

## **Annual cycles of development in ants: diversity, evolution, regulation\***

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**Abstract** - This is a review of the published data and the results of own long-term studies on the seasonality of development in ants. While primarily tropical ants penetrated into the temperate climate regions their predominantly homodynamous development was replaced by the heterodynamous annual cycles characterized by the appearance of winter diapause. Three types of annual cycles of development are distinguished by the author: (1) *Formica* type (only queen diapause, hibernation without a brood); (2) *Aphaenogaster* type (only larval diapause, hibernation with eggs and all instars larvae); (3) *Myrmica* type (diapause of both queens and larvae, hibernation with larvae of single or several instars). On the grounds of regulation nature the heterodynamous ant species are divided into two groups. The species with exogenously heterodynamous cycles are characterized by the possibility for continuous and unlimited development under optimal conditions and by the arising of ontogenetic delays only in response to the decline of temperature. The regulation of seasonal development in these ants is realized entirely by the external ecological factors and above all by temperature. Most of ants inhabiting the regions with temperate and cold climate possesses the endogenously heterodynamous cycles. They are distinguished by an obligatory diapause that arises in their colonies under any circumstances as a result of the endogenous physiological process of yet unknown nature (so-called "sand-glass device") determining the gradual decrease of the ability for development and the increase of the tendency for diapause during the summer. Temperature and more infrequently photoperiod (the exogenous modifying factors) participate in the regulation of seasonal development of these ants adjusting the date of diapause arising to the climatic characteristics of a given year. The diapause termination and the restoration of the capability for full development in northern ants are the result of cold reactivation proceeding at low positive temperatures during the hibernation. In species restricted to more southern regions of the temperate climate zone the reactivation could be of essentially endogenous nature and does not require the winter chilling.

**Keywords:** review, Formicidae, seasonality, climate, temperature, photoperiod, homodynamous, heterodynamous, development, diapause, exogenous, endogenous, regulation, spontaneous rhythms.

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\* This paper is dedicated to the memory of Dr. Michael V. Brian whose constant and so rare among the myrmecologists interest to the study of seasonality in ants and other social insects inspired the author for a long time.

## Introduction

The life of ants as of most other organisms is very closely connected and correlated with the seasonal climatic variation occurring during the year. The seasonality of ecological factors, such as temperature, rainfall, humidity, food, etc., usually expressed even in the tropics, causes the corresponding changes in behaviour and development of ants and other insects. As for the regions of the temperate and boreal climates, it should be emphasized that the life cycles of all organisms inhabiting them are strongly subordinated to the annual rhythm of climatic factors.

It is widely known that each ant species is characterized by a certain *annual cycle of behaviour*. A number of works by many authors were devoted to the study of seasonality in ant behaviour (for a review see Dlussky, 1967, 1981; Brian, 1983; Hölldobler, Wilson, 1990). At the same time the seasonality of development in the ant colony did not nearly evoke the specialists' interest during long periods despite of the obvious fact that it is the seasonal timing of developmental processes that makes up the base for annual behavioural cycle. The oviposition and brood rearing are necessary for colony maintenance, growth and reproduction and so for the species existence. As a rule all these processes have no possibility to proceed incessantly during the whole year. Thus, the *annual* or *seasonal cycle* of development usually exists in every colony of ants.

For the survival and prosperity of the colony its annual cycle should be organized in a way to use the whole warm period of a year for larvae rearing and to produce maximal quantity of new workers and alates. For this purpose the development of the brood should commence in spring as earlier as possible and continue as long as possible. Simultaneously only the stages capable to hibernate successfully should be present in the nest by the beginning of winter. To solve all these problems the ant colony should possess the appropriate *mechanisms of regulation* synchronizing the development with the annual climatic rhythm. It is utterly impossible to understand thoroughly the ant evolutionary strategies of adaptation to the existence in the temperate and boreal climate environment without a sufficiently detailed study of the nature and action of this regulation.

The special attention to the seasonality of development in ants was paid for the first time by I. I. Yozhikov (1929) who had collected the data on the phenology of development for several ant species in Middle Russia. A. E. Headly (1943, 1949) had firstly described the seasonal development of two North American species of the genus *Leptothorax* and *Aphaenogaster fulva aquia*. The similar study on two species of *Myrmica* ants was carried out by M. Talbot (1945). In 1943 H. Eidmann had published a thorough paper devoted to the overwintering of ants and among other things firstly reported that the species of the genus *Formica* hibernate without a brood.

After the second world war when the photoperiodic responses in insects were rediscovered the profound investigations of seasonal adaptations in various arthropods began (Danilevski, 1965; Beck, 1968). However, these studies did not almost touch ants and other social insects. The only myrmecologist specifically interested in annual cycles studies was M. V. Brian who has published since 1950 several papers concerning the regulation of seasonal development in ants, mainly in the species of *Myrmica*. He was, however, much more concerned in the studies on caste determination, productivity and development regulation and related problems. The annual cycles of development did not, thus, become a subject of Dr. Brian's purposeful investigations. Other specialists were even less interested in these problems. As a result the literature on this theme is extraordinarily scarce. The papers specially devoted to phenology and annual cycle regulation in ants and other social insects are extremely rare; more frequently these questions may be broached only parenthetically and stand behind the main problem under consideration (for examples see the review of Brian, 1977). In the fundamental treatise "Ants" by B. Hölldobler and E. O. Wilson (1990) the seasonality of development and the annual cycles are not even mentioned.

Our studies carried out from 1969 up to the present were devoted to the elimination of this gap in ant ecology and sociobiology. We have used two main study methods: eco-physiological experiments in

the laboratory and field phenological observations. In experiments the colony fragments (more rarely the whole natural colonies) consisting of workers, queens (or the single queen in monogynous species) and the brood were used. They were kept in artificial plastic nests at different photoperiods and constant temperatures (or thermoperiods) in photothermostats. Our culturing methods allow to observe and to study in the laboratory all stages of annual cycle including the hibernation in a refrigerator under 3-5°C.

We have already investigated in laboratory 60 ant species belonging to 19 genera and four subfamilies from different regions of the former USSR including North, Centre and South of European Russia, West Ukraine (Carpathians), The Crimea, Central Siberia, Turkmenistan and the Far East (Magadan region and Primorie). The results of these studies allowed us to classify the diversity of the ant annual cycles, to reveal the primary mechanisms of their regulation and to come to some ideas on the possible ways of their evolution (Kipyatkov, 1981, 1987, 1990).

### Diversity of ant annual cycles of development and possible ways of their evolution

The family Formicidae undoubtedly had its origin in some tropical or subtropical region because the most primitive ant groups now occur just in these climatic zones (Hölldobler and Wilson, 1990). Unfortunately, the seasonality of development in tropical and subtropical ants has been studied much more insufficiently than in temperate climate species. Nevertheless, even these scanty data allow us to draw some rather definite conclusions.

Evidently many ant species in tropics and subtropics have *homodynamous development*: in every time of a year all ontogenetic stages from egg to pupa are present in their nests and the prolonged delays of development (dormancy, diapause) do not occur. Such development has been discovered, for example, in *Camponotus sericeus* from India (Basalingappa et al., 1983) and *Cataulacus guineensis* from tropical Africa (Ackonor, 1983), and in some subtropical ants: *Camponotus detritus* from the Namib desert (Curtis, 1985) and *Pseudomyrmex* sp. from Texas, USA (Baldrige, DeGraffenried, 1988). As a rule, on the general background of homodynamous development a significant seasonal variation of certain ontogenetic stages' numbers can be observed as a rule; there also exists the seasonality in the winged reproductives rearing and in the nuptial flight timing. In *C. guineensis* the number of the brood has two maxima - in May and in September; alates are numerous in nests from July to October and are absent during other months. In *C. sericeus* the larvae of alates develop from October to July and the nuptial flight takes place in September - October. The proximate causes of this seasonality in tropical ants are unknown.

In our experiments we have observed homodynamous development in two tropical species: *Pheidole sexspinosa* from Tonga Archipelago and *Tetramorium semillimum* from the Seychelles. These species were kept in the laboratory during 1.5 years under various ecologically allowable temperatures (from 17 to 25°C) and photoperiods (from 10 to 16 hours of light per day). During all these experiments we have observed incessant development without any sign of delays. Another species investigated in our laboratory is Pharaoh's ant *Monomorium pharaonis*. This tropical by its origin species appeared to retain the homodynamous development in its present environment of large city houses. The colonies of this ant collected in St. Petersburg were kept in the laboratory at various temperatures and developed exactly like two above mentioned tropical species. Our results agree with the experimental data of M. Petersen Braun (1975).

At the same time many tropical and subtropical ants are characterized by the appearance of more or less durable delays of development in certain seasons. Such annual cycles should be called *heterodynamous*. For example, all five species of *Rhytidoponera impressa* group widespread in the forests of East Australia were found to have a distinct seasonality of development: only small and medium size larvae and very rarely some eggs but never large larvae and pupae are present in their nests during the

winter months, this seasonality being clear-cut both in the tropical and subtropical regions of Australia (Ward, 1981). *Prenolepis imparis* in the northern part of Florida, USA (Tschinkel, 1987) and *Polyrhachis vicina* in the subtropics of China (Chen and Tang, 1989, 1992) are also heterodynamous.

Apparently the heterodynamous development could arise in the tropics if only there exists some seasonality in the environment. As far as the seasonal climatic rhythms are usually quite distinct in the tropical countries, the heterodynamous cycles should be very common in tropical ants. The data concerning this problem are, however, very scarce. Recent investigations give ever more evidence that dormancy and diapause are widespread phenomena in tropical and subtropical insects, but the regulation of seasonal cycles in these species is yet insufficiently known (Denlinger, 1986). It is safe to say that the studies of seasonality in the development of tropical and subtropical ants will bring entirely new and fascinating information.

The evolution of several ant groups was associated with their penetration from the regions with the warm and mild climate to the temperate zone with cold and long winter (Dlussky, 1981; Dlussky and Fedoseyeva, 1988; Hölldobler and Wilson, 1990). What strategies of adaptation to the annual climatic rhythm did they select during this evolution?

Occasionally the existence of homodynamous ants in the regions with temperate but rather warm climate appeared to be possible without any changes in their development. For example, the fire ant *Solenopsis invicta* imported into the USA from the tropical regions of South America remains quite homodynamous in the southern states, but in the northern part of its area the oviposition and development in its colonies cease for the most cool months (Horton and Hays, 1974; Lofgren et al., 1975). The field observations have revealed that the fire ant development strictly depends on temperature and stops at an average environment temperature of 10°C (Markin et al., 1974). In this species the regulation of development had not been studied experimentally.

The primarily tropical army-ants of the genus *Neivamyrmex* in northern parts of their area exist in a temperate climate with rather cold winter. According to the observations of T. Schneirla (1971) in autumn when nights grow cooler these nocturnal ants cease foraging. Then the lack of the food forces the queen to stop laying, the workers destroy the remaining brood and the colony comprising only adult ants passes the winter somewhere in a shelter. Schneirla postulated the direct influence of inferior temperatures on the development of these ants. However, this statement has not been tested experimentally.

In our experiments we have revealed and studied the homodynamous development in two species of the genus *Pheidole*: *P. pallidula* occurring in the South Europe, Caucasus and Middle Asia (Dlussky, 1981) and *P. fervida* the area of which includes the South-East Asia, Japan, Southern Kurils and the south of Primorie (Kipyatkov and Lopatina, 1987; Kupyanskaya, 1990). In Primorie *P. fervida* is likely to persist from the Tertiary when the climate was much more mild (Kupyanskaya, 1990).

In both *Pheidole* species in experiments under any temperature above the lower developmental threshold the queens go on egg-laying and the larvae continue to develop and pupate. Thus, any form of dormancy or diapause is lacking in these ants. At optimal temperature 25-28°C we have observed the incessant and unlimited development in their colonies during more than two years.

In *P. pallidula* from Turkmenistan at 20°C the oviposition and larval development do not cease. After temperature dropping below the lower developmental threshold, which is about 17°C in this species, the queens continue to lay but the eggs do not develop, prepupae and pupae perish and all brood gradually dies out before the hibernation. The overwintering of this species without a brood was confirmed by our field studies in Turkmenistan and by the observations of L. Passera (1977) in the Southern France.

*P. fervida* is better adapted to the rather severe temperate climate of the Southern Primorie: its brood perishes only partially during the hibernation. After the temperature falls up to 10-12°C in autumn the workers begin to dismember and discard the pupae and prepupae and destroy gradually them all. These ants hibernate, therefore, with eggs and all instars larvae. However, some part of the eggs and

young larvae dies during the winter, whereas older larvae hibernate successfully (Kipyatkov and Lopatina, 1987).

It is, thus, possible to maintain that tropical ants retaining their homodynamous development turn out to be inadequately adapted to the temperate climate because their brood perishes during the winter entirely or partially. To prevent such brood losses it is imperative to get an ability for any form of dormancy, i.d. to evolve a heterodynamous annual cycle.

Evidently the tropical ants already possessing the diapause and the heterodynamous development can more easily penetrate to the regions with the temperate climate and to adapt to overwintering as compared with homodynamous species. Unfortunately, we can only speculate on this interesting question because the annual cycles of tropical ants remain mostly unstudied. Nevertheless, the facts that are now in our disposal allow to assume that the heterodynamous cycles of development have evolved in ants along two main paths.

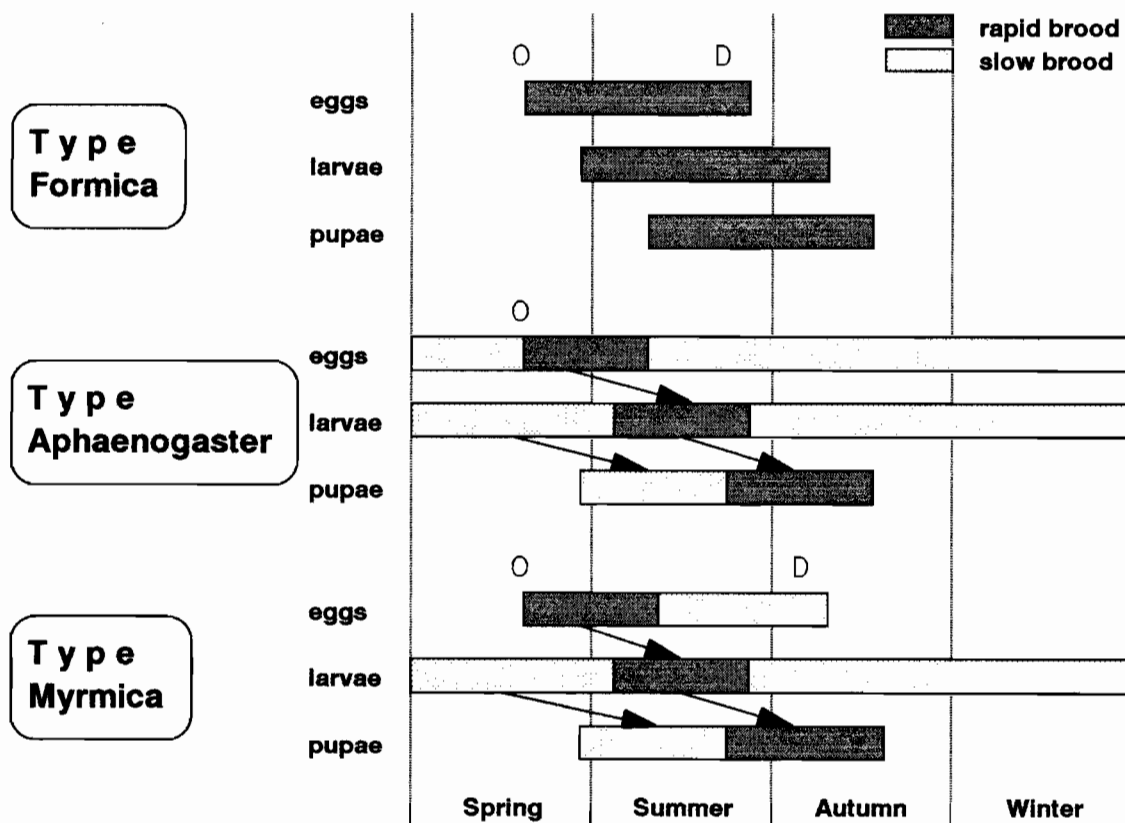
*The first path* of evolution was based on the reproductive imaginal diapause arising in queens. This diapause begins in summer long before the end of the warm season favourable for development and, therefore, all eggs and larvae, even the latest ones, manage to finish their development, all imagoes emerge from the pupae before the autumn cold weather and the ants hibernate without a brood. Such annual cycles we ascribe to the **type Formica** (Fig. 1). According to our observations and the published data (Dlussky, 1981) this type is characteristic for all genera of the tribe Formicini: *Alloformica*, *Cataglyphis*, *Formica*, *Proformica*, and also for *Prenolepis imparis* (Tschinkel, 1987) and the species of the genus *Pogonomyrmex* (MacKay, 1981) in the USA. Besides that we have discovered this cycle in *Ponera coarctata* from the Crimea.

The diapause induction in queens is a central point in the regulation of *Formica* type cycles as far as it determines the moment after which new eggs do not appear, the brood gradually vanishes and the ants begin to prepare for wintering. Queen diapause should not occur too early because it will not allow ants to use the whole warm season for brood rearing. At the same time if the diapause comes too late many larvae and pupae will not manage to complete their development and perish after the autumn temperature fall.

*The second path* of heterodynamous cycles arising in evolution is more prevalent in ants. It is based on larval dormancy and diapause, which enables larvae to hibernate without great mortality. Probably, it is larval diapause that arises first in species evolving along this path. It occurs at the end of summer to prevent the appearance of new pupae which will not succeed to finish their development before cold weather.

There is no yet queen diapause at this first stage of evolution. We have found this annual cycle (Fig. 1) in species of the genus *Aphaenogaster* and suggested to classify it as a distinct **type Aphaenogaster** (Kipyatkov and Lopatina, 1990). In three species studied, *A. gibbosa* (Caucasus, South-West Turkmenistan), *A. sinensis* (Southern Primorie) and *A. subterranea* (Europe), the stable diapause of the third (last) instar larvae arises in the end of summer but the queens have no diapause and do not cease laying until the late autumn. Therefore, not only the diapausing larvae but also the eggs and the first and second instars larvae hibernate and were found to survive, at least partially, during the winter both in nature and in the laboratory. Unfortunately, only quite recently I discovered a paper of Headley (1949) in which the hibernation of the eggs was described for the first time in *Aphaenogaster fulva aquia*.

The same type of annual cycle is characteristic for *Monomorium kusnezovi* (Turkmenistan) and for at least some species of the genus *Messor* but the eggs of these species do not survive during the winter; only the larvae of all instars hibernate successfully. At the same time the queens of *Messor capitatus* have stable winter diapause and the eggs could not be found in nests of this species in winter (Delage, 1968). Queen oviposition at low autumn temperatures and the overwintering of eggs were reported for subtropical ants *Leptothorax rabaudi* and *Temnothorax recedens* in the Southern France (Passera, Déjean, 1974).



**Figure 1.** Three types of ant annual cycles of development.

In our experiments the eggs of several species of the genera *Acantholepis*, *Lasius*, *Myrmica*, *Plagiolepis* were shown to perish in a short time at the temperature below the developmental threshold. The species of *Aphaenogaster* inhabiting the regions with rather long and cold winter seem, therefore, to have acquired some physiological mechanisms that rise the viability of eggs at inferior temperatures. Further studies are required to clarify this problem.

One can also assume that it was the inability of eggs to hibernate successfully that has caused the arising of queen diapause but this event, probably, took place somewhat later in evolution. As a result the annual cycles in which hibernating brood consists of only larvae have appeared. These are the cycles of the type *Myrmica* (Fig. 1). They are peculiar for most of ant species occurring in the temperate climate zone. In some of them (*Crematogaster*, *Diplorhoptrum*, *Manica*, *Myrmica*, *Tetramorium*) the larvae of only one (usually the last) instar are capable to hibernate but all other species have the larvae of several instars in the overwintering brood.

The annual cycles with the hibernating brood have a rather complex structure (Fig. 1) and are well adapted to the temperate and boreal climate environments with long winter and relatively short summer. All overwintered larvae pupate as a rule during the summer and make the first peak of pupae number in nests; the winged reproductives also usually develop from these larvae. Many larvae hatching from the eggs laid in spring and the beginning of summer may pupate during the same year forming the so-cold

*rapid brood* (Brian, 1951, 1957). This brood develops without diapause and makes the second peak of pupae number in the same season. All other larvae hatching from the eggs during the summer fall in diapause and their development completes only the next year. These larvae comprise *slow* or *hibernating brood* (Brian, 1951, 1957). The appearance of the hibernating brood in evolution provided ants with a unique way of adaptation to the boreal climate of the high altitudes regions. There are several advantages of such a structure of the cycles:

(1). *More rational utilization of the thermal and food resources during the year.* Since the larvae are always present in nests, the ants start feeding them in spring as soon as it gets warmer and go on with nursing until the colds in autumn (the diapausing larvae in ants can retain the ability for feeding and for slow growing - see Brian, 1955, 1968).

(2). *The possibility to extend the development of larvae over two or even three summer seasons.* Thus, the repeated hibernation of larvae was reported for *Camponotus aethiops* (Suzzoni et al., 1986), *Leptothorax nylanderii* (Plateaux, 1970), *L. acervorum* (Buschinger, 1973) and *L. grouwellei* (Espadaler et al., 1983). We have observed this phenomenon in some species of the genera *Camponotus*, *Lasius*, *Leptothorax*, *Manica*, *Myrmica*, and in *Aphaenogaster sinensis*. The possibility of repeated hibernation of larvae is most important for the ants inhabiting boreal zones. For example, in *Myrmica aboriginica* near the Kolyma river (the Magadan region) during the warmer summers all overwintered larvae pupate but during the cooler summers only a part of them finishes development (Zhigul'skaya et al., 1992).

(3). *The possibility to adapt to the duration of the warm season by changing of the rapid brood quantity.* For example, in *Leptothorax acervorum* the rapid brood is usually rather numerous, but in cooler summers it may be absent at all; the same may happen because of the food or workers lack in the colony (Plateaux, 1970). In the south of France *L. unifasciatus* has a large rapid brood, but in cooler Belgium it is quite small (Martin, 1988). According to our observations in *Lasius niger*, *Myrmica rubra* and *M. ruginodis* in the Middle Russia ("The Forest on Vorskla" reserve, the Belgorod region) all overwintered larvae complete their development during the spring and the first half of summer and then many larvae of the rapid brood pupate too. Simultaneously, at the latitude of St. Petersburg where the available for ants thermal resources are significantly lesser abundant only few larvae of these species hatching from the eggs pupate in the same season. What is more in the cooler years the rapid brood is absent at all and many of the overwintered larvae hibernate again.

From this point of view the cycles of *Formica* type exploit the thermal resources less effectively, since in species with such cycles in spring only eggs are present in nests whereas in autumn there are only pupae. Thus, the workers of these species are not fully occupied in the beginning and in the end of the warm season.

This deficiency is probably compensated by the rather high developmental rates that are characteristic for species of the genera *Formica* and *Cataglyphis*. As our data show in these ants the duration of ontogenesis from egg to pupa at optimal temperatures 25-26°C is only 20-25 days, whereas in *Myrmica rubra* it makes 34-35 days at 25°C and even 40-45 days at optimal for this species temperatures of 21-22°C, i.e. almost twice as more. Therefore, *Formica* ants rear their brood more intensively.

Thus in the Middle Russia the development from egg to imago in species of the subgenus *Serviformica* could be successively realized during the warm season two or three times but in *Myrmica* it is utterly impossible, these ants have only one full developmental cycle during the summer - the rapid brood; the larvae of the second brood cycle enter diapause and complete development after the hibernation.

It is now difficult to say whether such elevated developmental rates have appeared in evolution as a consequence of *Formica* annual cycles arising or these cycles could originate only in species that have already got high developmental rates as a preadaptation? To answer this question we need more comparative studies of developmental rates in various ant groups and in the first instance in tropical and more primitive ones.

## Regulation of annual cycles

Two forms of insect seasonal development control are known: exogenous regulation by the factors external for an organism (temperature, photoperiod etc.) and endogenous regulation based on the action of internal for an organism and autonomous mechanisms (Danilevsky et al., 1970; Zaslavski, 1984; Tauber et al., 1986).

As it was pointed out above, the exogenous regulation of development by temperature is typical for homodynamous species of ants first of all. As for heterodynamous species, they have substantially more complex regulation. The analysis of the data obtained in our experiments allowed me to classify the heterodynamous ant species into two groups (Kipyatkov, 1987) which are described below.

The first is characterized by the possibility for continuous and unlimited development under optimal conditions and by the arising of delays in development only in response to the decline of temperature. We designate such cycles as *exogenously heterodynamous*. They are peculiar for all investigated species of the genera *Diplorhoptrum*, *Messor*, *Monomorium*, *Tetramorium*, and also for *Camponotus xerxes* and *Tapinoma karavaievi*. At temperatures above 25°C and also under daily thermoperiods 20/30°C they all behave as true homodynamous species. We have observed several colonies of these species to develop at optimal temperatures for more than two years without any delay and changes for the worse in their viability.

While at non-optimal temperatures below 23-25°C the development in colonies of these ants shortly ceases. Both oviposition and pupation are restrained by the inferior temperature in *Monomorium ruzskyi*, *Tapinoma karavaievi* and all species of the genus *Tetramorium* but only pupation in *Monomorium kusnezovi* and some species of the genus *Messor* (these ants hibernate, therefore, with eggs). If the temperature is risen after that, the development will recommence, but it may be blocked again by the drop of temperature and then be resumed in response to a new temperature increase. We have succeeded to repeat similar experiments with the same ant colony several times with the identical result.

Thus, the delays of development in species of this group are of purely external origin and are induced by low temperature, i.d. by the factor exterior for the colony. This inhibition of development is hardly stable and could be easily broken by the temperature raising. However such delay of development is not the simple quiescence but a specific form of diapause. This statement could be proved by the experiments with cold reactivation: after the hibernation in a refrigerator under 3-5°C during 2-3 months the development in ant colonies resumes and goes on for a long period even at 20°C. The developmental delays characteristic for the exogenously heterodynamous ant species should be probably referred to the oligopause following the classification of dormancy forms by H. J. Müller (1970). Their physiological nature deserves, however, special investigation.

Most of temperate climate ants belong to the second species group distinguished by the *endogenously heterodynamous* annual cycles. The obligatory diapause is induced in these species in the first instance by the internal for the colony factors and no external circumstances could prevent the cessation of development. Even at long days and optimal temperature, including the daily thermoperiods i.d. the most favourable temperature conditions for ants (Lopatina and Kipyatkov, 1990, 1993), the development in colonies of these species ceases inevitably without fail and the inactive phase of their annual cycle begins. Certainly, the exogenous factors, such as temperature and photoperiod, also take part in the regulation (see below) but they are unable to alter the endogenous basis of these annual cycles.

Let us consider in detail the nature and action of the mechanisms regulating the ant annual cycles of development.



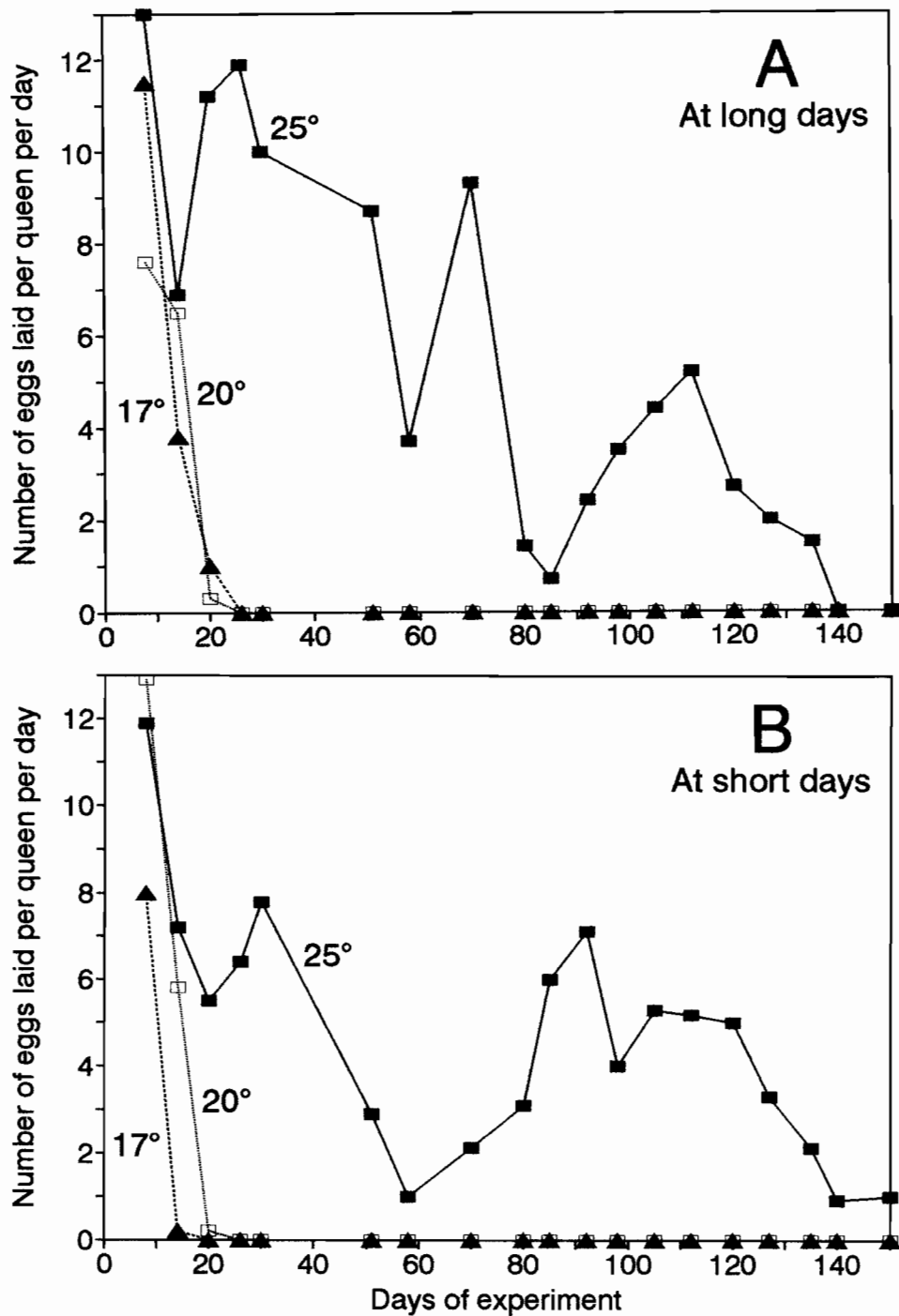
**Table 1.** *Spontaneous rhythms of development in ant colonies under constant laboratory conditions*

Species, places, experimental regimes, group numbers, years, brood stages etc.	Months and weeks (month quarters, ##)											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	#####											
<u>Camponotus japonicus</u> Mayr Primorie 25°C, 18 h. Group C.j.-8 1985 Eggs 1986 Pupae 1986 Eggs 1986 Pupae					X X	██████████ ██████████						
<u>Formica aquilonia</u> Yarr. St. Petersburg region 25°C, 20 h. Group F.a.-8 1976 Eggs 1977 Eggs 1978 Eggs 1979 Eggs 1980 Eggs						██████████ ██████████ ██████████ ██████████ ██████████						
<u>Leptothorax acervorum</u> (Fabr.) Magadan region 22°C, 22 h. Group L.a.-1 1984 Eggs 1984 Pupae 1985 Eggs 1985 Pupae						██████████ ██████████ ██████████ ██████████						
<u>Myrmica ruginodis</u> Nyl. Primorie 22°C, 17 h. Group M.rg.-2 1984 Eggs 1984 Pupae 1985 Eggs 1985 Pupae 1986 Eggs 1986 Pupae						██████████ ██████████ ██████████ ██████████ ██████████ ██████████						

Table 1. (Continued)

Species, places, experimental regimes, group numbers, years, brood stages etc.	Months and weeks (month quarters, ##)											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	#####											
<u><i>Acantholepis semenovi</i></u> Ruzsky Turkmenistan, Kopetdag 29°C, 18 h. Group A.s.-1												
1989 Eggs												
Pupae												
1990 Eggs												
Pupae												
1991 Eggs												
Pupae												
<u><i>Crematogaster bogojawlenskii</i></u> Ruzsky Turkmenistan, Kopetdag 20/30°C, 12 h. Group Cr.-1												
1989 Eggs												
Pupae												
1990 Eggs												
Pupae												
1991 Eggs												
Pupae												
1992 Eggs												
Pupae												
<u><i>Monomorium ruzskyi</i></u> Dlussky et Zabelin Turkmenistan, Kara-Kala 25°C, 12 h. Group Mo-2												
1987 Eggs												
Pupae												
1988 Eggs												
Pupae												

■ - eggs and pupae presence in ant colonies (for *Formica aquilonia* the presence of only eggs is given because the species of this genus do not have a diapause of larvae); [ - the start of experiment with ant colonies taken from the field; X - the start of experiments with colonies after a cold reactivation in laboratory; ] - the end of experiment.



**Figure 2.** The influence of temperature and photoperiod on the queen oviposition in the ant *Lasius niger* L. The experiment began on 1 July. Each line - data for one colony with one queen per colony. Long days - 18 h; short days - 12 h. (The data of V. E. Kipyatkov and V. Voitas).

### Exogenous regulation

The main external regulators of seasonal development in ants and in other arthropods are temperature and photoperiod.

*The temperature regulation of development* is widespread in ants and is characteristic to one or other degree for all their species. In each experimentally studied species the decrease of temperature promotes the arising of diapause and hastens the cessation of development in the end of the summer season. For example, in summer colonies of *Lasius niger* at 20°C oviposition and pupation cease in a very short period while at 25°C the diapause in queens and larvae follows as a result of endogenous processes (see below) much later (Fig. 2). Similarly the fall of temperature advances the diapause induction in *Myrmica rubra* (Fig. 3; see also Kipyatkov, 1977a), *Aphaenogaster sinensis* (Kipyatkov and Lopatina, 1990) and some species of *Formica* (Kipyatkov and Shenderova, 1989, 1991; Kipyatkov and Lopatina, 1993).

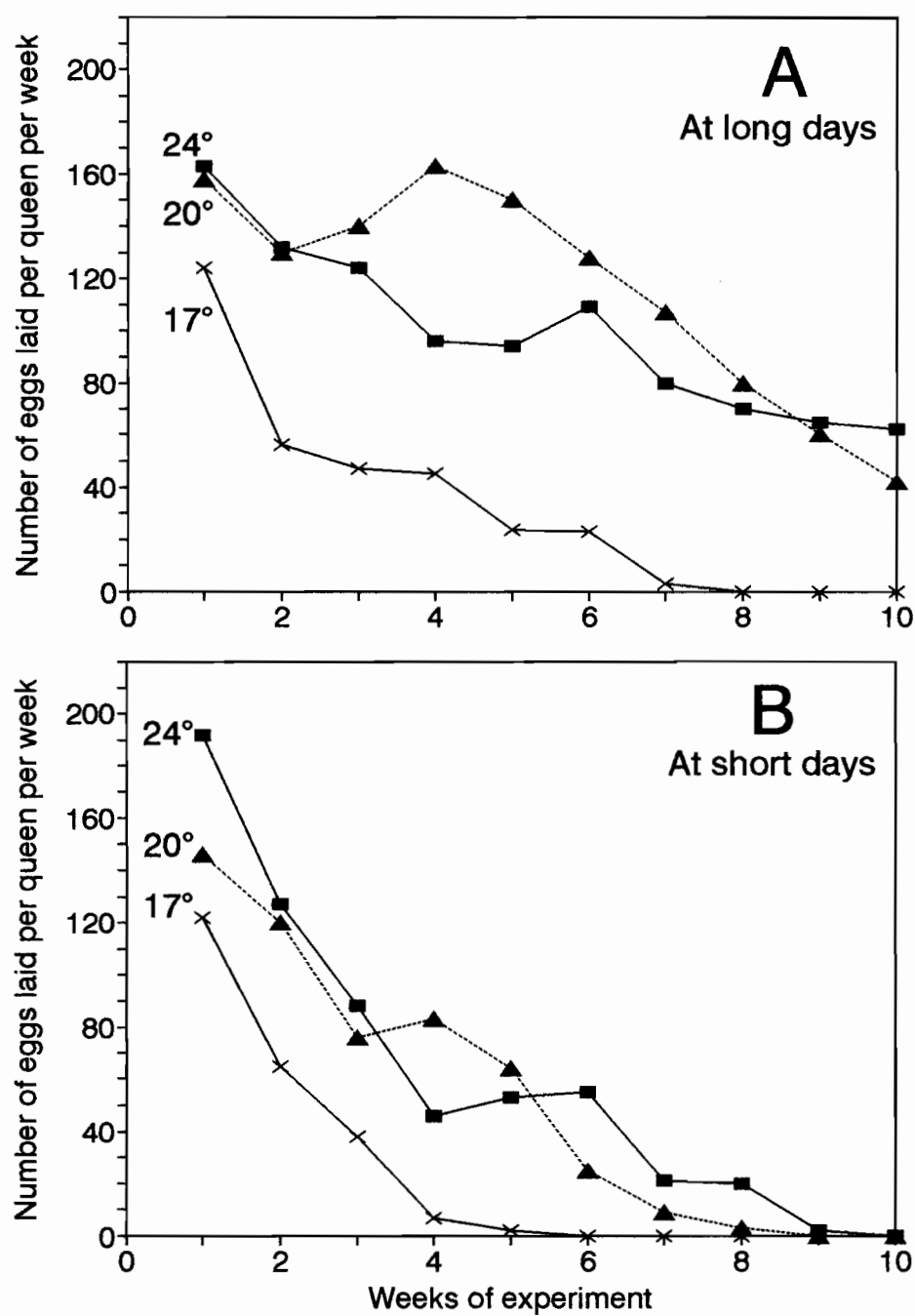
The adaptive significance of such a regulation by temperature is quite evident: this mechanism allows to adjust the date of the diapause arising in the end of summer season; if the summer is cooler the development will stop earlier but the warmer autumn will enable ants to rear some additional amount of brood and new adults.

*The photoperiodic regulation of development* occurs rather scarcely among ants. For example, photoperiods do not affect the development of larvae and the egg-laying by the queens in *Lasius niger* (Fig. 2) and *Formica polyctena* (Fig. 7). The most apparent photoperiodic response of the long-day type has been found and thoroughly studied in the ants of the genus *Myrmica* (Kipyatkov, 1972-1979). In summer at temperatures near the optimum (21-22°C) the short (less than 15 hours of light) days evoke in a while the cessation of pupation and some later of oviposition in colonies of *M. rubra* whereas at long (more than 17 hours) days the diapause of larvae and queens ensues as the effect of endogenous regulators (see below) substantially later (Fig. 3-4). Comparably (Fig. 5) the diapause arising depends on photoperiod in *Aphaenogaster sinensis* (Kipyatkov and Lopatina, 1990) and *Acantholepis semenovi*. In *Aphaenogaster sinensis*, *Camponotus herculeanus*, *Leptothorax acervorum*, *Manica rubida* and the species of *Myrmica* we have revealed the increase of the diapausing larvae percent in colonies at short days comparing with the similar colonies at long days.

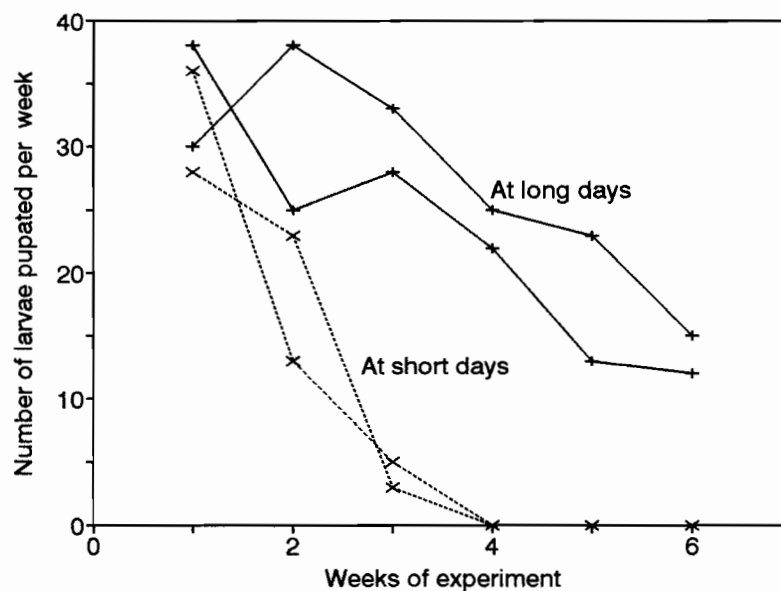
It is widely known that photoperiod is a quite universal factor of seasonality regulation (Danilevski, 1965; Beck, 1968; Zaslavski, 1984). In this connection it is rather surprising that the photoperiodic regulation plays so a modest role in the ant seasonality.

A quite distinct place among exogenous regulation mechanisms belongs to *the cold reactivation* (according the terminology of Danilevski, 1965), i.d. the termination of diapause and the restoration of ability for normal development as a result of exposition at low positive temperatures during the hibernation. The role of the winter chilling in the seasonality regulation was reported in literature for some species. The influence of autumn and winter cooling was found necessary for the renewal of egg-laying by the queen of *Messor capitatus* (Delage, 1968). When the workers of *Plagiolepis pygmaea* being kept at optimal temperature have ceased to oviposit they could be provoked to renew the egg-laying by quite long chilling (Passera, 1969). For *Leptothorax nylanderii* colonies the cooling during autumn and winter is indispensable for the resumption of full development in spring (Plateaux, 1970, 1971).

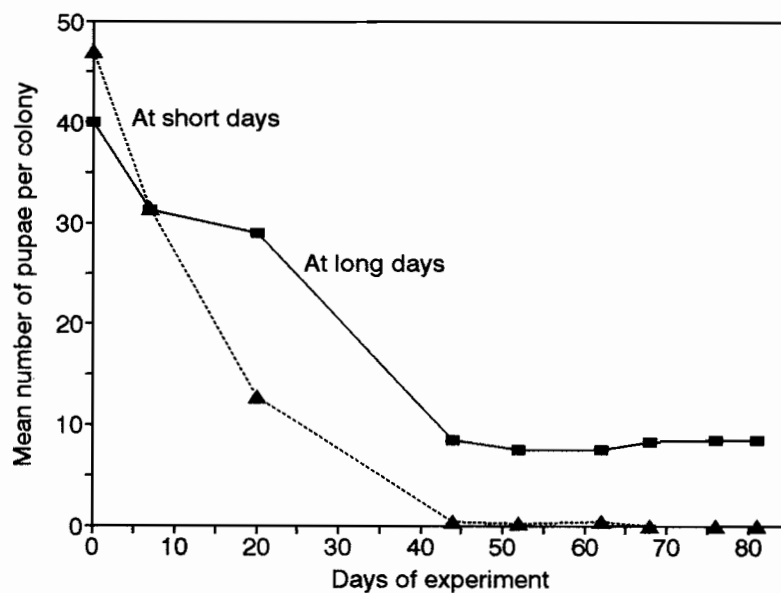
Our experiments have also shown that the role of cold reactivation in the regulation of the heterodynamous cycles in temperate climate ants is quite significant (see below). For full reactivation the ant colony usually needs from one to four months (depending on species) of the exposition at 3-5°C. The development commences after such treatment even at 17-20°C, i.d. at temperatures that cause the immediate diapause induction in the same colonies in summer.



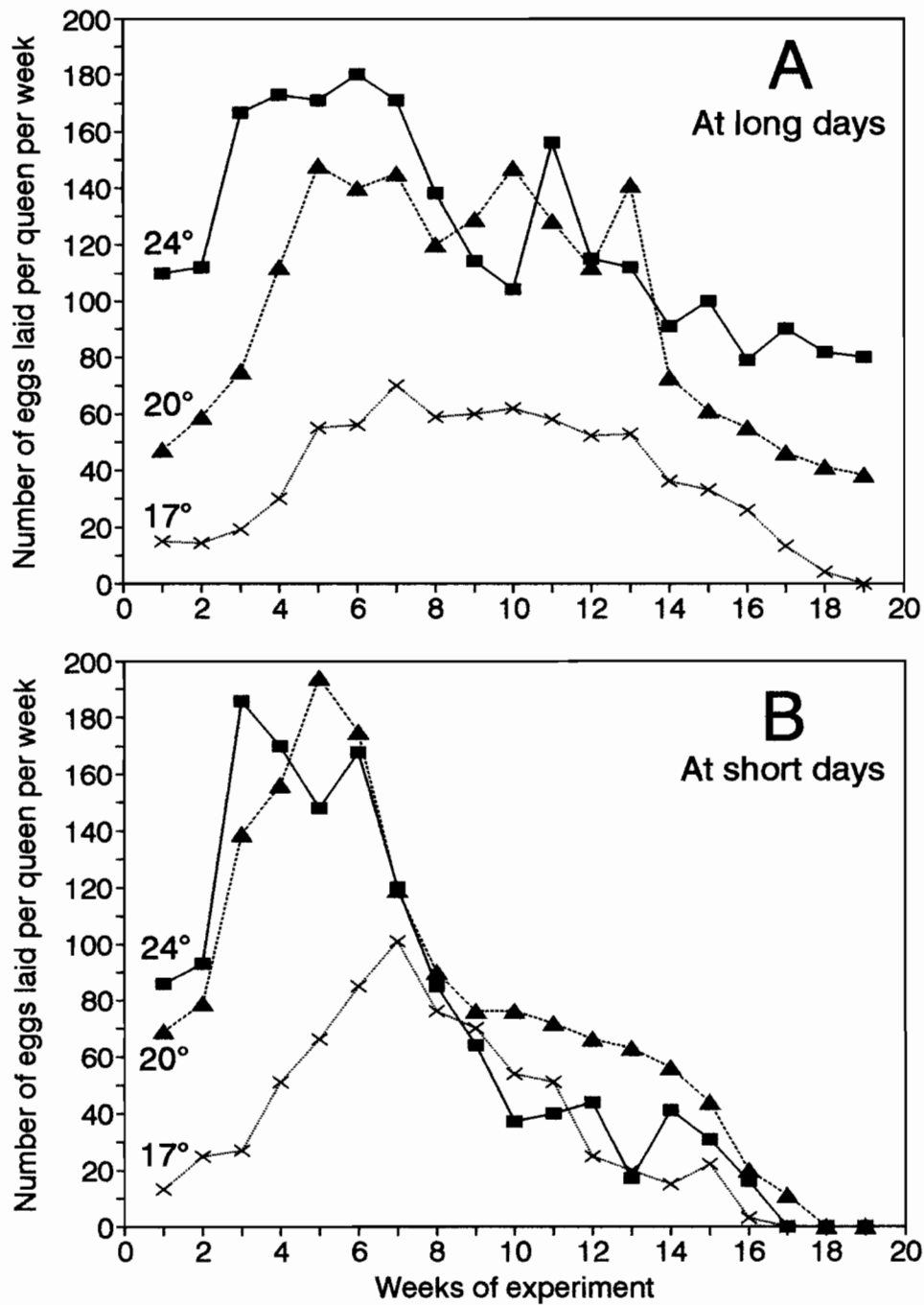
**Figure 3.** The influence of temperature and photoperiod on the oviposition of queens in the ant *Myrmica rubra* (L.). Each line is the mean data for two colonies with two queens per colony. The experiment was started on 19 July. Long days - 18 h; short days - 12 h.



**Figure 4.** Photoperiodic response in *Myrmica rubra* (L.): the influence of the long (18 h) and short (12 h) days on the larval pupation at 24 °C. Experiment was started on 1 August. Each line - the pupation in one colony.



**Figure 5.** Photoperiodic response in *Aphaenogaster sinensis* Wheeler: the pupation of larvae in colonies under the long (17 h) and short (12 h) days and 23 °C. The experiment was started on 30 June. Each line - the mean number of prepupae and pupae present per colony on a day of census (5 colonies in each photoperiod).



**Figure 6.** The oviposition cycle of the queens of *Myrmica rubra* (L.) at different temperatures under long (18 h) or short (12 h) days. The experiment was started on 17 May. Each line - the mean data for two colonies with two queens per colony.

### Endogenous regulation

In colonies of many ant species maintaining under constant laboratory conditions one can observe the *spontaneous rhythms of development*: the egg-laying and pupation of larvae cease at first, but then recommence after more or less durable interval, these periods of development and of diapause being able to recur repeatedly.

Such spontaneous rhythms were observed for the first time by B. Hölldobler (1961) in *Camponotus herculeanus* and *C. ligniperda*. During inactive periods of the cycles these ants formed the aggregations with diapausing larvae in the chambers of their artificial nests and the workers of *C. herculeanus* even plugged the nest entrance in this time. According to the observations of L. Plateaux (1970) in *Leptothorax nylanderi* the development in the overwintered colonies goes on at 24–25 °C during 90–100 days and then the obligatory period of rest follows and continues for not less than 100 days; after this diapause stage the development could restart.

S. Bruniquel (1978) had maintained a colony of *Aphaenogaster subterranea* in a laboratory nest with horizontal temperature gradient for a year and found the ants to have the annual rhythm of thermo-preferendum variation: in summer they aggregated with their brood in a zone with the temperature of 16–22 °C but in winter preferred temperatures of 9–12 °C. Similar results were obtained by J. Billen (1984) for groups of *Formica sanguinea* workers maintained in nests with horizontal gradient of temperature.

In our long-term investigations started in 1976 we have succeeded in finding the spontaneous rhythms of development in the ants of the genera *Acantholepis*, *Aphaenogaster*, *Camponotus*, *Cataglyphis*, *Crematogaster*, *Formica*, *Lasius*, *Leptothorax*, *Myrmica*, *Monomorium*, *Plagiolepis*, i.d. in almost all exogenously heterodynamous species studied (Kipyatkov, 1994). This phenomenon was most thoroughly explored in the red wood ants of *Formica rufa* group: the data for several dozens of experimental groups maintained at various constant temperatures and photoperiods for 1–5 years were obtained (Kipyatkov and Shenderova, 1990). The queens' ovaries were shown to contain no eggs and developing oocytes during the inactive phases of the cycles. Thus, the queens underwent a true reproductive diapause in these periods. The duration of full period of the spontaneous rhythm (time when eggs are present plus that of their absence) was on average 212 days in *F. aquilonia* and 179 days in *F. polycтена* and proved to be independent of temperature in the optimal range from 20 to 25 °C; at higher temperatures this parameter decreased and at lower temperatures increased to some extent (Kipyatkov and Shenderova, 1989, 1990).

Examples of the spontaneous rhythms of development in constant laboratory conditions for some ant species studied are given in Table 1. It is noteworthy that there exists a significant variability of the development and diapause stage durations both between different experimental colonies and between different cycles observed in the same colony. Furthermore, the complete absence of any agreement between the ant developmental cycles and calendar (i.d. natural succession of seasons) is evident. What is more, the periods of oviposition do not always coincide precisely with the periods of pupation as it occurs in nature. All these facts exactly reveal the pure endogenous basis of the rhythms observed and the entire absence of their external synchronization.

During a long experiment with ants kept in laboratory nests with horizontal gradient of temperature from 5 to 33 °C we have observed even more apparent rhythms of development in *Acantholepis semenovi*, *Camponotus ligniperda*, *Lasius niger*, *Myrmica ruginodis* and *Tapinoma karavaievi* (Lopatina and Kipyatkov, 1991; Kipyatkov, 1994). When the queens laid eggs and the larvae developed and pupated the ants with their brood were found in those nest chambers that had rather high temperatures around the optimum of development. Then, as the diapause arose in colonies, the workers with diapausing larvae and queens gradually moved in cool chambers with the temperatures from 5 to 12 °C (depending on species) and stayed there for several weeks or even some months. After such period of "overwintering" the workers transported the brood into the warm chambers where its development began. Thus, the



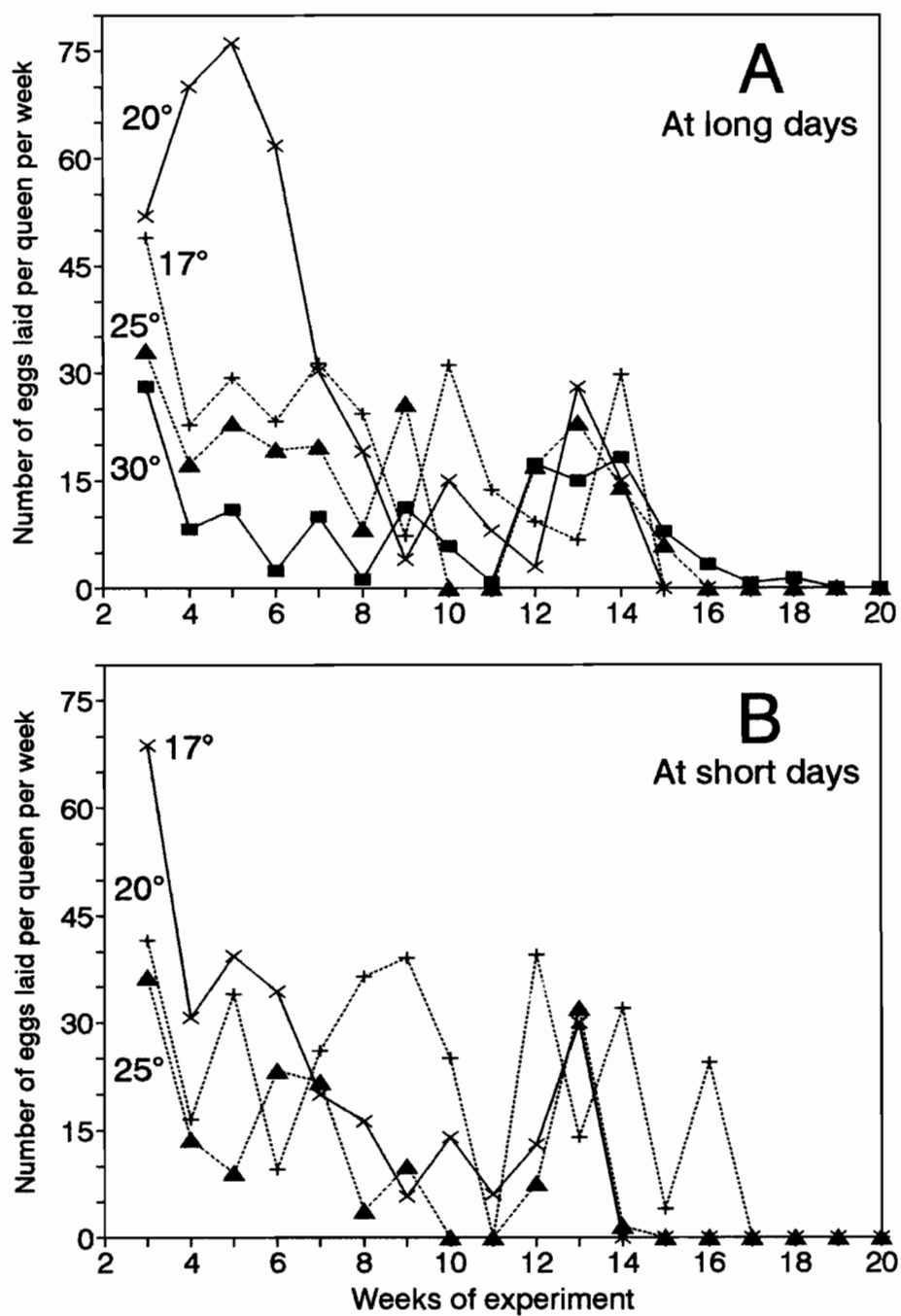
intimate relation between developmental and behavioural periodicity has been apparently displayed in all five species studied. The similar relation has been revealed earlier in *Formica polyctena* also in the nests with a temperature gradient but in an experiment that had proceeded from May to September (Kipyatkov and Shenderova, 1986).

To evaluate correctly the role of endogenous processes in the regulation of the ant annual cycles it is essential to consider first the typical endogenously heterodynamous species inhabiting the northernmost regions of Palaearctic. They all belong to the genera *Camponotus s. str.*, *Formica*, *Lasius*, *Leptothorax s. str.* and *Myrmica*. The necessity of chilling during the inactive stage of the annual cycle is obvious for these ants. In the nests with temperature gradient after the diapause arising they moved into the cold chambers and stayed there for a long time. Elevated temperatures that are optimal for the development of these species are apparently unfavourable for them during the inactive phase of the annual cycle. This phenomenon is characteristic for most of temperate insects (Danilevski, 1965). Consequently we have succeeded in a long-term maintenance of these ants under constant conditions only at temperatures somewhat below the optimum and even in such circumstances the excess mortality of the brood and workers during the diapause stages occurred.

It should be also emphasized that after the spontaneous renewal of development the latter could never be so adequate as following the normal hibernation at low temperature: queen productivity is rather low, not all diapausing larvae pupate and there is no rapid brood as a rule. This feature of the spontaneous recommencement of development was first noticed by L. Plateaux (1970) for *Leptothorax nylanderi*; we have observed it in all northern species studied. After each new developmental cycle at constant temperature the productivity decreases ever more and the callow workers appear in fewer and fewer numbers. As a result, the number of ants in the colony gradually declines, their viability diminishes and the colony dies up in the end. In our especially long experiments with red wood ants we were sometimes compelled to add some pupae from natural nests into the ant colonies under experiment to prevent their decline and loss (Kipyatkov and Shenderova, 1990). Consequently, all these northern ants require the winter chilling, i.d. cold reactivation, for adequate restoration of their ability for full and productive development.

The endogenously heterodynamous ant species belonging to the genera *Acantholepis*, *Aphaenogaster*, *Crematogaster*, *Plagiolepis* and occurring in more southern regions do not require so inferior temperatures for a successful hibernation and reactivation. We have never observed in their colonies maintained at optimal temperatures so catastrophic mortality as in northern species. Although it should be noted that constant high temperatures are not, of course, ideal for them, too. The spontaneous reactivation in these species is quite similar to the natural renewal of development in spring and results in rather prolonged oviposition and pupation. *Acantholepis semenovi* and *Crematogaster bogojawlenskii*, which developed at thermoperiod 20/30 °C almost without significant breaks, as if they were homodynamous, may represent a good example (Tab. 1).

At last, several exogenously heterodynamous species studied turned out to exhibit in certain circumstances some indications of endogenous periodicity. For example, in *Monomorium ruzskyi* at constant suboptimal temperature of 25 °C the breaks in larval pupation for 1-1.5 months occurred sometimes during the experiment (Table 1). A colony of *Tapinoma karavaievi*, which was maintained for two years in a nest with a temperature gradient, displayed two short periods of rest during which the larvae did not pupate and were kept by workers in the chambers with the temperatures of 18-22 °C while in the periods of active development the thermopreferendum was 26-33 °C (Kipyatkov, 1994). The ants of the genus *Tetramorium* at 23-25 °C behave alike homodynamous species, i.d. the development in their colonies goes on without any delay and diapause incessantly and unlimitedly. However, if they are maintained after a hibernation at 20 °C, the oviposition and pupation cease in 2-3 months but then the development recommences some months ago, i.d. the typical endogenous rhythm arises.



**Figure 7.** The oviposition of *Formica polycetena* queens at different temperatures under long (18 h) or short (12 h) days. The start of experiment - on 30 April. Each line - the mean data for three colonies with one queen per colony.

Thus, the border between the exogenously and the endogenously heterodynamous species groups is not so distinct and we can find species with more or less intermediate pattern of annual cycle regulation.

The spontaneous processes are well known to participate in the regulation of seasonal development in many insects either exerting influence upon the diapause termination or modifying the tendency for diapause in a row of successive insect generations (Zaslavski, 1984). In ants, according to our results, spontaneous processes are involved not only in diapause termination (reactivation) but also in its arising (induction). In this connection it is believed that in the tropics and subtropics endogenous rhythms could play an important and even a principal role in the regulation of seasonality in ants. This problem, however, deserves special study.

The existence of cold winter in the temperate climate environment makes the independent progression of endogenous rhythms impossible. In ant species distributed in the southern regions of the temperate climate zone (*Acantholepis* et al.) the termination of diapause, according to our data, is essentially spontaneous, their reactivation being already accomplished in autumn as a result of endogenous processes, but the advance of cold weather makes the development impossible until the spring warmth.

The ant species penetrating far to the north (*Camponotus* s. str. et al.) are well adapted to the climate with a long and cold winter. They have acquired true cold reactivation that requires a long period of chilling for its realization. The spontaneous reactivation is possible in these ants exclusively in an artificial situation and could not be of full value. Consequently, the cold reactivation is absolutely indispensable for complete restoration of the capability for development in these species.

Thus, in northern ants only the part of the endogenous rhythm, which determines the gradual decrease of the capability for development and the increase of the inclination for diapause during the active (summer) period of the annual cycle, has an ecological significance. This endogenous physiological mechanism of yet unknown nature operates like a sand-glass and play a cardinal role in the regulation of seasonality in true endogenously heterodynamous ant species (Kipyatkov, 1987). Some signs of its existence have been observed in earlier works. For example, orphan workers of *Plagiolepis pygmaea* after the hibernation lay eggs for 2-3 months, their productivity gradually decreasing up to zero; for the renewal of oviposition the winter chilling is needed (Passera, 1969). The egg-laying and the pupation of larvae in the overwintered colonies of *Leptothorax nylanderi* cease in 90-150 days under any experimental regime, temperature exerting almost no influence on the duration of this period (Plateaux, 1970, 1971). The same author revealed some physiological changes in thermal reactions occurring in workers of *P. nylanderi* during the summer season: in June-July ants are rather active and agile at 11-18°C while in September-October they are inactive and motionless at the same temperatures. And lastly, in *Cataglyphis cursor* the endogenously restricted cycle of oviposition both in queenright and queenless groups maintained under constant laboratory conditions was discovered by H. Cagniant (1979, 1980).

In our experiments the "sand-glass device" has been revealed in nearly all ant species excluding entirely homodynamous ones. Let us consider as a good example *Myrmica rubra*, a species possessing a clear-cut photoperiodic response (Kipyatkov, 1979). After the winter cold reactivation the larvae of this ant quickly develop and nearly all of them pupate independently of temperature and photoperiod; the queens also start laying in spring even at short days and temperature of 17°C and their productivity rapidly increases (Fig. 6). Eventually, the ants' reaction on temperature and photoperiod changes and in the middle of summer the short days or the temperatures below 20°C provoke the fast diapause induction in larvae (Fig. 4) and in queens (Fig. 5B). To cause the entire cessation of larval pupation at 20°C the short days should affect a colony for 7 weeks in the middle of May, 5-6 weeks in the beginning of June, 3-4 weeks in the middle of July and 3 weeks in the beginning of August. Thus, ant sensitivity to photoperiod gradually appears and rises during the summer.

The queens of *Myrmica rubra* possess an endogenously restricted cycle of oviposition. Their productivity increases in spring, attains its maximum in the beginning of summer and then begins to

decline; the egg-laying stops after all under any conditions (Fig. 6). The same oviposition cycle was observed in the experiments of M. V. Brian and A. F. Kelly (1967). In the middle of summer short days and low temperatures substantially accelerate the diapause induction in queens while at long days and temperature of 25°C, which exceeds significantly the optimum (21-22°C) of this species, the queens lay eggs continuously for several months without diapause (Kipyatkov, 1979).

All these facts confirm the existence in a colony of *M. rubra* of an endogenous physiological process, which causes the gradual modification of the ants' reaction on temperature and photoperiod, the decline of queen productivity and of the competence for development in larvae, and the rise of the total bias for diapause.

The "sand-glass device" participates in the regulation of seasonal development in all heterodynamous species always in combination with the exogenous factors, such as temperature and photoperiod, as it was just shown on the example of *M. rubra*.

## Conclusions

Relying on the results of our studies, it is now possible to outline the following base scheme of the annual cycle regulation in the heterodynamous species of ants inhabiting the temperate climate zone.

During the autumn and winter at low positive temperatures the cold reactivation of diapausing ants occurs. It ends well before the end of hibernation and results in a restoration of the ants' capability for full development, as if the ant colony's "sand-glass" turns over and their reservoir full of sand is above. In spring the ants awake as soon as the nest temperature exceeds a certain threshold and the development in different colonies of the same habitat starts, therefore, almost synchronously owing to the similarity of temperature regimes in their nests.

In spring and in the end of summer the tendency for non-diapause development is extremely high and it can go on even at rather low temperatures that cause the immediate diapause induction in the end of summer. The sensitivity to photoperiod is also absent after the hibernation.

During the active period of the annual cycle, i.d. in summer season, the gradual decrease of the competence for development and the increase of the bias for diapause occurs as a result of the endogenous physiological process, as though the sand in the ants' "sand-glass" pours little by little from the upper reservoir to the lower one. The photoperiodic sensitivity also appears in ants and their reaction on temperature alters entirely, too. Now the fall of temperature and the short days (in some species) rapidly induce the diapause.

Thus, the cessation of oviposition and development is controlled by both the endogenous process and the exogenous factors. The latter play a modifying role adjusting the date of diapause arising to the climatic characteristics of a given year. So, if in the end of summer the weather is cold the development in ant colonies will cease earlier while in the warm autumn the development will be somewhat prolonged.

In different ant groups one can find significant deviations from the base scheme described above to the predominance of either exogenous or endogenous regulation mechanisms. Thus, in species with the exogenously heterodynamous development the endogenous regulation apparently plays a subordinate role but can be revealed in specific experiments, as it was shown above. In several endogenously heterodynamous species the external regulators can alter the duration of the active period of the annual cycle within the rather broad limits. The regulation of development in *M. rubra* discussed above is an example of such a situation. The species of the genera *Aphaenogaster*, *Crematogaster*, *Lasius*, *Tapinoma* belong to the same group. Finally, the development of the species belonging to the third group is controlled predominantly by the endogenous regulators, i.d. the time of diapause arising in the colonies of these ants only slightly depends on the environmental conditions. Thus, temperature nearly does not affect the endogenously determined duration of queen oviposition in red wood ants (Fig. 7; see also Kipyatkov and Shenderova, 1989, 1991) and in species of the subgenus *Serviformica* (Kipyatkov and Lopatina, 1993).

The development of ants of the genera *Camponotus* s. str., *Cataglyphis*, *Leptothorax* s. str. is comparably independent of the environment.

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