ("timesetter" according to Gvinner, 1984) and ensuring a virtually simultaneous beginning of egg laying in the spring.

Thus, only the part of the reproductive rhythm determining the spontaneous onset of diapause in the queens may have ecological significance. Do there exist any external factors capable of affecting the duration of this phase of the rhythm, i.e., changing the times when diapause is entered? Our data presented above demonstrate that different constant photoperiods do not affect the parameters of the reproductive rhythm. Perhaps, gradual seasonal changes in photoperiod may play a synchronizing role, as was demonstrated in some birds (Gvinner, 1984a). Thus, the question requires additional experimental study.

We also have data demonstrating that periodic exposure of ants to temperatures below the optimal range somewhat accelerates the onset of diapause in queens. Perhaps this mechanism to some degree adjusts the duration to the reproductive period in nature, speeding up the onset of diapause at low temperatures in the second half of the summer. However, if we consider that red wood ants are capable of active temperature regulation and maintain an elevated temperature in the nest throughout the entire summer (Otto, 1962; Dlusskiy, 1967), then the importance of such a temperature adjustment should not be overestimated.

Thus, when red wood ant queens enter diapause is probably determine primarily by an endogenous reproductive rhythm functioning in this case on the hourglass principle (Kipyatkov, 1987). Although endogenous regulation of seasonal development arose in evolution on the basis of exogenous regulation, the advantages of circumannual systems of regulation compared to systems entirely dependent on external regulatory factors are by no means obvious (Gvinner, 1984). Especially worthy of attention is the fact that in red wood ants, which are one of the most advanced ant groups (Dlusskiy, 1967; Zakharov, 1972), it is the endogenous mechanisms of regulating seasonal development that dominate.

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