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Role of Endogenous Rhythms in Regulation of Annual Cycles of Development in Ants (Hymenoptera, Formicidae)*

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Abstract. Ants were collected in natural nests in spring and summer and kept in artificial plastic formicaria at optimal or suboptimal temperatures and constant daylength for several (up to 5) years. The spontaneous rhythms of queen oviposition and larval pupation were observed under constant laboratory environment in all 17 species studied belonging to the genera *Acantholepis, Aphanogaster, Camponotus, Crematogaster, Formica, Leptothorax, Monomorium,* and *Myrmica.* Oviposition and pupation stopped at a certain time and queens and larvae entered diapause. Development then recommenced spontaneously in several weeks or months. The rhythm period and its phases (development phase and diapause phase) varied greatly in duration and were not synchronized with natural seasons. This is an indication of the endogenous nature of the rhythms observed. *Acantholepis semenovi* Ruzs., *Camponotus ligniperda* (Latr.), *Lasius niger* (L.), *Myrmica ruginodis* Nyl., and *Tapinoma karavajevi* Em. were kept in the artificial nests with a horizontal temperature gradient from 8 to 35° for 2 years. Spontaneous rhythms of development correlated with the thermopreferendum cyclic variation were observed in all five species. During the developmental phase of the rhythm workers preferred nest chambers with a higher temperature to keep their brood but when the ants entered the diapausal phase of the rhythm they moved diapausing larvae to the cooler parts of the nest. The role of endogenous rhythms in the regulation of seasonality is discussed.

Key words: Formicidae; Hymenoptera; oviposition and larval pupation rhythms; endogenous regulation of natural rhythms.

The behavior and development of ants, as well as many other organisms, depend strongly on changes of ecological factors during the year. This dependence is particularly distinct in regions with temperate and cool climate, where life cycles of all living organisms rigidly follow an annual cycle of climatic changes. However, the seasonal association of processes of development in a colony of ants and mechanisms of its regulation did not attract the attention of myrmecologists despite the obvious importance of their investigation. For example, in the fundamental monograph of Hölldobler and Wilson (1990) dedicated to seasonality and annual cycles of development of ants they are simply never mentioned.

In 1969 at the initiative of A. S. Danilevskiy at the Faculty of Entomology of St. Petersburg University, I began investigation of the regulation of seasonal development in ants. In various years students, postgraduate students, and workers of the Faculty assisted me in my experiments and obser-

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vations. We managed to collect a considerable amount of data which allowed us to sort out the diversity of annual cycles of ants and to obtain some knowledge about the mechanisms regulating them and plan the most likely directions of their evolution (Kipyatkov, 1981, 1987, 1990, 1993).

Many tropical and subtropical ants have a homodynamic development: all ontogenetic stages from egg to pupa are present in their nests at any time of the year, and long-term retardation in development such as a winter suspension, or diapause, does not take place. The expansion of ants into regions with temperature and cool climate became possible only on the basis of formation of heterodynamic annual cycles, which are characterized by somewhat long retardation of development and even its complete termination with formation of stable diapause at certain periods of the year.

Based on results of the investigation of mechanisms regulating seasonal development, I distinguished two groups of yearly cycles of ants (Kipyatkov, 1987). The first is characterized by the possibility of continuous and unlimited development under optimal conditions and emergence of retardation of ontogenesis only at a lower temperature. Such cycles I call exogenous-heterodynamic. They are present in all species of *Diplorhotrum, Messor, Monomorium,* and *Tetramorium,* which I investigated, and are also characteristic of *Camponotus xerxes* For. and *Tapinoma karavajevi* Em. In species of this group diapause is exogenous and emerges under the influence of external ecological factors, primarily low temperatures not optimal for development.

The majority of ants in temperate-climate areas belong to the second group of species, which is characterized by endogenous-heterodynamic yearly cycles. Emergence of diapause in these species is caused primarily by inner factors for the colony, and any external conditions cannot prevent it. Even under conditions of a long day and optimal temperature, including daily thermorhythms that are most favorable for the ants (Lopatina and Kipyatkov, 1990), development of ants in colonies of these species finally is terminated and is replaced by the inactive phase of their yearly cycle. Exogenous factors such as the photoperiod and temperature, of course, play an important role in the regulation of yearly cycles of these species (for details, see Kipyatkov, 1993), but they cannot change their endogenous basis.

In individual endogenous-heterodynamic ants kept under constant laboratory conditions some researchers observed spontaneous rhythms of development: ovipositing and pupation of larvae first ended, and then spontaneously resumed after a long or short interval of time, and such cycles could be repeated. Such spontaneous cycles of development and behavior under constant conditions in the laboratory were first described by Hölldobler (1961) in *Camponotus herculeanus* (L.) and *C. lignioperda* (Latr.). In nonactive periods of cycles ants formed aggregations together with nondiapausing larvae in the nest, and workers during this time even closed the entrance to the nest with a plug made of litter. According to Plateaux (1970), in *Leptothorax nylanderi* (Fabr.) at 24-25°, development continues after overwintering when only diapausing larvae are present in the nest: after this period of diapause has continued for not less than 100 days, development may be resumed.

While maintaining a colony of *Aphaenogaster subterranea* (Latr.) in a laboratory nest with horizontal temperature gradient, Bruniquel (1978) observed a year-long cycle of changes of the thermopreferendum: in the summer ants concentrated in parts of the nest with temperature 16-22°, and in the winter they preferred to be at 9-12°. A similar pattern of association between the cyclicity of development and behavior of ants in nests with horizontal gradient was discovered by Billen (1984) in groups of workers of *Formica sanguinea* Latr. maintained without queens, and in my experiment with *Formica polyctena* Förster (Kipyatkov and Shenderova, 1986).

In our joint investigation with S. S. Shenderova, extensive data on spontaneous rhythms in *Formica* sp. s. str. were obtained. Experiments were conducted with several diels of experimental groups maintained at different constant temperatures and photoperiods from 1 to 5 years long (Kipyatkov and Shenderova, 1989, 1990). It was established that the spontaneous rhythms of ovipositing of queens do not have any association with the calendar, in other words with seasons of year replacing each other outside the walls of the laboratory. This is an apparent indication of their endogenous nature. Ovaries of queens in inactive periods of the reproductive rhythm do not contain eggs and developing oocytes. Therefore, queens during this time are in a state of true reproductive diapause. That the existence of a high variation in duration of periods of ovipositing and diapause among these endogenous rhythms should also be noted. The duration of the complete period of spontaneous rhythm (period of presence of eggs + period of their absence) on the average is 212 days in *F. aquilonia* Yarr. and 179 days in *F. polyctena* and does not depend on the photoperiod or temperature within an optimal range which is 20-25°; at a higher temperature this parameter declined and at a lower temperature increased (Kipyatkov and Shenderova, 1989, 1990).

In this work, the results of a multiannual experimental investigation of endogenous rhythms of development of 25 species of ants belonging to 12 genera are offered. In most of these investigations, beginning in 1984, E. B. Lopatina took the most active part and I sincerely thank her for her assistance in the work and estimation of its results.

MATERIALS AND METHODS

Ants were collected from natural colonies most often in spring and maintained in the laboratory in portable plastic formicaria without nesting material, allowing us to conduct a survey of all stages of development. Each such formicarium consisted of a darkened and humidified nest part, where ants kept their brood and a nonhumidified "arena" open to the light in which feeders with food were placed twice a week. The food consisted of 20% sugar solution with ground cockroaches or puparia of calliphorid flies. Each experimental group of ants had a complete composition: workers, brood and queens (or one queen in monogynous species). Formicaria with ants were kept in photothermostatic chambers at various photoperiods and temperatures. In several cases, 24-hour period П-shaped thermorhythms with 12-hour periods of high and low temperature were used. Transition from high to low temperature and vice versa occupied about one hour. Scotophase in the photoperiodic cycle in cases when it was shorter than 12 hours (at the long day) always remained in the middle of the low-temperature period of the thermorhythm.

Experimental groups of ants were kept under constant laboratory conditions for not less than 1 year, usually 2-3 years, and sometimes up to 5 years. During this time a survey of all stages of development was conducted weekly, and in some cases more often.

Experiments with free choice by ant of the preferred temperature was conducted in a laboratory device consisting of a concrete plate 140 × 30 × 5 cm placed on an aluminum plate 0.5 cm thick. In the concrete plate 6 rows connected with 30 passages were made and covered with glass forming chambers 25 × 20 × 10 mm. Each such row served as a nest for one group of ants and in one of central chambers had exit through the pipe to separate plate arena, where the food was placed. The nest was covered with a darkening and thermoinsulating lid. One end of the plate was cooled with a compressor refrigerator, and another end was heated with an electric heater. As a result a temperature gradient from 8° (in the first chamber) to 35° (in the 30th chamber) was maintained along the plate. Temperature was recorded with thermometers inserted into the concrete plate. The entire device was kept at the ambient room temperature and light for 20 hours a day. One to two times a week the distribution of ants and brood among the chambers along the temperature gradient were recorded visually.

Since 1976 the following species of ants were used in experiments: *Acantholepis semenovi* Ruzs. (Turkmenia, vicinity of Ashkhabad), *Aphaenogaster sinensis* Wheeler (S Maritime Terr., Kedrovaya

Pad' Reserve), *Camponotus herculeanus* (L.) (St. Petersburg [formerly Leningrad] Prov., Vyritsa and Moscow Prov., Solnechogorsk Distr.), *C. japonicus* Mayr (Maritime Terr., Lazovskiy Reserve), *C. ligniperda* (Latr.) (Ukraine, Carpathian Mountains, Kolochava), *Cataglyphis aenescens* (Nyl.) (Turkmenia, Kopetdag), *Crematogaster bogojawlenskii* Ruzs. (Turkmenia, vicinity of Ashkhabad), *Formica aquilonia* Yarr. (St. Petersburg Prov., Novolisino), *F. fusca* L. (Moscow Prov., Solnechnogorsk Distr.), *F. gagatoides* Ruzs. (Magadan Prov., Vetrenyy), *F. lemani* Bondr., (same locality), *F. picea* Nyl. (same locality), *F. polyctena* Först. (Belgorod Prov., Borisovka, Les-Na-Vorskle Reserve), *Lasius flavus* De Geer (Ukraine, Carpathian Mountains, Kolochava), *L. niger* (L.) (St. Petersburg Prov., Vyritsa and Ukraine, Carpathian Mountains, Kolochava), *Leptothorax acervorum* (Fabr.) (St. Petersburg Prov., Vyritsa and Magadan Prov., Vetrenyy), *Monomorium ruzskyi* Dlussky & Zabelin (Turkmenia, Kara-Kala and vicinity of Ashkhabad), *Myrmica rubra* L. (Belgorod Prov., Borisovka, Les-Na-Vorskle Reserve and St. Petersburg Prov., Vyritsa), *M. ruginodis* Nyl. (Belgorod Prov., Borisovka, Les-Na-Vorskle Reserve, St. Petersburg Prov., Vyritsa and S Maritime Terr., Kedrovaya Pad' Reserve), *M. scabrinodis* Nyl. (Belgorod Prov., Borisovka, Les-Na-Vorskle Reserve), *M. transsibirica* Radtschenko (S Maritime Terr., Kedrovaya Pad' Reserve), *Plagiolepis karawajewi* Ruzs., *P. pallescens* For., *P. vladileni* Radch. (Crimea, Kara-Dag and Turkmenia, Kopetdag), *Tapinoma karavaievi* Emery (Turkmenia, vicinity of Ashkhabad).

RESULTS OF DISCUSSION

In all endogenous heterodynamic species of ants that we investigated we observed spontaneous resumption of ovipositing and pupation of larvae during long-term maintenance of groups under conditions identical to those in which development of ants became suspended. Depending on the species, conditions of maintenance and other factors, discussion of the nature of which is premature, development may resume after a few weeks or after several months, and sometimes even after almost a year. Ovipositing and pupation continue for some time, but then a gradual decline is observed, and finally development became suspended again. We observed such an alternation of periods of development and suspension under constant conditions in 17 species of ants (Table 1). Also, in *Catoglyphis aenescens, Lasius flavus, L. niger* and species of *Plagiolepis*, resumption of development under constant conditions was recorded, but complete cycles with alternation of development and diapause were not investigated for technical reasons.

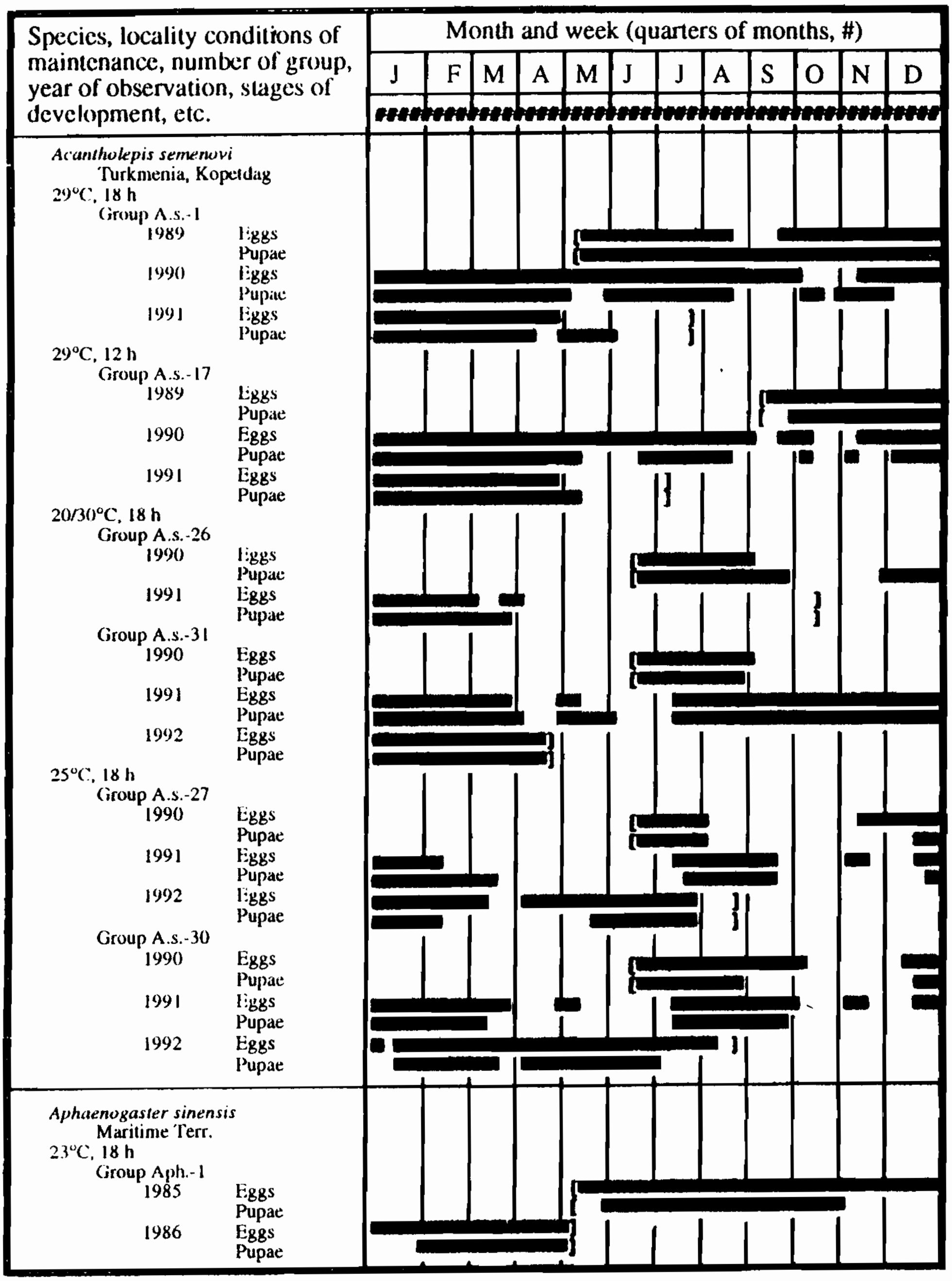
In nests with horizontal temperature gradient in which ants were permitted to make a free choice, we observed even more distinct spontaneous rhythms of development (Table 2). They were closely associated with changes in the thermopreferendum: in periods of active development ants kept their brood in chambers with sufficiently high temperature, and in periods of diapause in cool chambers. These rhythmic changes of the thermopreferendum have been described in detail (Kipyatkov and Lopatina, 1991).

There was a considerable variation of the duration of periods of development and diapause in different experimental groups and within the same group. As well, a complete absence of any coordination with natural change of seasons is completely obvious. Also periods of ovipositing do not always "regularly" (as happens under natural conditions) coincide with periods of pupation and sometimes follow in general disorder (Table 1). All this clearly indicates the endogenous nature of observed rhythms and absence of external synchronizers in them.

In the analysis of obtained results, typical endogenous-heterodynamic ants associated in their distribution with the northernmost areas of the Palearctic Region should be considered first. These are species of *Camponotus* s. str., *Formica, Lasius, Leptothorax* s. str., and *Myrmica*. They apparently need lower temperature during the inactive phase of the annual cycle. In nests with a thermogradient these ants moved into the cool chambers with the onset of diapause and remained there for a long time.

Table 1

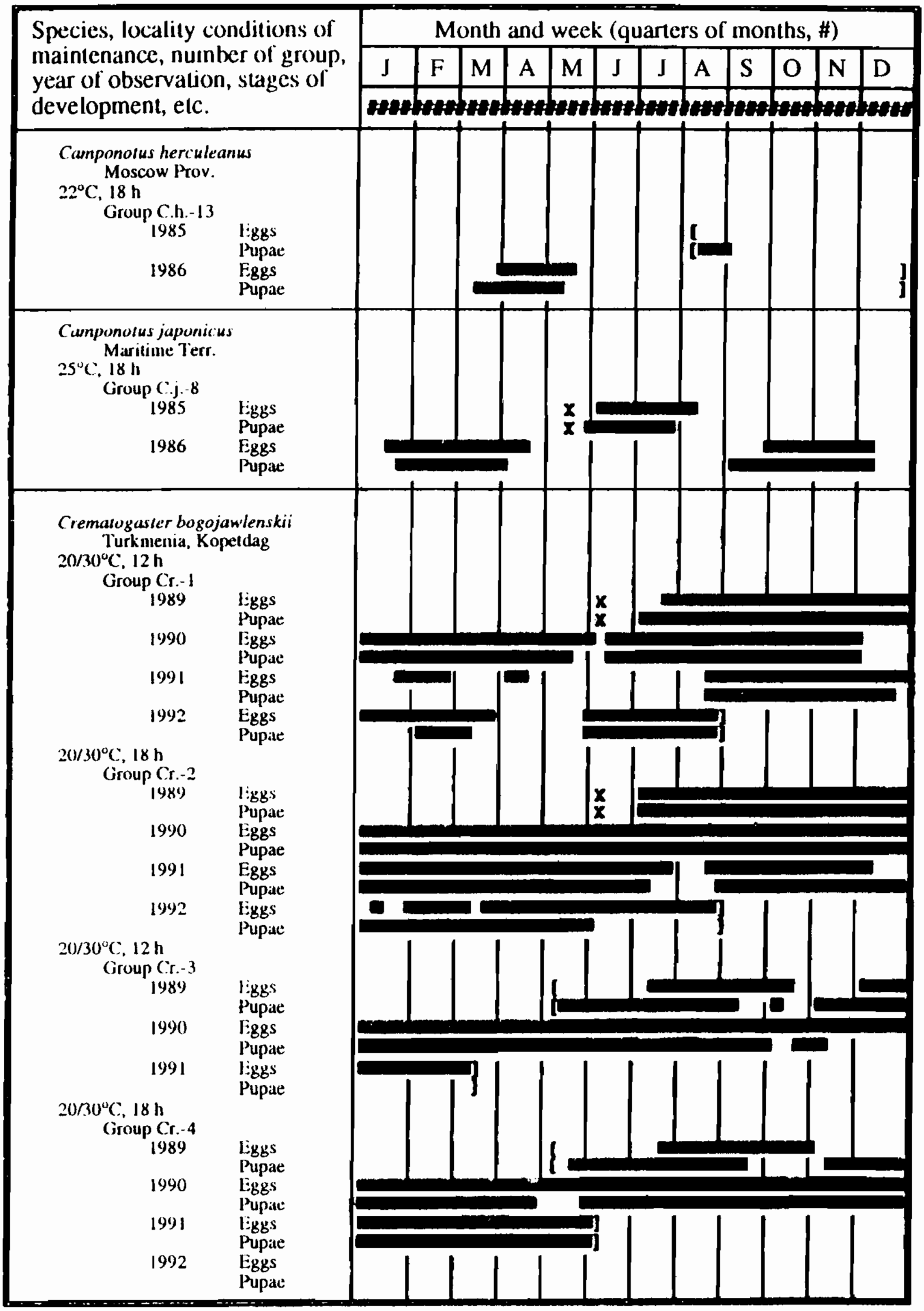
Spontaneous rhythms of development of ants during long-term maintenance under constant laboratory conditions



Acantholepis semenovi
Turkmenia, Kopetdag
29°C, 18 h
Group A.s.-1
1989 Eggs
Pupae
1990 Eggs
Pupae
1991 Eggs
Pupae
29°C, 12 h
Group A.s.-17
1989 Eggs
Pupae
1990 Eggs
Pupae
1991 Eggs
Pupae
20/30°C, 18 h
Group A.s.-26
1990 Eggs
Pupae
1991 Eggs
Pupae
Group A.s.-31
1990 Eggs
Pupae
1991 Eggs
Pupae
1992 Eggs
Pupae
25°C, 18 h
Group A.s.-27
1990 Eggs
Pupae
1991 Eggs
Pupae
1992 Eggs
Pupae
Group A.s.-30
1990 Eggs
Pupae
1991 Eggs
Pupae
1992 Eggs
Pupae

Aphaenogaster sinensis
Maritime Terr.
23°C, 18 h
Group Aph.-1
1985 Eggs
Pupae
1986 Eggs
Pupae

Table I (continued)



Species, locality conditions of maintenance, number of group, year of observation, stages of development, etc.

Month and week (quarters of months, #)

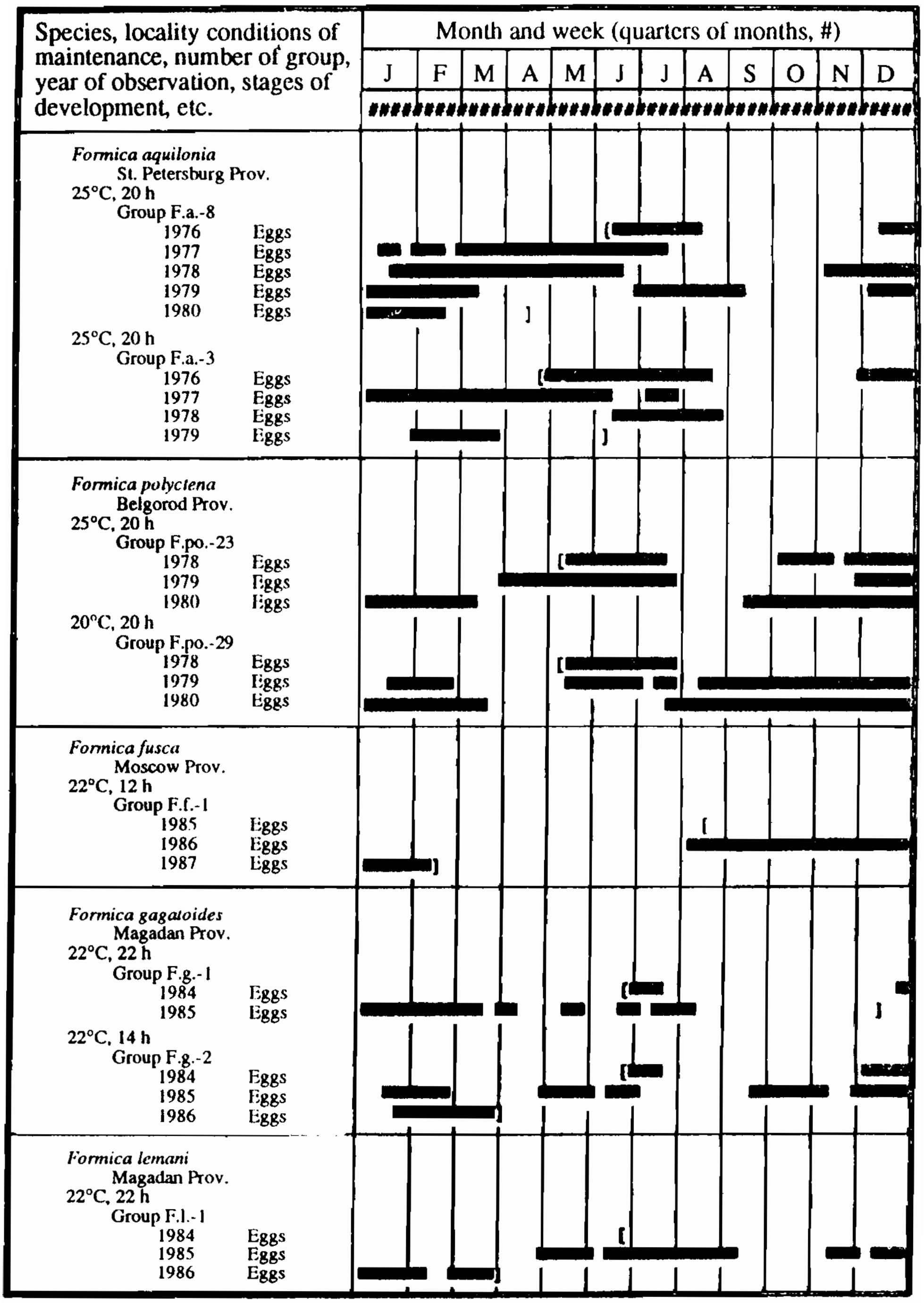
J F M A M J J A S O N D

Camponotus herculeanus
Moscow Prov.
22°C, 18 h
Group C.h.-13
1985 Eggs
Pupae
1986 Eggs
Pupae

Camponotus japonicus
Maritime Terr.
25°C, 18 h
Group C.j.-8
1985 Eggs
Pupae
1986 Eggs
Pupae

Crematogaster bogojawlenskii
Turkmenia, Kopetdag
20/30°C, 12 h
Group Cr.-1
1989 Eggs
Pupae
1990 Eggs
Pupae
1991 Eggs
Pupae
1992 Eggs
Pupae
20/30°C, 18 h
Group Cr.-2
1989 Eggs
Pupae
1990 Eggs
Pupae
1991 Eggs
Pupae
1992 Eggs
Pupae
20/30°C, 12 h
Group Cr.-3
1989 Eggs
Pupae
1990 Eggs
Pupae
1991 Eggs
Pupae
20/30°C, 18 h
Group Cr.-4
1989 Eggs
Pupae
1990 Eggs
Pupae
1991 Eggs
Pupae
1992 Eggs
Pupae

Table 1 (continued)



Species, locality conditions of maintenance, number of group, year of observation, stages of development, etc.	Month and week (quarters of months, #)
	J F M A M J J A S O N D

Formica aquilonia
St. Petersburg Prov.
25°C, 20 h
Group F.a.-8
1976 Eggs
1977 Eggs
1978 Eggs
1979 Eggs
1980 Eggs
25°C, 20 h
Group F.a.-3
1976 Eggs
1977 Eggs
1978 Eggs
1979 Eggs

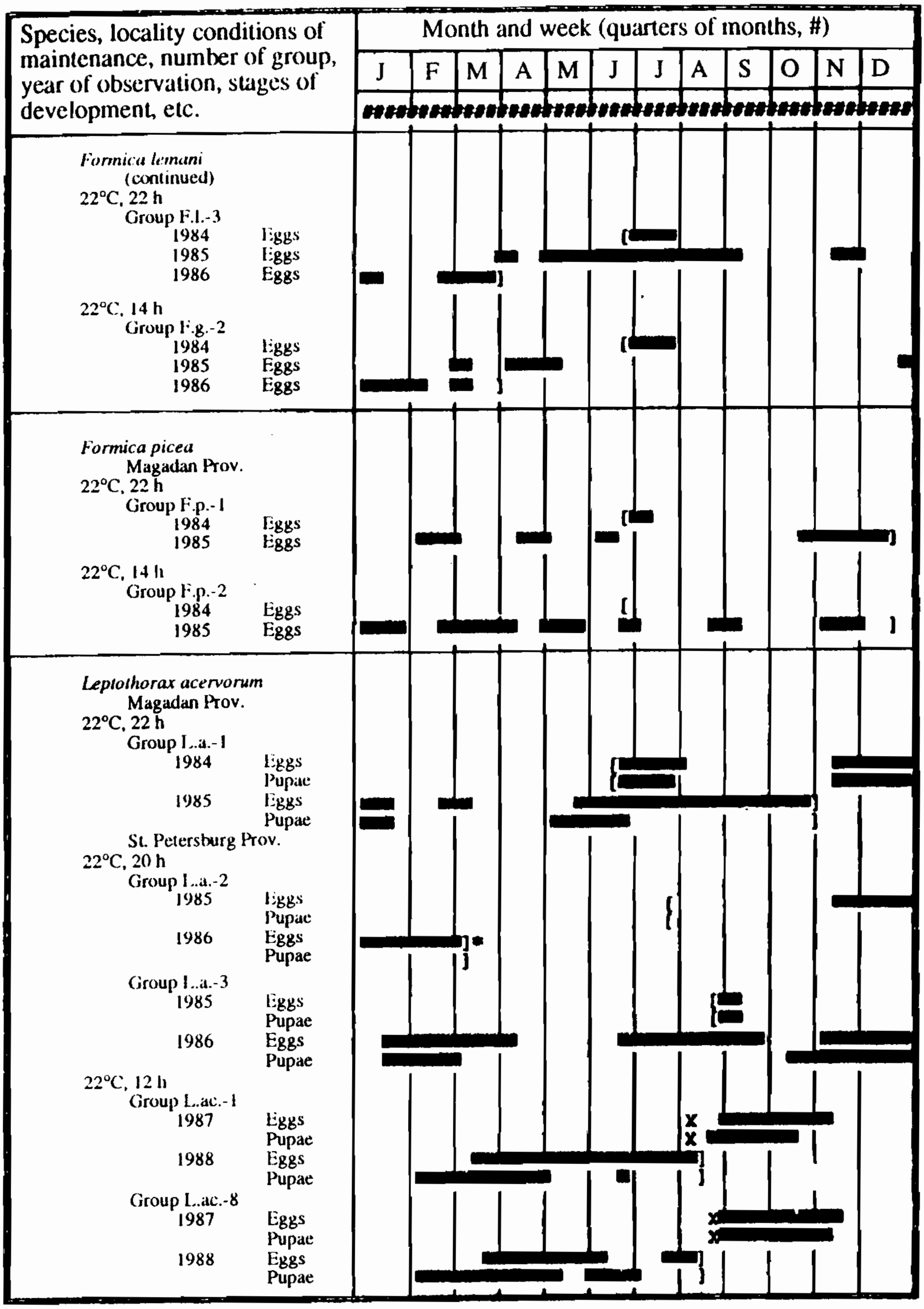
Formica polyctena
Belgorod Prov.
25°C, 20 h
Group F.po.-23
1978 Eggs
1979 Eggs
1980 Eggs
20°C, 20 h
Group F.po.-29
1978 Eggs
1979 Eggs
1980 Eggs

Formica fusca
Moscow Prov.
22°C, 12 h
Group F.f.-1
1985 Eggs
1986 Eggs
1987 Eggs

Formica gagatoides
Magadan Prov.
22°C, 22 h
Group F.g.-1
1984 Eggs
1985 Eggs
22°C, 14 h
Group F.g.-2
1984 Eggs
1985 Eggs
1986 Eggs

Formica lemani
Magadan Prov.
22°C, 22 h
Group F.l.-1
1984 Eggs
1985 Eggs
1986 Eggs

Table 1 (continued)



Species, locality conditions of maintenance, number of group, year of observation, stages of development, etc.

Month and week (quarters of months, #)

J F M A M J J A S O N D

Formica lemani
(continued)
22°C, 22 h
Group F.l.-3
1984 Eggs
1985 Eggs
1986 Eggs

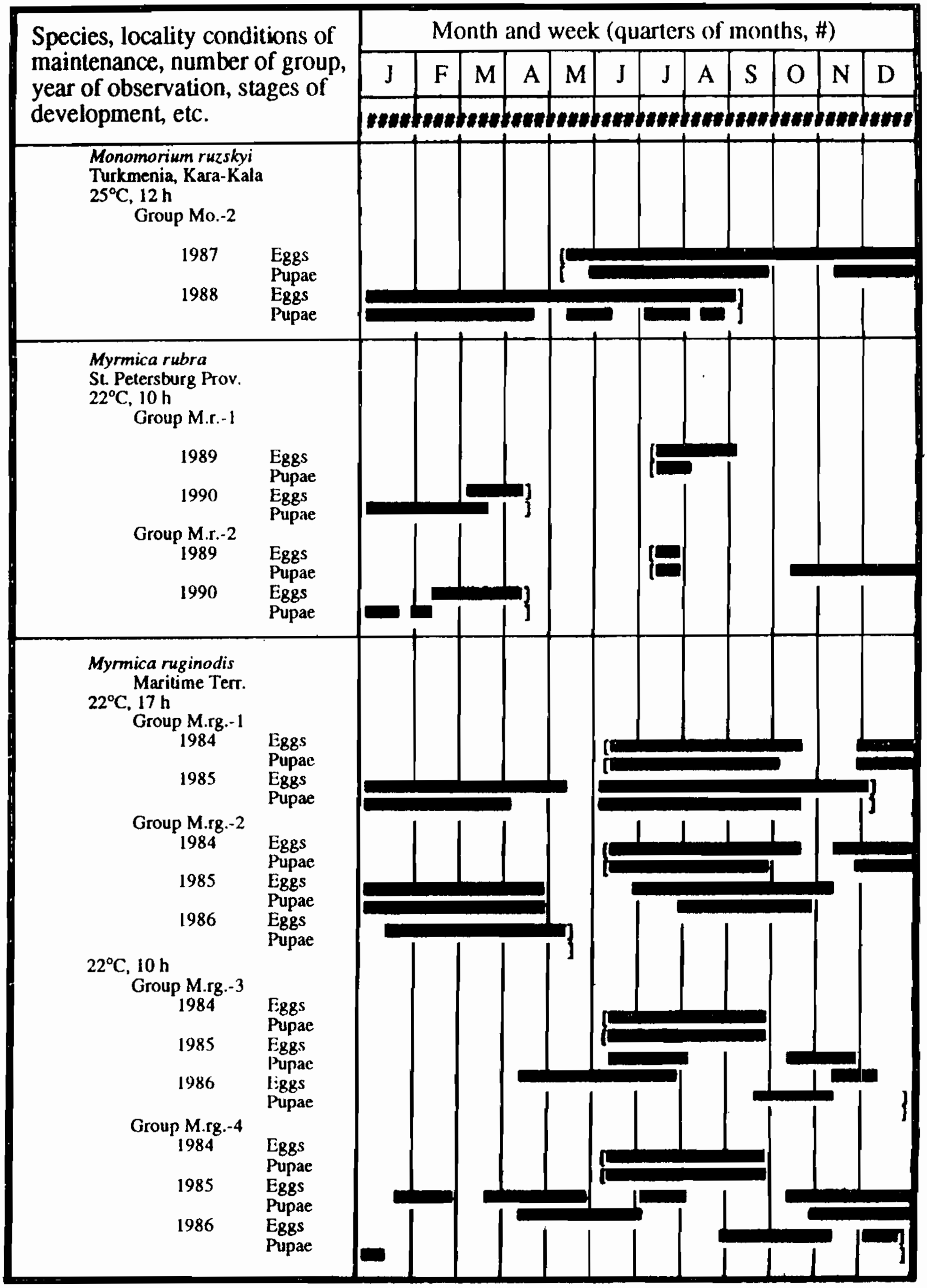
22°C, 14 h
Group F.g.-2
1984 Eggs
1985 Eggs
1986 Eggs

Formica picea
Magadan Prov.
22°C, 22 h
Group F.p.-1
1984 Eggs
1985 Eggs

22°C, 14 h
Group F.p.-2
1984 Eggs
1985 Eggs

Leptothorax acervorum
Magadan Prov.
22°C, 22 h
Group L.a.-1
1984 Eggs
Pupae
1985 Eggs
Pupae
St. Petersburg Prov.
22°C, 20 h
Group L.a.-2
1985 Eggs
Pupae
1986 Eggs
Pupae
Group L.a.-3
1985 Eggs
Pupae
1986 Eggs
Pupae
22°C, 12 h
Group L.ac.-1
1987 Eggs
Pupae
1988 Eggs
Pupae
Group L.ac.-8
1987 Eggs
Pupae
1988 Eggs
Pupae

Table 1 (continued)

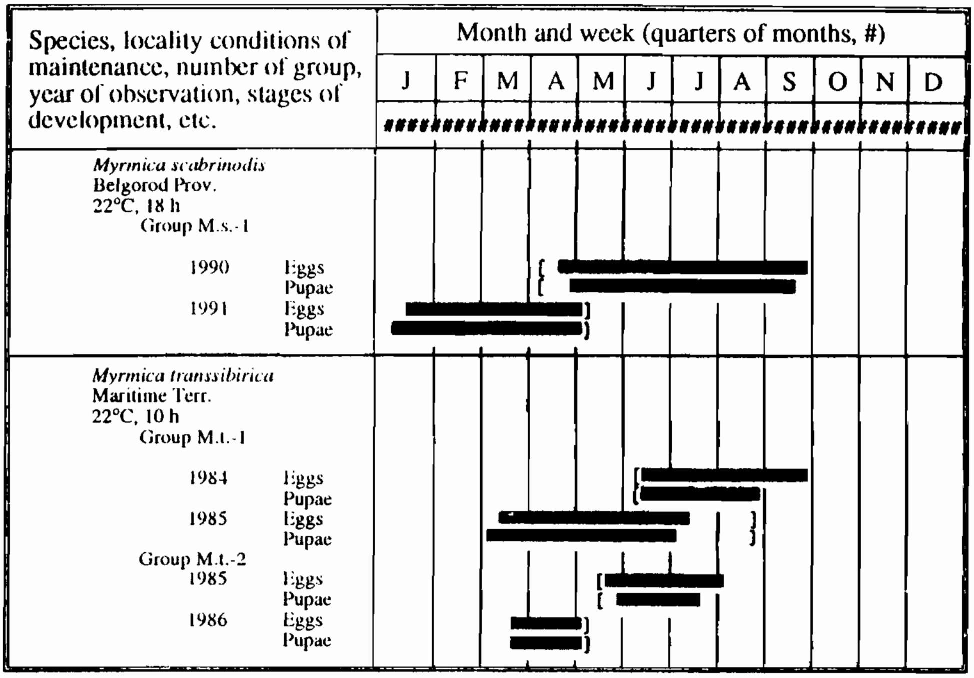


Monomorium ruzskyi
Turkmenia, Kara-Kala
25°C, 12 h
Group Mo.-2
1987 Eggs
Pupae
1988 Eggs
Pupae

Myrmica rubra
St. Petersburg Prov.
22°C, 10 h
Group M.r.-1
1989 Eggs
Pupae
1990 Eggs
Pupae
Group M.r.-2
1989 Eggs
Pupae
1990 Eggs
Pupae

Myrmica ruginodis
Maritime Terr.
22°C, 17 h
Group M.rg.-1
1984 Eggs
Pupae
1985 Eggs
Pupae
Group M.rg.-2
1984 Eggs
Pupae
1985 Eggs
Pupae
1986 Eggs
Pupae
22°C, 10 h
Group M.rg.-3
1984 Eggs
Pupae
1985 Eggs
Pupae
1986 Eggs
Pupae
Group M.rg.-4
1984 Eggs
Pupae
1985 Eggs
Pupae
1986 Eggs
Pupae

Table 1 (continued)



Comments. In the table only presence of eggs and pupae (together with prepupae) is indicated because larvae were not always present. In species of *Formica* only eggs are marked because larvae do not diapause and do not overwinter. The constant presence of eggs in the group *Aphaenogaster sinensis* is explained by the fact that some ants of this genus are characterized by a special type of annual cycle without diapause of the queen, as a result of which eggs remain in nests to overwinter.

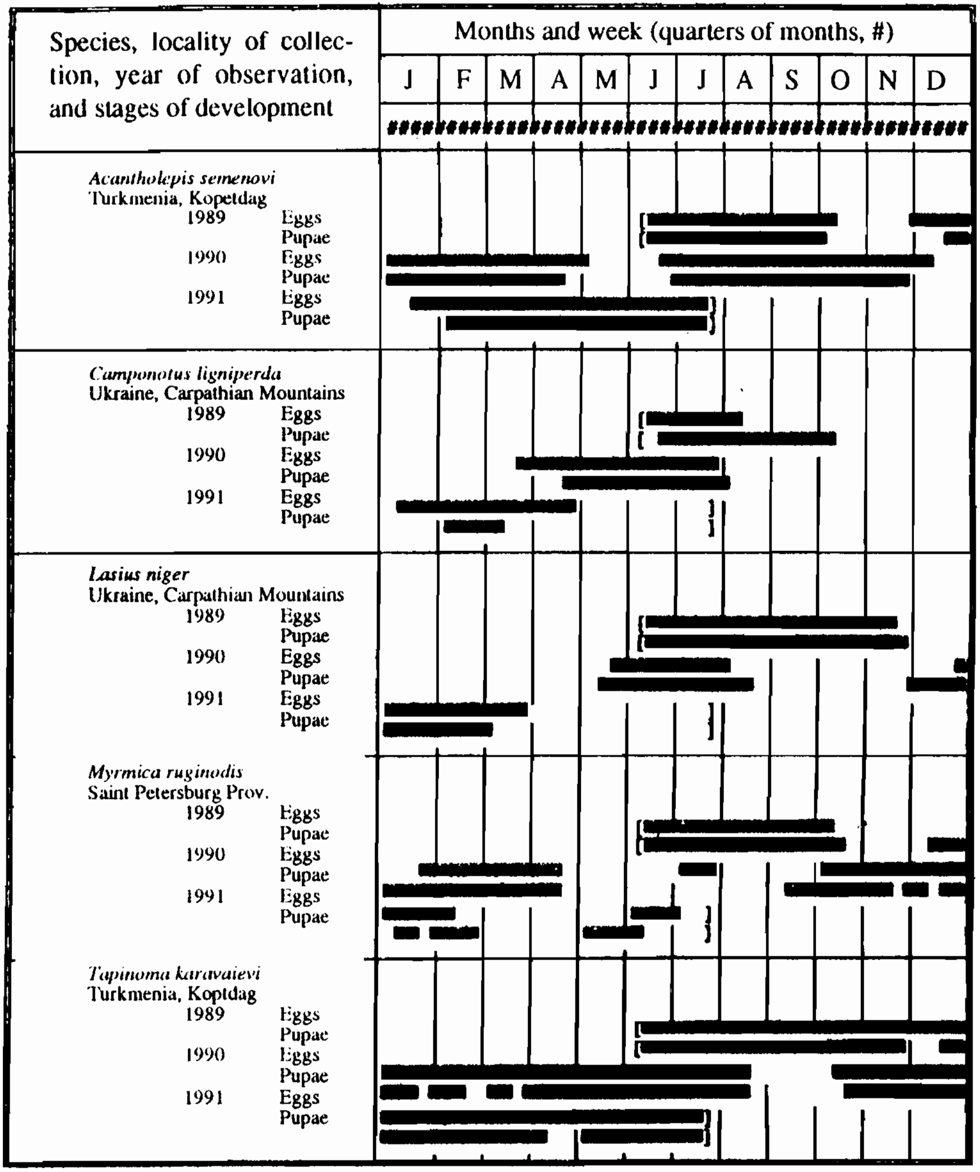
_____ - indicates presence of eggs or pupae and prepupae in the group; [- indicates the beginning of experiment with ants collected under natural conditions; X - indicates the beginning of experiment with ants after reactivation under cool conditions in the laboratory; | - indicates the end of the experiment; * - queen in the nest died.

The high temperatures which are optimal for development of these ants during the active phase of the annual cycle are obviously unfavorable for them during periods of winter suspension, which generally is characteristic of most insects of the temperate zone (Danilevskiy, 1961). Therefore, we could keep these species for a long time at temperatures slightly lower than the optimum. However, even under these conditions high mortality of the brood and workers in periods of diapause was observed.

It should also be emphasized that during the spontaneous resumption of development of these ants it is never as perfect as after normal overwintering: the productivity of queens is low, not all larvae go into diapause, and quick brooding (individuals completing development in one season) usually does not occur at all. Such a peculiarity of spontaneous resumption of development was recorded first in *Leptothorax nylanderi* (F.) (Plateaux, 1970); in our experiments we observed this

Table 2

Spontaneous rhythms of development of five species of ants maintained in nests with horizontal temperature gradient



Comments. See Table 1.

phenomenon in all northern species. In each reproductive cycle under constant conditions the indices of viable development decline steadily, the number of young workers gradually declines, and therefore the population density of the ants also declines, their viability declines, and finally they all die. In most lengthy experiments with *Formica* sp. we sometimes added pupae from other colonies in order to maintain the density of ants in experimental groups and prevent their dying out (Kipyatkov and Shenderova, 1990). In some cases resumption of development under constant conditions takes place with difficulty and not quickly (see *Formica fusca* in Table 1) or does not resume at all as in some of our experiments with *Lasius niger* and *L. flavus*. Therefore for a valid restoration of the capability to develop and for preservation of the viability, all these species need overwintering, or reactivation under condition at lower temperature (Kipyatkov, 1993).

Endogenous-heterodynamic species of ants of the genera *Acantholepis, Aphaenogaster, Crematogaster,* and *Plagiolepis* distributed in more southern regions do not require any lower temperature for successful overwintering and reactivation. When they were kept at a temperature optimal for development during diapause, we did not observe such a catastrophic mortality as in northern species, although a high constant temperature is not an ideal condition for these ants. The *A. semenovi,* which we investigated, may serve as an example.

In the nest with thermogradient it was characterized by a high cyclicity of development with very long (5-8 months) active phase and short (1-1.5 months) phase of suspended development (Table 2). The thermopreferendum during development was 28-32°, and during diapause 15-25°. Temperature distinctly influenced the display of endogenous rhythm of development. At a constant high temperature of 29° development was almost continual, with rare short periods of suspension; at 25° and thermorhythm 20/30° (average 24-hours period temperature 25°) spontaneous rhythms were more distinct with longer and more frequent periods of diapause (Table 1). *Crematogaster bogojawlenskii* was similar. At a thermorhythm of 20/30° it developed almost like homodynamic species (especially after overwintering in the laboratory, see groups Cr.-3.4 in Table 1), in other words without interruptions.

Finally, the exogenous-heterodynamic species *Monomorium ruzskyi* and *Tapinoma karavaievi,* which at normal optimal temperature are capable, as well as homodynamic ants, of continuous development without any decline in viability (Kipyatkov, 1993), may under certain conditions display some characteristics of endogenous rhythms. Thus, in *M. ruzskyi* at a constant suboptimal temperature of 25° in the pupation of larvae 1-1.5-month-long, interruptions (Table 1) were observed. The *T. karavaievi* group in the nest with temperature gradient over 2 years had two short periods of diapause (Table 2): from October 1989 to February 1990 many larvae were in diapause, but some continued to develop, and ovipositing also did not stop; in August-October, 1990, ovipositing and pupation ended completely for two months, queens and brood during this time were in chambers at temperature 18-22°, whereas during active development their thermopreferendum was 26-33°.

Therefore, among groups of exogenous-heterodynamic ants, as should be expected, there are no sharp borders and we can find species with mixed, intermediate regulation of the annual cycle.

CONCLUSION

The spontaneous rhythms of development of the ants we investigated are physiologically endogenous, which is clearly proven by the absence of external synchronizing factors and considerable deviation from the 12-month period of rhythms (Ashoff, 1984; Gvinner, 1984b). They should be considered as near-annual, although as compared with annual rhythms described in other animals (Gvinner, 1984b) rhythms of ants differ most from annual periodicity and, as well, they differ in the great variation of the duration of phases and entire period of the rhythm.

However, for us it is not the physiological nature of the phenomenon, but its ecological role that is most interesting. It is known that spontaneous processes participate in the regulation of seasonality of development of many insects affecting either termination of diapause or changing the tendency toward it in series of consecutive generations (Zaslavskiy, 1984; Vinogradova, 1991). In ants, as shown above, these processes may participate not only in the termination of diapause (reactivation), but also in its induction.

Despite extremely scanty information concerning the phenomena of seasonality in tropical ants, it is known that they can have not only homodynamic, but also heterodynamic development (Kipyatkov, 1993). It is possible that under conditions of tropical and subtropical climates endogenous rhythms may play an important, and even leading, role in the regulation of seasonal development of ants. However, this problem requires special investigation.

Under conditions of a temperate climate, the cold winter makes possible the free flow of endogenous rhythms. In species distributed in southern regions of the temperate zone (*Acantholepis*, etc.) reactivation, as our data show, is essentially spontaneous and takes place in the fall because of effects of endogenous mechanisms, but approaching cool weather makes the resumption of development impossible until warmer weather in the spring.

Species of ants distributed far to the north (*Camponotus* s. str., etc., see above) became adapted to the long, cold winter. They developed a true reactivation brought about by the cold weather, which requires a long period of life at low positive temperature (Danilevskiy, 1961; Danilevskiy and Sheldeshova, 1968). In these ants spontaneous reactivation is possible only under artificial conditions and is not complete. For the complete restoration of the capability to develop and for preservation of viability they need a cool reactivation.

Therefore in northern ants only that part of the endogenous rhythm is ecologically meaningful which determines the gradual decline of the potential for development and an increase in the tendency to diapause during the active (summer) period of the annual cycle. This endogenous physiologic mechanism is not yet known in nature. It acts by the "sand clock" principle (Kipyatkov, 1987) and occupies a central place in the regulation of annual cycles in a way typical of endogenous-heterodynamic species. It acts jointly with correcting exogenous factors such as temperature and photoperiodicity. In our investigations this mechanism was discovered in all species except the completely homodynamic species (Kipyatkov, 1993). Cold reaction is a major synchronizing factor (a "time setting" mechanism according to Gvinner, 1984a) in coordinating rhythms of development of individual colonies of ants and securing simultaneous start of development in the spring. However, discussion of the role of the "sand clock" mechanism in the regulation of the cycle of endogenous-heterodynamic ants in greater detail exceeds the limits of this work and has been published earlier (Kipyatkov, 1993).

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