

Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea)

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Received August 15, 2000; accepted August 30, 2001
Published October 2, 2001

Abstract. The forms of dormancy found in ants range from simple quiescence to profound diapause. Most tropical ants are *homodynamic* and have no developmental arrests: all ontogenetic stages from egg to pupa are present in their nests throughout the year. Some of them (*quasi-heterodynamic* species) have penetrated into the regions with warm temperate climates but did not evolve real diapause. The development of their brood ceases only at temperatures below the threshold of development (consecutive dormancy) and ants overwinter in a quiescent (cold coma) state suffering from more or less strong mortality. Most temperate ants, however, are *true heterodynamic*, i.e. they possess real winter diapause (prospective dormancy). In *exogenous-heterodynamic* species diapause in larvae and queens is *facultative* and arises in direct response to falling temperatures in autumn, but diapause begins after some delay and when temperatures are still well above the threshold of development. The diapause in *endogenous-heterodynamic* species is *obligatory at a colony level* in a sense that it ensues sooner or later under any circumstances. Their intrinsic brood-rearing cycle is limited by an endogenous timer called a *sand-glass device* and is also controlled by environmental cues – temperature and photoperiod (in some species), which can only advance or delay the onset of diapause to some extent. Larval dormancy in these ants is *facultative diapause* induced by social influences of the nurse workers and temperature cues. Adult dormancy is *obligate diapause* characterized by inactive state of ovaries and also by inability of workers to maintain high growth rate and non-diapause development of larvae and normal egg production of queens. The adult and larval diapause in some endogenous-heterodynamic species is quite stable even at high temperatures and long days but in many others diapause can easily be terminated in such circumstances. In many ants, both endogenous- and exogenous-heterodynamic, the diapause larvae in the last instar continue to feed and to grow slowly and can attain significantly larger size before overwintering. The diapause completion in temperate ants is normally a result of cold reactivation, i.e. the winter exposure to low temperatures, which also leads to (1) the restoration of the colony's "spring physiology" and full capability to realize a new brood-rearing cycle, and (2) the changes of the norm of reaction to photoperiod (general loss of sensitivity in species that have photoperiodic responses) and temperature (ability to produce eggs and rear larvae without diapause at rather low temperatures that induce diapause in summer).

Seasonality, climate, temperature, photoperiod, development, diapause, exogenous, endogenous, social, control, Hymenoptera, Formicoidea, Formicidae

INTRODUCTION

Despite extensive studies of arthropod dormancy and seasonality during the last several decades, most ant specialists remained indifferent to this subject. As a result the papers specially devoted to phenology, diapause and seasonal cycle control are rather scarce in myrmecological literature; more frequently these questions are discussed only parenthetically and given less prominence than the main problem under consideration (for examples see the review of Brian 1977). In the fundamental modern treatise "The Ants" by Hölldobler & Wilson (1990) the seasonality of development is not even mentioned.

Our studies were, therefore, devoted to the elimination of this gap in ant ecophysiology and sociobiology. Since 1969 more than 70 ant species belonging to 21 genera and four subfamilies from different regions of the former USSR have been studied in our laboratory. We used two main research methods: laboratory experiments and field phenological observations. In experiments the colony fragments (more rarely the whole natural colonies) consisting of workers, queens (or a single queen in monogynous species) and the brood were used. They were kept in artificial plastic nests under different constant temperatures (or thermoperiods) and photoperiods. Our culturing methods allowed us to observe and to study in the laboratory all phases of ant annual cycle including the overwintering in a refrigerator under 3–5 °C. This research resulted in a classification of the structural diversity of ant annual cycles, revealed the primary factors of their control and led to some ideas on the possible ways of their evolution (Kipyatkov 1981, 1993, 1994, 1996, Kipyatkov & Lopatina 2002b, c).

The main purpose of this paper is to consider the types of seasonal development and the forms of dormancy found in ants in connection with the mechanisms of their control. This review is based on the results of our studies and also on data in the literature.

MAIN TERMS AND DEFINITIONS

The terms *seasonal development* and *seasonal life cycle* are traditionally used to designate the seasonal differences in the development and physiology of individuals of a species at different times of year (e.g., Danilevskii 1961). The annual cycle of development of a species is, therefore, a succession of the individual life cycles of different generations (in polyvoltine species), the whole life cycle of a single generation (in monovoltine species) or a sum of different parts of the life cycles of several successive generations (in semivoltine and perennial species). Ants are social insects and their colonies are not only perennial but usually even have unlimited life cycle i.e. are potentially immortal unless environment becomes too adverse (Bourke & Franks 1995); adult ants (especially queens) also live for several years (Hölldobler & Wilson 1990). The brood and workers in an ant colony may all belong to the same genetic generation (in monogynous species having a single queen in each colony) during several successive years (while the same mother queen is alive) or they may belong to different but overlapping generations (in polygynous species having several queens in each colony). But the seasonal life cycle of a colony has nothing in common with the differences between generations. Instead, it involves the regular seasonal changes in developmental paths, physiological states and behaviour of individuals of all generations composing a colony. This is why the seasonal life cycle of an ant colony should be better referred to as *the annual cycle of development, physiology and behaviour* (Kipyatkov 1993, 1996).

In spring ants awake from the winter dormancy and begin their routine activity, the workers start to rear larvae (if the species overwinter with brood), a queen (or queens) begins to lay eggs from which new larvae originate, the larvae grow, pupate and become new workers or alate reproductive females and males. The oviposition and brood development continue through the whole warm season until queens enter diapause and stop laying. Before the onset of winter all the eggs and young larvae develop into adults or up to a stage at which dormancy ensues and the colony moves to a overwintering place with diapause larvae or without brood. The workers also enter diapause in autumn and accumulate the nutrients in their bodies necessary for overwintering and early spring activity. Thus, each individual ant (queen, worker and even some larvae) can enter diapause and resume non-diapause activity several times in its life. This situation is unique for ants and other social insects with perennial colonies and only partly resembles extremely long perennial life cycles found in a few non-social insect species (cf. Danks 1992).

Roubaud (1922a, b, 1925) first distinguished *homodynamic species* of insects which have no diapause but only quiescence (“pseudo-diapause” of Roubaud) due simply to low temperature conditions and immediately resume their activity after the rise of temperature and *heterodynamic species* possessing true diapause (“diapause vrais” of Roubaud) that arises well in advance of the onset of adverse conditions and cannot be easily terminated by the rise of temperature. This valuable dichotomy is used for the classification of ant annual cycles of development described below. I also follow Müller (1965, 1970) in distinguishing two main forms of arrested development: *consecutive dormancy or quiescence* and *prospective dormancy or diapause*.

Ants have diverse forms of dormancy ranging from simple quiescence to profound diapause (Tab. 1). Only larvae and adults can enter diapause; embryonic (egg) diapause and pupal diapause are unknown in ants as well as in most other Hymenoptera (Danks 1987). Some authors (e.g., Tauber & Tauber 1981, Tauber et al. 1986) insisted on a narrower definition of diapause as “hormonally mediated state of low metabolic activity”. However, the known cases of arrested development in arthropods range from total cessation of activity to suppressed development with less extensive effects on growth (Danks 1987). This appears especially true for ants (see below) and I therefore prefer to follow Danks (1987) in using a wider and most appropriate definition of diapause that does not require low metabolic activity and growth arrests, but only definitive suppression of development or reproduction.

Another term, *cold reactivation* (Danilevskii 1961), used in this paper needs some comments. Temperature evidently plays multiple roles during insect diapause which are not yet completely understood; moreover, the diapause-development responses are not limited to the effects of temperature and in fact can be much more complex (see Danks 1987, Hodek & Hodková 1988). In particular, the role of low temperatures in termination of diapause as well as the relevance of the term “cold reactivation” itself have been disputed by some authors (Hodek & Hodková 1988, Zaslavski 1988, Hodek 1996). Although their arguments seem to be very sound in regard to the proximate causes of the diapause termination itself, I still find it appropriate to use the term “cold reactivation” to describe the apparent effects the overwintering at cool temperatures on an ant colony, namely, the restoration of colony’s “spring physiology” and full capability to realize a new brood-rearing cycle (to be detailed below). As applied to ants I employ this term in addition to commonly used Andrewartha’s “diapause development” (Danks 1987) and Hodek’s “diapause completion” (Hodek 1983, 1988, Hodek & Hodková 1988) because the expression “cold reactivation” helps to emphasize in the best way the restoration of colony’s spring physiological state rather than simply diapause completion.

HOMODYNAMIC DEVELOPMENT

Most ant species living in the tropics and warm subtropics have homodynamic seasonal development (Kipyatkov 1993, 1996). All ontogenetic stages from egg to pupa are always present in their nests, which means that development continues without any arrests throughout the year (Tab. 1). However, significant seasonal variations in the abundance of certain brood stages and especially of the winged reproductives can usually be observed. For example, in *Cataulacus guineensis* in tropical Africa 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 (Ackonor 1983). The larvae of alates of *Camponotus sericeus* in India develop from October to July and the nuptial flight takes place in September–October (Basalingappa et al. 1986, 1989). The seasonality of alate production has also been reported for *Anoplolepis longipes* in Papua New Guinea (Baker 1976) and in the Seychelles (Haines & Haines 1978), *Camponotus detritus* in the Namib desert (Curtis

Tab. 1. Description of main types of dormancy and seasonal life cycles in ants

species group	homodynamic	quasi-heterodynamic	exogenous-heterodynamic	endogenous-heterodynamic
area of occurrence	Tropics, warm temperate climates	Subtropics, regions with warm of temperate zone	subtropics, southern part of temperate zone	temperate zone, regions with boreal climates; up to the subarctic; tropics and subtropics (probably)
seasonal cycle and overwintering in nature	all ontogenetic stages throughout the year, no overwintering	all ontogenetic stages remain at the onset of winter	eggs and larvae of all instars can overwinter or only diapause larvae	overwintering with diapause larvae or without brood
Adaptations to cold winters	No adaptations; quick death at temperatures below the threshold	Some adaptations exist; more or less severe mortality of brood and adults at temperatures below the threshold	Good adaptations High winter survival	Good adaptations High winter survival
Forms of winter dormancy in larvae	No developmental arrest or dormancy	Consecutive dormancy: <i>simple quiescence</i> at temperatures below the threshold	Prospective dormancy: <i>facultative diapause</i> induced by suboptimal (but exceeding the threshold) temperatures after some delay	Prospective dormancy: <i>facultative diapause</i> induced by temperature cues and social influences
in adults	No delays of oviposition, no forms of physiological rest	Consecutive dormancy: <i>simple quiescence</i> at temperatures below the threshold	Prospective dormancy: <i>facultative diapause</i> induced by suboptimal (but exceeding the threshold) temperatures after some delay	Prospective dormancy: <i>obligate diapause</i> , environmental cues (temperature and sometimes photoperiod) can only advance or delay its onset
Stability of diapause	—	—	<i>Reversible</i> : can easily be ended by reentering the optimal temperature range (after some delay)	<i>Unstable</i> : can easily be interrupted by above-optimum temperatures or long days (many species) <i>Extremely stable</i> , cannot be broken by high temperatures and long days (some species)
Brood-rearing cycle in constant optimal conditions (in a laboratory)	Unlimited and incessant oviposition and brood-rearing	Unlimited and incessant oviposition and brood-rearing	Unlimited and incessant oviposition and brood-rearing	Intrinsic cycle of oviposition and brood-rearing limited by an endogenous sand-glass device

1985), *Pseudomyrmex* sp. in Texas, USA (Baldrige & DeGraffenried 1988) and for many species of Neotropical army-ants (Schneirla 1977, Rettenmeyer et al. 1983). The proximate causes of this seasonality in tropical ants are unknown.

Uninterrupted homodynamic development was also observed in prolonged laboratory experiments under optimal temperatures in tropical ants *Tetraponera anthracina* (Terron 1977) and *Monomorium pharaonis* (Peacock & Baxter 1949, 1950, Peacock 1950b, Peacock et al. 1955, Petersen Braun 1975, 1977). Our experiments revealed the homodynamic type of development for three tropical species – *M. pharaonis* collected in St. Petersburg, *Pheidole sexspinosa* from Tonga Archipelago and *Tetramorium semillimum* from the Seychelles. These species were kept in the laboratory during 1.5–2 years under various ecologically feasible conditions (temperature from 18 to 25 °C, photoperiods from 10 to 16 hours of light per day) and incessant development without any sign of arrest was invariably observed.

However, when colonies of Pharaoh's ant *M. pharaonis* were kept at temperatures close to or below the threshold of development, which is about 17.7–17.8 °C (Kipyatkov & Lopatina 2002a), the mortality of brood and workers became too high and the colonies died out in a month. This finding is in good accordance with the fact that Pharaoh's ant occurs in Europe only in well-heated buildings (Berndt & Eichler 1987). Unfortunately, other tropical ants are still unexplored in this respect. It is well known, however, that true tropical insects are unable to survive long at temperatures near or below the threshold for development and especially below the cold coma point i.e. in the state of quiescence (Leather et al. 1993). Thus, most homodynamic tropical ants are not preadapted to cold weather and would not survive even in warm temperate regions.

QUASI-HETERODYNAMIC DEVELOPMENT

The term *quasi-heterodynamic* can be applied to tropical ants that are adapted to exist in the regions with cold winters but unlike true heterodynamic (see below) species do not have real diapause (Kipyatkov 1996). In optimal conditions the egg-laying of their queens and the development of their brood can proceed indefinitely and cease in nature only at temperatures below the threshold of development (consecutive dormancy). The colonies overwinter in a quiescent (cold coma) state suffering from more or less strong mortality (Tab. 1). These species differ from true homodynamic ants only in this ability to survive somehow during cold winters. Several examples are described below.

The red and black imported fire ants, *Solenopsis invicta* and *S. richteri*, were accidentally introduced into the United States from South America about 60 and 80 years ago, respectively, at the port of Mobile, Alabama (Lofgren 1986). Today, the red imported fire ant is distributed throughout most of the southeastern United States and the black imported fire ant is primarily restricted to northern Alabama and Mississippi and southern Tennessee (Lofgren 1986). Thus both species now occur in the regions with relatively cold winters. In fact they are homodynamic in the Southern United States since all developmental stages occur in their nests throughout the year, although the amount of brood can be very low during mid-winter (Markin & Dillier 1971, Horton & Hays 1974, Lofgren et al. 1975). However, in the northern parts of the fire-ant range, oviposition in colonies ceases during the coldest period of the winter and most larvae and pupae disappear (Markin et al. 1974, Lofgren et al. 1975). As long as the lower threshold of larval development in *S. invicta* is about 17 °C (Porter 1988) many larvae (and also adult workers) may perish during the winter in northern populations of this species. Such winter mortality of workers is documented for *S. invicta* (e.g., Morrill 1977, Morrill et al. 1978).

The Argentine ant, *Linepithema humile*, from South America has infested many territories all over the world. The seasonal life cycle of this species studied in the South of California, USA (Markin 1970) and in the South of France (Benois 1973) appeared rather similar to that of the fire ants. Only a few larvae (mainly small) and very few eggs can be found in the nests of *L. humilis* during the winter when adults make up more than 90% of colony biomass. In summer the brood constitutes about 50% of the biomass but in October it quickly declines and reaches a minimum by December.

The primarily tropical army-ants of the genus *Neivamyrmex* in northern parts of their range exist in a temperate climate with rather cold winters. According to the observations of Schneirla (1958, 1971) in autumn when nights grow cooler these nocturnal ants cease foraging. Then the lack of food forces the queen to stop laying, the workers destroy the remaining brood and the colony, comprising only adult ants, passes the winter in a shelter. In spring when temperatures rise the queen starts laying and the colony gradually restores the periodicity of brood-rearing and nomadic behaviour typical of the summer season (Schneirla 1963, 1971). Schneirla postulated the direct influence of low temperatures on the development of these ants. However, this statement has never been tested experimentally.

We have studied the quasi-heterodynamic development in three species of myrmicine ants. *Pheidole pallidula* occurs in South Europe, the Caucasus and Middle Asia (Dlussky 1981); the range of *P. fervida* includes South-East Asia, Japan, Southern Kurils and the South of Primorie (Kipyatkov & Lopatina 1987, Kupyanskaya 1990). In Primorie *P. fervida* is likely to have persisted from the Tertiary when the climate was much warmer (Kupyanskaya 1990).

In experiments on both *Pheidole* species (Kipyatkov 1993, 1996) the queens laid eggs and the larvae continued to develop and pupate uninterruptedly under any temperature above the lower developmental threshold. Thus, any form of diapause is absent in these ants. We have observed incessant and unlimited development in their colonies at optimal temperatures of 25–28 °C during more than two years. In *P. pallidula* from Turkmenistan oviposition and larval development did not cease at 20 °C. After temperature decreased below the developmental threshold, which is about 18 °C in this species (Kipyatkov & Lopatina 2002a), the queens still continued to lay but the eggs did not develop, prepupae and pupae began to perish and all the brood gradually died out. The overwintering of this species without brood was confirmed by our field studies in Turkmenistan and by the observations of Passera (1977) in Southern France.

P. fervida, appeared to be better adapted to the rather severe winters of the Southern Primorie because its brood perished only partially during artificial overwintering. After temperature decreased up to 10–12 °C in an experiment the workers began to dismember and discard the pupae and prepupae and gradually destroyed all of them. The ants overwintered, therefore, with eggs and larvae of all instars. However, some proportion of eggs and young larvae died out during the artificial overwintering, whereas older larvae overwintered successfully (Kipyatkov & Lopatina 1987).

In *Monomorium kusnezovi* from Turkmenistan (Kipyatkov 1996) the growth and pupation of larvae continued without delays at all temperatures above the threshold of development (between 20 and 21.5 °C for eggs, larvae and prepupae – Kipyatkov & Lopatina 2002a). Thus, the larvae of this species have no diapause. At 20 °C and below the larvae ceased to grow but the queens continued to lay eggs. Therefore, the ant colonies contained eggs and larvae of all instars before the artificial overwintering. Most eggs died during overwintering but larvae survived more successfully. The overwintering of *M. kusnezovi* larvae was also confirmed by our field observations in Turkmenistan (Kipyatkov 1996).

Most temperate ants are true heterodynamic, i.e. they have a period of prospective dormancy (winter diapause) in their annual life cycle. However, heterodynamic development has been found in some tropical species as well. 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 no 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 warm subtropics of China (Chen & Tang 1989, 1992) are also heterodynamic. As long as seasonality of the environment is usually quite apparent in the tropics, heterodynamic development with true diapause might be very common in tropical ants. Unfortunately, the data are still very scarce. Recent investigations give ever more evidence that various forms of dormancy and diapause are widespread phenomena in tropical and subtropical insects but the factors controlling dormancy in these species are as yet insufficiently known (Denlinger 1986, Danks 1987). It is worth emphasizing that heterodynamic development can serve as a preadaptation for survival during cold winters and facilitate the expansion of some tropical ants to temperate regions (Kipyatkov 1993, 1996).

In a pioneering study of life history evolution in social insects Oster & Wilson (1978) primarily concentrated on the scale and timing of the allocation of resources between worker and sexual production. They distinguished three main stages in a colony's life cycle: *foundation stage* when the solitary queen attempts to start its colony, *ergonomic stage* in which the colony grows by producing all-worker broods for a number of years, and *reproductive stage* in which the colony each year produces a mixture of workers and sexuals. For the perennial species, such as ants, Oster & Wilson (1978) predicted so-called "*bang-bang*" strategy which maximizes colony's fitness (sexual production) by alternation ergonomic and reproductive phases within each year. The ergonomic phase within each season should be as long as possible so that more workers are available to raise the largest number of sexuals during the second part of the year. Such seasonal switches to sexual production resulting in clear oscillations in numbers of worker present in a colony were indeed observed in several species, such as *Solenopsis invicta* in the USA (Tschinkel 1993).

However, the perennial colonies also have to invest in workers to promote winter survival and subsequent reproduction. Considering this constraint Oster & Wilson (1978) predicted that the switch to producing sexuals should occur later within a season as the colony overwintering survival rise. Since then little attention has been paid to the role of seasonality in life history evolution in ants (e.g., Bourke & Franks 1995). Recently, the thorough analysis of literature and own data collected during many years of field work allowed Kipyatkov (1996) to conclude that most temperate ants evidently differ in seasonal timing of worker and sexual production from the predictions of Oster and Wilson. First, most species raise their alate reproductives not in late summer after the worker brood is already produced, but quite the reverse – just after the overwintering. In some of them sexuals originate from the first egg portion laid by queens in early spring. This group comprises species belonging to the tribe Formicini (genera *Alloformica*, *Cataglyphis*, *Formica* and *Proformica*) and the genera *Dolichoderus* and *Pogonomyrmex* (Kipyatkov 1996). Another, much larger group consists of all other temperate species in which alates develop from the overwintered larvae (Kipyatkov 1996). Anyhow, the rearing of sexuals always precedes the period of worker production in an annual cycle of most temperate ant species. The second departure from the predictions of Oster and Wilson is that the production of sexuals is always accompanied by rearing of workers which can emerge even in greater numbers than winged reproductives (Kipyatkov 1996). It means that a complete switch from worker to alate production does not in fact occur.

Thus, most temperate ants use *the strategy of preceding production of sexuals* in their annual cycle (Kipyatkov 1996). This strategy demands that the colony's annual cycle should be organized in a way to maximize the quantity of diapause larvae and new workers produced by the end of each brood-rearing season; these workers will facilitate colony's winter survival and will rear alate females and males from overwintered larvae or from eggs next spring. For this purpose the brood-rearing should start in spring as early as possible and continue as long as possible. At the same time the brood stages and adults present in the nest by the beginning of winter should be capable of overwintering. To resolve this problem the temperate ants should evolve appropriate forms of winter dormancy and efficient mechanisms controlling its onset and completion at the proper time (Kipyatkov 1993, 1996).

Temperate ants use two main *seasonal strategies of brood-rearing* (Kipyatkov 1996, Kipyatkov & Lopatina 1995, 1996a, b). The most widespread is *the strategy of prolonged brood-rearing* distinguished by delaying development of a large proportion of larvae (so-called *slow brood*) which continue to grow in autumn, overwinter in diapause and pupate during the next summer; thus, only some larvae develop from egg to pupa within the same summer season without overwintering (so-called *rapid brood*). The strategy of prolonged brood-rearing has several evident advantages important for adaptation to temperate and boreal climates (Kipyatkov 1993, 1996): (1) the larvae can be reared from early spring up to late autumn thus utilizing the whole warm period of a year; (2) the quantity of rapid brood can be changed to adapt to long-term and short-term climatic

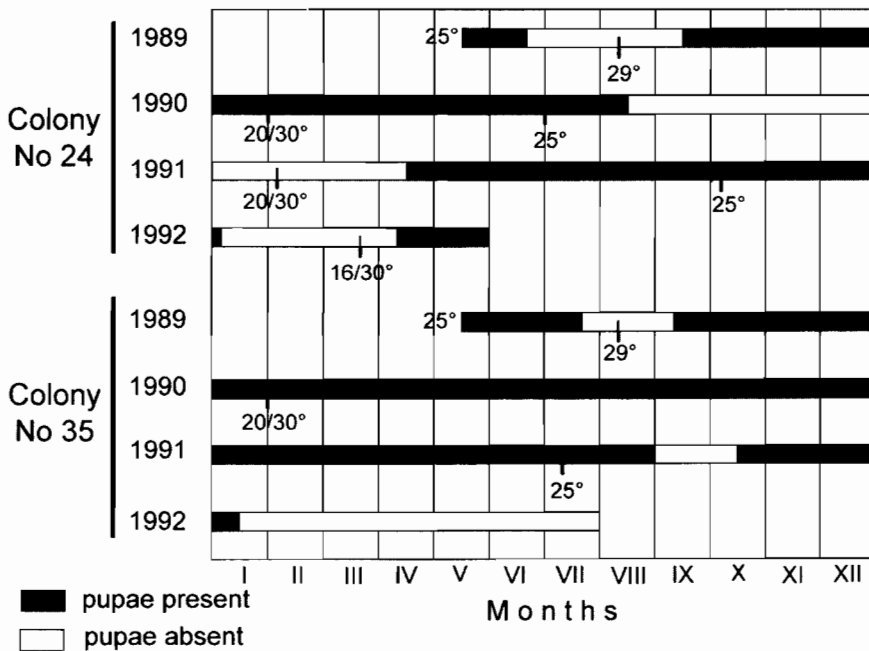


Fig. 1. Repeated induction and termination of larval diapause in two laboratory colonies of *Tapinoma karavaievi* collected in summer 1989 in Turkmenistan as a result of successive changes of temperature regimes during a period of three years. The absence of pupae in a colony indicates that larvae are in diapause.

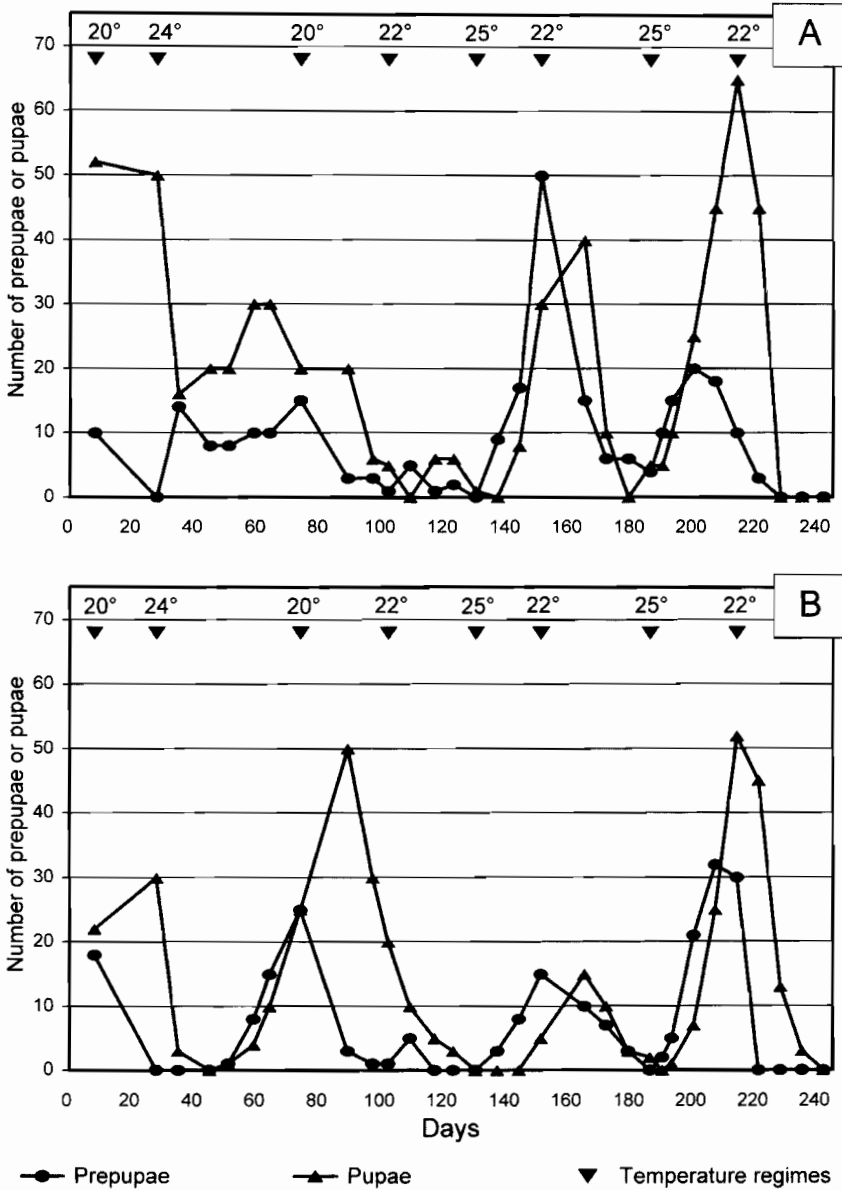


Fig. 2. Repeated induction and termination of larval diapause in two laboratory colonies (A and B) of *Tetramorium jacoti* from South Primorie (near Vladivostok) by successive alterations of temperature. Start of experiment on 17 September. The numbers of prepupae and pupae present in a colony at each census date are depicted. Since the prepupal stage lasts only several days, the absence of prepupae in a colony is a good evidence that larvae do not pupate.

variations and to the duration of the warm season; (3) the development of larvae can be extended to two or even three summer seasons.

Two *structural types* of annual cycles have been distinguished among heterodynamic species with prolonged brood-rearing (Kipyatkov 1993, 1996). In ***Aphaenogaster* type** the larvae enter diapause at the end of summer but the queens have no diapause and do not cease laying until the late autumn; therefore, not only diapause larvae but also eggs and young larvae overwinter and survive, at least partially, during the winter (Kipyatkov & Lopatina 1990). Ants with this type of cycle are apparently restricted to the subtropics and the southernmost regions of the temperate zone. It was discovered in all hitherto studied species of *Aphaenogaster* (Kipyatkov & Lopatina 1990) and in a few species of *Leptothorax*, *Messor*, *Monomorium*, *Polyrhachis*, *Tapinoma* and *Temnothorax* (Kipyatkov 1993, 1996).

Most species with prolonged brood-rearing have the second structural type of annual cycle – ***Myrmica* type**. They all have winter diapause both in larvae and adults and overwinter without eggs but only with diapause larvae of one or several instars depending on species (Kipyatkov 1993, 1996). According to the stages in which larvae can enter diapause five species groups have been distinguished (Kipyatkov 1996): (1) species with diapause in early (1–3) instars (*Lepisiota*, *Plagiolepis*, *Tapinoma*, some *Camponotus*; full number of instars – 5), (2) species with diapause in middle (2–4) instars (*Camponotus* s. str.), (3) species with diapause in the two last (3–4) instars (*Harpagoxenus*, *Leptothorax* s. str., *Messor*), (4) species with diapause in a final (usually the third) instar (*Diplorhoptum*, *Leptanilla*, *Monomorium*, *Myrmica*, *Tetramorium*), (5) species with dia-

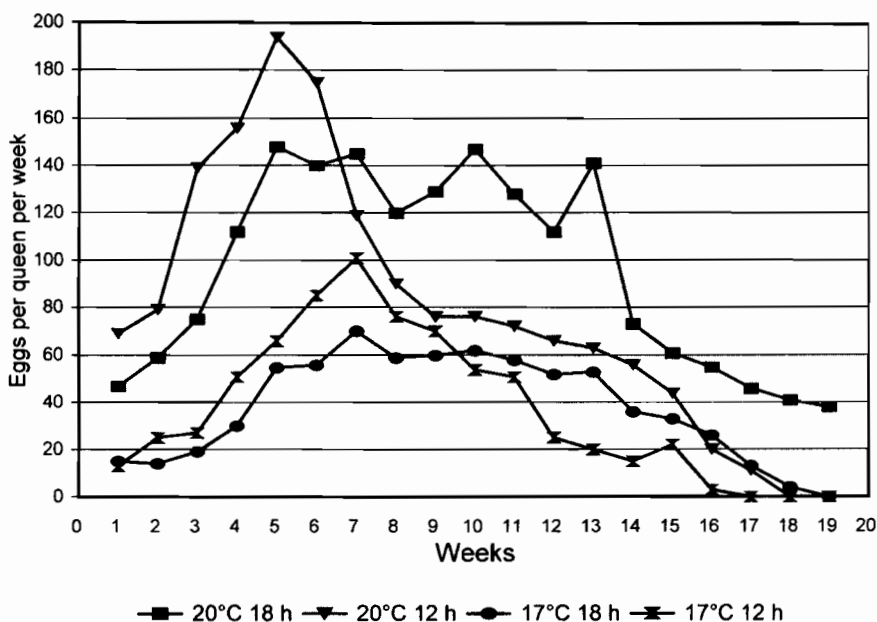


Fig. 3. Internally limited intrinsic cycle of oviposition in *Myrmica rubra* queens in cultures collected in spring in Belgorod region and kept under two temperatures and two photoperiods (according to the data of Kipyatkov 1979). Start of experiment on 17 May. Each line – the average value for 4 queens in separate cultures. Evidently, short days and lower temperature decreased the egg production and advanced the onset of diapause in queens.

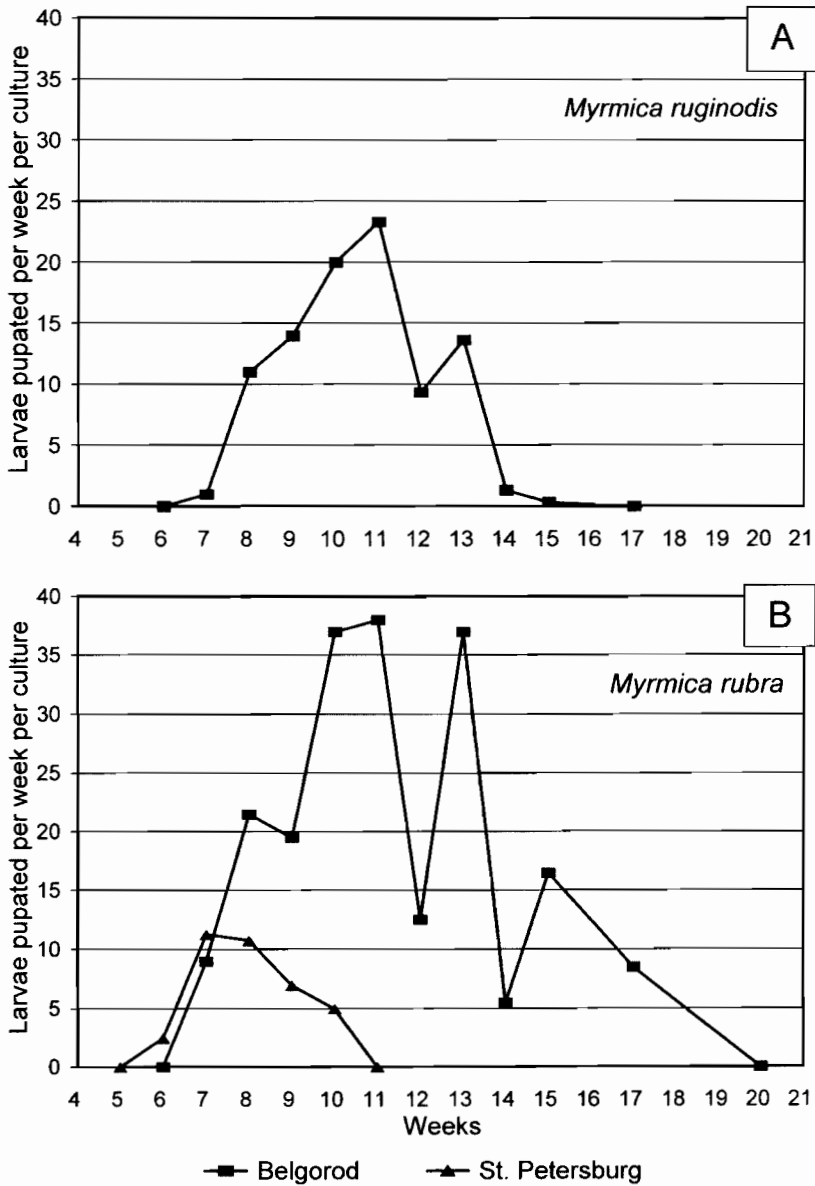


Fig. 4. Specific and geographic differences in the length of the intrinsic seasonal cycle of rapid brood production in *Myrmica ruginodis* (A) and *Myrmica rubra* (B) (according to the data of Kipyatkov & Lopatina 1997a). Ants were collected in early spring in Belgorod and St. Petersburg regions and cultured under long days (20 h) and 20 °C. Start of experiments – 13 April (Belgorod), 2 June (St. Petersburg). Each line – the average value for 4 experimental cultures. The cultures of *M. rubra* had significantly longer period of pupation and produced more rapid brood pupae than *M. ruginodis* cultures. *M. rubra* cultures from northern population (St. Petersburg) had much shorter cycle of rapid brood-rearing and produced significantly less pupae in comparison with cultures from southern population (Belgorod). *M. ruginodis* cultures from St. Petersburg did not produce any rapid brood at all.

pause in all instars (*Crematogaster*, *Lasius*, *Paratrechina*, s.g. *Tanaemyrmex* of the g. *Camponotus*; full number of instars – 5–6).

The strategy of concentrated brood-rearing is employed by ant species with another structural type of annual cycles which I call **Formica type** (Kipyatkov 1993, 1996). The development of all brood stages is restricted to the warm season in these ants. Only queens (and also workers) are able to diapause. Larvae have no dormancy and all finish their development during the summer, all new workers emerge from pupae until autumn cold weather and ants overwinter, therefore, entirely without brood. According to our observations and published data this strategy is characteristic for all genera of the tribe Formicini (*Alloformica*, *Cataglyphis*, *Formica*, *Proformica*) and for some species of the genera *Dolichoderus*, *Pogonomyrmex*, *Ponera* and *Prenolepis* (Kipyatkov 1993, 1996).

The onset of diapause in queens is a central point in the cycles of *Formica* type because it determines the moment after which new eggs do not appear, the brood gradually vanishes and the ants begin to prepare for overwintering. Queen diapause should not occur too early because it would not allow ants to use a part of the warm season for brood-rearing. At the same time if diapause ensues too late many larvae and pupae would not manage to finish their development and would perish due to low temperature. Evidently, the strategy of concentrated brood-rearing is only appropriate for temperate and boreal ants in combination with very fast brood development, allowing them to rear sexuals and new workers from eggs during a short warm season. In fact among temperate ants *Formica* species have the shortest developmental times and their development is more temperature dependent, which allows *Formica* workers to rear the brood much faster at higher temperatures (Kipyatkov & Lopatina 2002a).

Among ants inhabiting the temperate zone and adapted to cold winters two main groups can be distinguished according to the nature of dormancy and the type of seasonal cycle control: *exogenous-heterodynamic* and *endogenous-heterodynamic* (Kipyatkov 1993, 1996).

EXOGENOUS-HETERODYNAMIC SPECIES

In ants belonging to this group winter diapause in larvae and queens is *facultative* and arises in direct response to suboptimal temperatures in the autumn, but unlike simple quiescence in quasi-heterodynamic species this diapause begins when temperatures are still well above the threshold of development. Another important property is that the diapause ensues not immediately following the temperature fall but after some delay and is reversible, i.e. may be ended by reentering the optimal temperature range, also after a delay (Tab. 1).

We have found diapause of this kind in several species of the genera *Diplorhoptrum*, *Messor*, *Monomorium*, *Tapinoma* and *Tetramorium* which are limited in their distribution to southern regions of the Palaearctic region, i.e. they live in rather warm temperate climates (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002b). These species are also remarkable by their ability for continuous and unlimited development under optimal temperatures, behaving as true homodynamic species in these circumstances. In our experiments several colonies of these species were kept at temperatures above 25 °C or under daily thermoperiods of 20/30 °C for more than two years and during the whole period queens continued to lay eggs, larvae emerged from eggs, grew and pupated without any delay or any changes for the worse in colony viability (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002b).

At the same time, at suboptimal temperatures, i.e. below 23–25 °C but well above the lower threshold, development ceased after a short period. If temperatures rise after that, development will soon recommence, but it may be blocked again by the fall of temperature and then be resumed in

response to a new temperature increase. We succeeded in repeating such alterations with the same ant colonies several times with similar results (Kipyatkov & Lopatina 2002b). Three examples are given below.

When summer colonies of *Tapinoma karavaievi* from Turkmenistan were kept at 28–30 °C or daily thermoperiod of 20/30 °C they displayed continuous development for months, but at 25 °C, i.e. well above the threshold of development, which is about 20 °C (Kipyatkov & Lopatina 2002a), the larvae ceased to pupate in 1–2 months and then resumed development only after the restoration of optimal temperature conditions, not immediately but after a delay of a month or more; these successive changes could be repeated over and over again (Fig. 1). Since this polygynous species has an annual cycle of the *Aphaenogaster* type, queens never stop laying except at too low temperatures and, thus, eggs are always present among the brood. Another Turkmenian species, *Monomorium ruzskyi*, has a lower threshold for larval development of 21.8 °C (Kipyatkov & Lopatina 2002a), but its larvae ceased to pupate in summer at 23–25 °C whereas under 27–28 °C or a thermoperiod of 16/30 °C the new pupae appeared in colonies for many months. A third example is the repeated induction and termination of larval diapause produced in two colonies of *Tetramorium jacoti* from South Primorie (near Vladivostok) by successive alterations of temperature (Fig. 2).

Another important feature of exogenous-heterodynamic species is the distinct change of their norm of reaction to temperature during overwintering as a result of cold reactivation. In spring oviposition and development begins in their colonies at threshold temperatures as a result of the

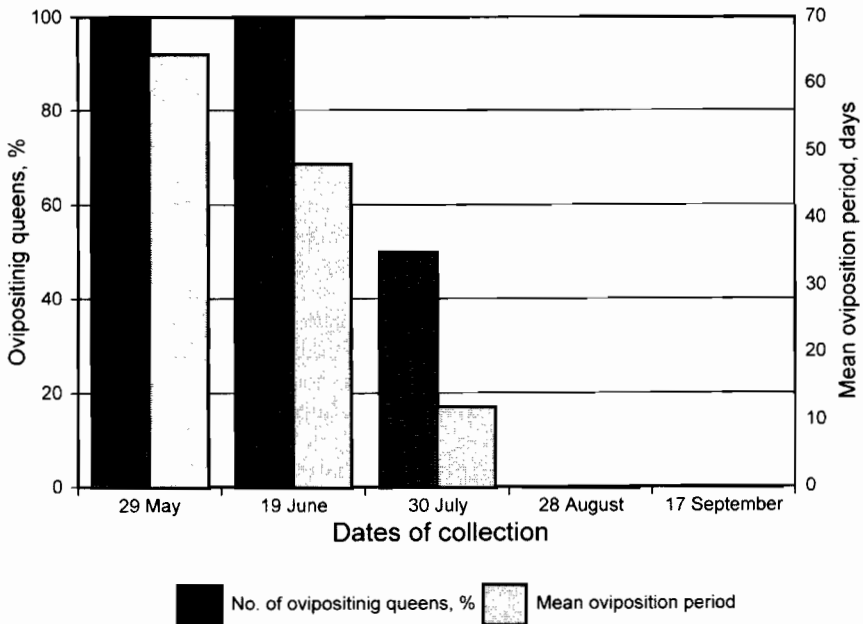


Fig. 5. Seasonal changes of intrinsically limited oviposition period in queens of *Formica aquilonia* from St. Petersburg region (according to the data of Kipyatkov & Shenderova 1989). Samples of queens and workers were collected from natural nests on five dates during May–September (from 4 to 14 queens per date) and cultured in laboratory at 25 °C and long days (20 h) until the queens stopped egg-laying. The later in the season samples were collected, the lower was the percentage of queens still laying eggs after the collection and the shorter was the mean length of their oviposition period.

absence of diapause. After natural overwintering or after exposure in a refrigerator to 3–5 °C during 2–3 months the development and pupation of larvae recommenced and proceeded for a long period at 20 °C and even at 18 °C (in some *Tetramorium*) in all species studied (Kipyatkov 1993, Kipyatkov & Lopatina 2002b). This difference in the norm of reaction to temperature, which can be easily revealed in experiments, is another indication of the existence of diapause in exogenous-heterodynamic species.

ENDOGENOUS-HETERODYNAMIC SPECIES

Most ants inhabiting the temperate zone and all northern species belong to this group. Their diapause is *obligatory at a colony level*, i.e. it is mostly due to factors internal for the colony and no external conditions can prevent the definitive cessation of oviposition and development. Even at long days and optimal temperatures, including the daily thermoperiods which are the most favourable temperature conditions for ants (Lopatina & Kipyatkov 1993, 1997), queen egg-laying capacity and worker ability to rear larvae without diapause tend to decline step-by-step in colonies of these species until oviposition and larval development stop and diapause ensues sooner or later as a result of an endogenous timer effect (Tab. 1). This timer mechanism, internal for the colony, was called *sand-glass device* to depict the gradual loss of colony's capability to produce eggs and to rear larvae without diapause (see Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c for details).

Thus, a colony of an endogenous-heterodynamic species has an internally limited (by a sand-glass device) *intrinsic seasonal cycle of brood-rearing*. Such an endogenous physiological cycle in constant laboratory conditions was first observed in *Myrmica* by Brian for worker (1953) and queen (Brian & Hibble 1964, Brian & Kelly 1967) oviposition, and then for rapid brood production (Brian 1957, 1962, 1963). Similar results were also obtained for *Camponotus herculeanus* and *C. ligniperda* (Hölldobler 1961), several *Leptothorax* species (Cagniant 1968, Plateaux 1970, 1986, Espadaler et al. 1983, 1984), *Plagiolepis pygmaea* (Passera 1969) and *Cataglyphis cursor* (Cagniant 1979, 1980).

In our experiments internally restricted cycles of queen oviposition and/or larval development in constant laboratory conditions were found in more than 60 species of the genera *Aphaenogaster*, *Camponotus*, *Cataglyphis*, *Crematogaster*, *Formica*, *Harpagoxenus*, *Lasius*, *Lepisiota*, *Leptothorax*, *Manica*, *Myrmica*, *Plagiolepis*, *Ponera*, *Proformica* and *Tapinoma* (Kipyatkov & Shenderova 1990, Kipyatkov 1993, 1994, 1996, Kipyatkov & Lopatina 1993, 2002c, Lopatina & Kipyatkov 1990, 1993). It was then found that the intrinsic length of colony's annual cycle of brood-rearing differed not only between close species but also between geographical populations of the same species, which reflects their adaptations to local climate conditions (Kipyatkov & Lopatina 1997a,b). Examples are shown in Figs 3–6.

The best evidence for the endogenous and obligatory nature of colony diapause was provided by experiments with free choice by ants of the preferred temperature. In the first one (Kipyatkov & Shenderova 1986) two small colonies of *Formica polyctena* were kept from early spring in nests with a horizontal temperature gradient from 5 to 40 °C in which ants were permitted to make a free choice. A normal seasonal cycle of queen oviposition and larval development was observed in both colonies, during which ants with brood concentrated in parts of the nests with temperatures of 20–30 °C. In August queens stopped laying and ants began to move gradually to the cooler parts of the nests, finishing the brood-rearing process. The length of the brood-rearing cycle in experimental colonies appeared to be just the same as in nature as well as in colonies simultaneously maintained in the laboratory at constant temperature of 25 °C (Kipyatkov & Shenderova 1986). Thus, the seasonal cycle of queen oviposition is completely limited in this species by some internal

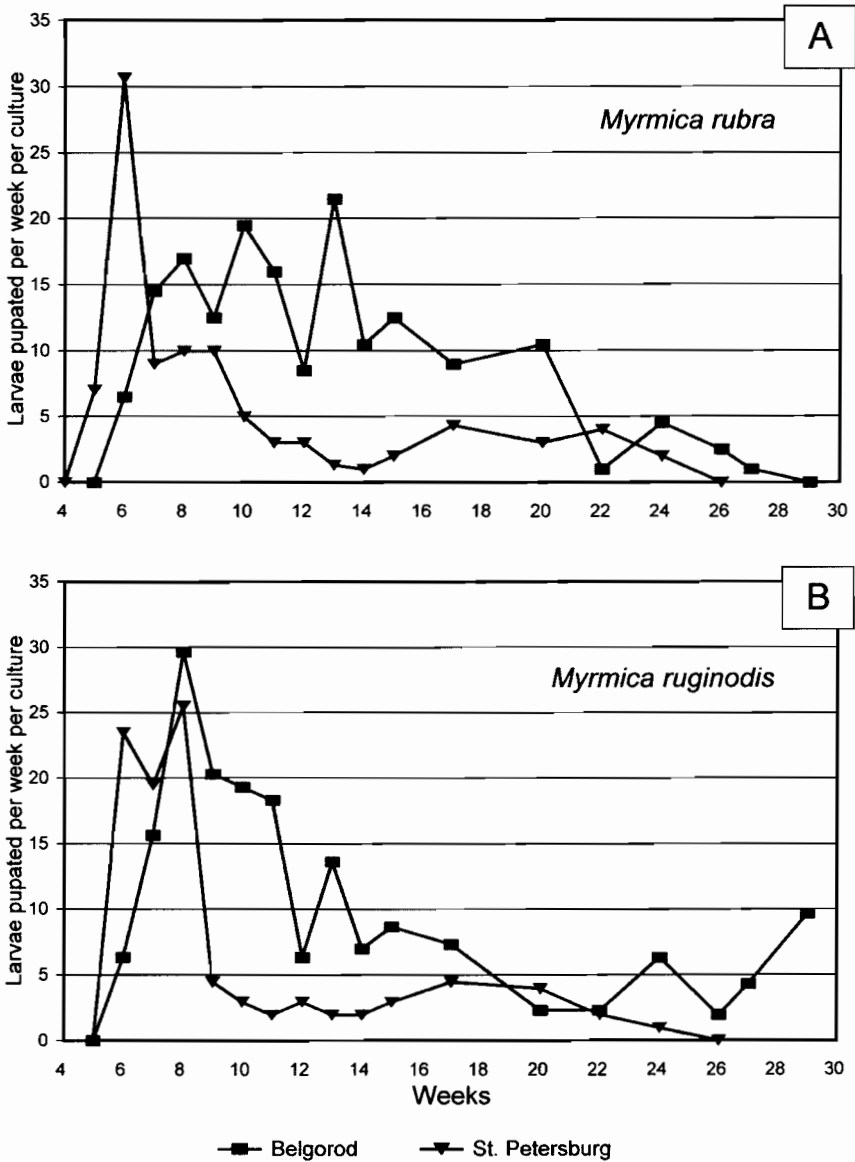


Fig. 6. Extremely prolonged production of rapid brood pupae in *Myrmica rubra* (A) and *Myrmica ruginodis* (B) cultures collected in spring in Belgorod and St. Petersburg regions and maintained under long days (20 h) and above-optimum temperature 25 °C (according to the data of Kipyatkov & Lopatina 1997a). Start of experiments – 13 April (Belgorod), 2 June (St. Petersburg). Each line – the average value for 4 experimental cultures. Even under such high temperature that strongly provoked development and pupation of larvae ant cultures from northern population (St. Petersburg) had shorter cycle of rapid brood-rearing and produced less pupae in comparison with cultures from southern population (Belgorod).

factors and cannot be extended even in favourable conditions. Similar results were later obtained for several endogenous-heterodynamic species in our prolonged experiments in nests with horizontal temperature gradients (Kipyatkov 1994, 1996).

Another confirmation for the endogenous nature of diapause control came from the observations of the *spontaneous rhythms of oviposition and development* in colonies of many ant species maintained under constant laboratory conditions for a long time: the egg-laying of queens and the development of larvae first ended, and then resumed after longer or shorter intervals, and these periods of direct development and of diapause could be repeated. Such a rhythm was first described by Hölldobler (1961) in *C. herculeanus* and *C. ligniperda*. During inactive periods of the cycle these ants formed dense aggregations in the nest together with larvae in diapause, which were fed only a little at that time, and the workers of *C. herculeanus* even closed the nest entrance then with a plug made of litter. According to the observations of Plateaux (1970) in *L. nylanderi* development in the overwintered colonies at 24–25 °C proceeded during 90–100 days and then the obligatory period of rest ensued and lasted for not less than another 100 days; after this diapause stage development could restart.

In our long-term experiments the spontaneous rhythms of oviposition and development were found in all endogenous-heterodynamic species that we studied, namely in the genera *Aphaenogaster*, *Camponotus*, *Cataglyphis*, *Crematogaster*, *Formica*, *Lasius*, *Lepisiota*, *Leptothorax*, *Myrmica* and *Plagiolepis*. In diapause ant colonies kept under conditions identical to those in which the diapause has ensued a new developmental cycle could begin after a few weeks or after several months, and sometimes after almost a year. Oviposition and pupation continued for some time, but then a gradual decline was observed, and finally development became arrested again (Kipyatkov 1993, 1994, 1996). This phenomenon was most thoroughly explored in the red wood ants *Formica aquilonia* and *F. polyctena*: the data for several dozens of experimental cultures of each species maintained at various constant temperatures and photoperiods for 1–5 years were obtained and analysed (Kipyatkov & Shenderova 1989, 1990). In nests with horizontal temperature gradients we observed even more distinct spontaneous rhythms of oviposition and development which were closely associated with changes in the thermopreferendum: during periods of direct development ants kept their brood in chambers with sufficiently high temperature, and during periods of diapause in cool chambers (Kipyatkov 1993, 1994, 1996).

There was considerable variation in the duration of periods of direct development and diapause in different experimental colonies and within the same colony. Furthermore, there was no coordination with the natural change of seasons. All this clearly indicates the endogenous nature of observed rhythms and the absence of external synchronizers (Kipyatkov 1993, 1994). This situation seems to be very similar to that found in some non-social insects which diapause as adults in which alternations of ovipositional arrest and resumption of oviposition can also be repeated in constant conditions (Hodek 1979, 1983). After analysing the available data Hodek (1998) came to the conclusion that this rhythmic alternation in the bug *Aelia acuminata* is endogenous and may be governed by internal timer(s), which is clearly analogous to my idea of a sand-glass device in ants. It is premature to discuss possible physiological mechanisms underlying these spontaneous rhythms. It should only be added that the available data distinctly demonstrate a rather complex nature of the sand-glass device in ants, which includes not only some unknown physiological mechanisms operating inside the bodies of individual ants but also a set of intricate social mechanisms functioning among individuals in a colony which control the onset and the end of diapause (Kipyatkov 1981, 1996, Kipyatkov et al. 1997a,b, Kipyatkov & Lopatina 1999). The latter mechanisms have so far been much better studied and understood (see below).

It should be emphasized, however, that in most endogenous-heterodynamic ants, especially in species occurring in the northern regions of Palaearctic, after the spontaneous completion of diapause in the laboratory the reproduction and development are never as perfect as after normal overwintering at low temperatures: the productivity of queens is low, not all overwintered larvae pupate and there is no rapid brood at all. Such a peculiarity of spontaneous resumption of development was first recorded by Plateaux (1970) in *L. nylanderi*. In our experiments we observed this phenomenon in all northern species studied. After each brood-rearing cycle under constant conditions the indices of productivity decrease steadily, the number of pupae produced and the number of ants in a culture gradually declines, their viability diminishes and finally they all die. In most prolonged experiments with red wood ants we sometimes added pupae from other colonies in order to maintain the number of workers in experimental cultures and prevent their dying out (Kipyatkov & Shenderova 1990). In fact, all endogenous-heterodynamic species require not only diapause completion but exactly cold reactivation, i.e. the winter exposure to low temperatures, to adequately restore their ability for productive brood-rearing (Kipyatkov 1994, 1996, Kipyatkov & Lopatina 2002c).

The necessity of winter chilling for diapause completion in ants was first revealed by Delage (1968) for queen diapause in *Messor capitatus* and by Cagniant (1968) for larval diapause in *Leptothorax monjanzei*. Then Passera (1969) discovered that when the workers of *P. pygmaea* kept without a queen at optimal temperature stopped laying after a long period of oviposition they could be provoked to renew egg-laying by keeping them at 10 °C for no less than 15 days. Plateaux (1970, 1971) showed a 3–4 months exposure of *L. nylanderi* colonies to cold during autumn and winter to be crucial for the resumption of full development in spring. In some ants after a nuptial flight the inseminated queens establish new nests at the end of summer but start egg-laying only in spring and need winter chilling for this (Benois 1972, Plateaux 1970). Finally, the overwintering at cool temperature was shown to be obligate for the production of alate sexuals, especially females, in numerous species of temperate ants (Wesson 1940, Chauvin 1947, Brian 1955, Otto 1962, Passera 1969, Plateaux 1970, 1971, Buschinger 1973, Schmidt 1974, Cagniant 1988). Brian (1955) first demonstrated experimentally that overwintering at low temperatures was crucial for workers of *Myrmica ruginodis* to gain the ability to terminate diapause in autumn larvae and for large diapause larvae to acquire the potency to develop into reproductive females. He called this process “vernalisation”.

In our experiments such an essential role of cold reactivation was revealed for all endogenous-heterodynamic species studied (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c). According to our data a period of 1–4 months (depending on species) of exposure to 3–5 °C is required for full reactivation. After such a treatment oviposition and development begin even at short days and 17–20 °C, i.e. in circumstances that cause quick diapause onset in the same colonies in summer (see below). Thus, besides the completion of diapause, which may happen spontaneously or as a result of the influence of long days, the apparent effects of cold reactivation, unachievable for temperate ants without winter cooling, include: (1) the restoration of the colony’s “spring physiology” and full capability to realize a new brood-rearing cycle (normal queen fecundity, potency of some larvae to develop into female reproductives, ability of workers to rear overwintered and rapid brood larvae without diapause and to produce alate sexuals), and (2) the changes of the norm of reaction to photoperiod (general loss of sensitivity in species that have photoperiodic responses – see below) and temperature (ability to produce eggs and rear larvae without diapause for a long period at rather low temperatures that induce diapause in summer). One could say that as a result of cold reactivation the ant colony’s “sand-glass” turns over (Kipyatkov 1993, 1996).

During the summer season the gradual decrease of a colony’s capability to produce new eggs and to rear larvae without diapause and the increase of the bias for diapause occur as a result of the

endogenous physiological and social processes, as though the sand in the ants' "sand-glass" pours little by little out the upper reservoir to the lower one. Also, the photoperiodic sensitivity of a colony appears and the reaction to temperature distinctly changes due to this process. As a result, in late summer lower temperatures and shorter days (only in some species) advance the onset of diapause, thus curtailing the period of oviposition and development. Such effects of external conditions were found in our experiments in all species studied (Kipyatkov 1974a, 1977a, 1979, 1981, 1993, 1996, Kipyatkov & Shenderova 1989, 1991, Kipyatkov & Lopatina 1990, 1993, 2002c, Lopatina & Kipyatkov 1993). Thus, the duration of a colony's annual cycle of brood-rearing in nature is controlled both by an endogenous timer (sand-glass device) and by exogenous environmental cues – temperature and photoperiod (in some species), which adjust the date of diapause onset to the climatic characteristics of a given year (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c).

Temperature control of diapause is really universal in ants. In all species tested in our experiments higher temperatures delayed and lower temperatures advanced the onset of diapause both in larvae and adults (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002b,c). On the contrary, *photoperiodic control of diapause* is unexpectedly uncommon among ants. The photoperiodic responses in these insects were revealed for the first time in *M. rubra* and *M. ruginodis* (Kipyatkov 1972, 1974a). It has been shown that diapause arose sooner in larvae and queens the shorter was the day-length in the interval from 16 to 13 h characteristic for the study region in July–September (Kipyatkov 1974a, 1977a, 1979). When ant colonies in the autumn state were subjected to day-lengths of 15 h, diapause ended both in queens and larvae (Kipyatkov 1977b). Subsequently the existence of photoperiodic responses in *M. rubra* was confirmed by Hand (1983) and Brian (1986).

Nevertheless, the following extensive studies demonstrated that only some ants besides *Myrmica* used day-length as an environmental cue controlling oviposition, development and diapause onset. The diapause induction was found to depend on photoperiods only in *Aphaenogaster sinensis* (Kipyatkov & Lopatina 1990) and *Lepisiota semenovi* (Kipyatkov & Lopatina 2002c). In addition in *A. sinensis*, *Camponotus herculeanus*, *Leptothorax acervorum* and *Manica rubida* we have observed higher incidence of diapause in larvae at short days compared with larvae in similar cultures at long days (Kipyatkov 1996). The genus *Myrmica* thus represents a rather curious exception among temperate ants since all its species studied so far possess clear-cut photoperiodic responses controlling the induction and termination of diapause (Kipyatkov 1972, 1974a, 1993, 1996, Kipyatkov & Lopatina, 1997b, 1999). Possible factors that prevent most ants from evolving photoperiodic control of diapause are discussed by Kipyatkov (1996).

Thus, most temperate ant species rely upon internal clocks as well as on ambient temperatures in triggering the onset of diapause. In several endogenous-heterodynamic ants (most species belonging to genera *Aphaenogaster*, *Crematogaster*, *Lasius*, *Myrmica*, *Tapinoma*) environmental cues can alter the duration of the annual brood-rearing cycle within rather broad limits. For example, in *Myrmica rubra* and *M. ruginodis* short days and suboptimal temperatures of 17–20 °C in the middle of summer substantially advance the onset of diapause in larvae and queens (Kipyatkov 1974a, 1977a) while at long days and a temperature of 25 °C, which is well above the optimum of these species (21–22 °C according to Brian 1973), egg-laying by queens and the development and pupation of rapid brood larvae continues for several months without a break (Kipyatkov 1979, Kipyatkov & Lopatina 1997a). An example is given in Fig. 6.

The seasonal cycle of oviposition and development in other species is controlled predominantly by the endogenous mechanisms, and the time of the onset of diapause depends only slightly on environmental conditions in these ants. Thus, temperature hardly modifies the intrinsic length of the queens' oviposition period in all studied species of the genus *Formica* (Kipyatkov & Shenderova 1989, 1991, Kipyatkov & Lopatina 1993). The annual brood-rearing cycle in species belong-

ing to the genus *Cataglyphis* and the subgenera *Camponotus s. str.* and *Leptothorax s. str.* is also comparably independent of the environment (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c).

FORMS AND PROPERTIES OF DIAPAUSE IN ENDOGENOUS-HETERODYNAMIC ANTS

Larval diapause

In most cases the diapause of larvae in ants is *facultative*, i.e. a given larva can either develop directly or enter diapause depending on the circumstances (Tab. 1). The diapause is induced by external factors and is normally ended due to diapause development at low temperatures (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c). In a few instances, however, the larval diapause can be obligate to some extent. Brian (1962, 1963) found that some *Myrmica* larvae emerging from the first eggs laid in spring had “a bias” for diapause and therefore they grew slowly, entered diapause and did not pupate without overwintering. Only at 24 °C and above could these larvae pupate if they were fed by workers with spring physiology (Brian 1963).

Evidently, temperature can affect larval development and induce diapause both directly and through the nurse workers, although the latter route has been investigated so far in only one instance. Brian (1955) carried out experiments with separate chilling of diapause larvae and workers of *M. ruginodis* and found that the process of vernalisation (see above) took place only in larvae, because larvae before overwintering never developed into alate females even if they were fed by workers in a spring state, whereas larvae subjected to cold and reared by autumn workers sometimes became alates under the relatively high temperature of 25 °C.

The ways by which the photoperiodic conditions can control larval diapause were studied in detail in *M. rubra* (Kipyatkov 1974b, 1976, 1981, 1988). Surprisingly, the larvae appeared to be entirely insensitive to the direct influence of photoperiods. Their development was instead controlled by workers who perceived the photoperiodic cues from the environment. Thus, non-diapause nurse workers (i.e. maintained under long days from the spring or activated by long-day photoperiods in autumn and, hence, physiologically active) stimulated rapid growth and pupation of summer larvae and terminated diapause in autumn larvae, whereas diapause workers (i.e. subjected to 3–4 weeks influence of short days and, hence, physiologically inactive) were unable to maintain a high growth rate of larvae and instead induced diapause in them (Kipyatkov 1974b).

In fact, this was an example of *social control of larval diapause by the workers*. However, the first case of such a control was described by Brian (1955) in *M. ruginodis*. He found that the spring workers (i.e. ants immediately following prolonged overwintering in a refrigerator) stimulated fast growth and pupation of diapause autumn larvae both at 20 and 25 °C. However, similar diapause larvae did not develop at all when fed by autumn workers (i.e. ants which performed a complete cycle of brood-rearing at optimal temperature during three months after overwintering). The results of Brian were then confirmed by Weir's (1959) experiments on the same species; Weir revealed also that young workers recently emerged from pupae were similar in their influence on larvae to the autumn workers. Plateaux (1971) made analogous experiments on *L. nylanderi* and showed that spring workers of that species are able to terminate diapause of autumn larvae. In subsequent experiments Brian (1963) found one more highly interesting form of social control of larval diapause: the stimulating effect of a queen whose presence in a culture led to a 4–5-fold increase of the percentage of pupating rapid brood larvae in comparison with ant cultures without queens.

Afterwards, Kipyatkov (1979) repeated experiments of Brian (1955) on *M. rubra* including naturally overwintered (spring) larvae as well. Spring larvae did not pupate at all under the care of diapause autumn workers, whereas naturally overwintered (spring) workers provoked growth and pupation in the majority of both spring and diapause autumn larvae. Significantly later we studied

the phenomenon of worker social control in several ant species and made experiments according to the same exchange scheme with four combinations: (1) overwintered workers with overwintered larvae, (2) overwintered workers with diapause larvae, (3) diapause workers with overwintered larvae, (4) diapause workers with diapause larvae.

The results of these experiments differed significantly among species (Kipyatkov & Lopatina 1994, 1999, Kipyatkov et al. 1996, 1997). In *Camponotus herculeanus*, *C. japonicus* and several *Tetramorium* species non-overwintered diapause larvae fed by spring workers developed rapidly and pupated within a short period whereas overwintered larvae placed into the nests with autumn workers did not develop and pupate at all or only a few of them pupated sometimes. Thus, the workers of these ants exercise full control over the development and the diapause of their larvae. However, in *Leptothorax acervorum* we found an entirely opposite situation: autumn workers could not prevent development of spring larvae and they all pupated. At the same time overwintered workers stimulated development of less than half of diapause larvae. In *Myrmica rubra*, *M. ruginodis*, *M. lobicornis* and *Lasius niger* we observed an intermediate situation: only some spring larvae pupated when fed by autumn workers and also far from all autumn larvae finished development under the care of spring workers.

Thus, the forms of social influence on diapause by workers are diverse in ants and range from nearly absolute control (in *Camponotus* and *Tetramorium*), when the physiological state of workers completely defines the fate of larvae, to rather weak effects when diapause workers are unable to prevent the pupation of most overwintered larvae and spring workers are capable of inducing the development and pupation of only a few diapause autumn larvae (in *Leptothorax*). In most species (*Lasius*, *Myrmica*), however, the intermediate variants of diapause control are realized. There is some evidence that *Myrmica* workers can manipulate the development of larvae via changing the intensity of tactile stimulation and the frequency of feedings (Kipyatkov & Lopatina 1988, 1989a, b).

The stability of larval diapause differs significantly among ant species. In some species the diapause is quite stable and cannot be broken by the influence of high temperature and long days. Hölldobler (1961) observed that *C. herculeanus* and *C. ligniperda* larvae did not grow and stayed in diapause for a long time under high temperature. The same appeared true for *C. vagus* (Benois 1972). Passera (1969) showed that autumn larvae of *Plagiolepis pygmaea* did not grow even at high temperature and could pupate only after normal overwintering. We also found such stable larval diapause in several species of *Camponotus s. str.* as well as in *Camponotus aethiops*, *Plagiolepis compressus* and *Tapinoma erraticum*. The diapause larvae of all such species do not take food and grow while in diapause (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

At the same time, in many endogenous-heterodynamic species larval dormancy is unsteady and they all need lower temperature for diapause maintenance. Brian (1955) found that the diapause in autumn *Myrmica* larvae was rather unstable at 25 °C and many of them pupated in this situation. We observed such *thermal termination of diapause* with the pupation of almost all or of only part (depending on species) of diapause larvae in many endogenous-heterodynamic species belonging to the genera *Aphaenogaster*, *Crematogaster*, *Lasius*, *Lepisiota*, *Leptothorax*, *Manica* and *Myrmica*. Unlike the exogenous-heterodynamic species thermal termination of larval diapause in endogenous-heterodynamic ants occurs only at temperatures well above the optimum (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

In many ants, both endogenous- and exogenous-heterodynamic, which are characterised by diapause in the last larval instar, the diapause larvae continue to feed and to grow slowly and can attain a significantly larger size before overwintering. This trait was first recorded by Ezhikov (1929) in *Leptothorax* but it was Brian (1955, 1968) who first understood its significance. He found that

such *diapause growth* plays a peculiar role in the process of caste differentiation in *Myrmica*. The diapause larvae grow in size but do not develop in fact, since their imaginal buds remain the same size and do not differentiate. Only such large diapause larvae well grown in autumn have the potential to develop into female reproductives in spring. Later, the same situation was discovered in *L. nyländeri* by Plateaux (1970). According to our data diapause growth is a property of species belonging to the genera *Diplorhoptum*, *Lasius*, *Leptothorax*, *Lepisiota*, *Manica*, *Messor*, *Myrmica*, *Tetramorium*, *Camponotus* (some species), *Crematogaster* and *Monomorium* (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

Adult diapause

The winter dormancy is inevitable for all adult insects (except most winged reproductives) in a colony of temperate ants since all of them normally live for several years. Therefore, in the life cycle of each individual and of the colony as a whole the diapause arises and is completed repeatedly. Besides perennial social insects a recurrent reproductive diapause is known only in a few solitary species with diapause in the adult stage (Hodek 1979, 1983, 1998).

The adult diapause in endogenous-heterodynamic species is always *obligate* in a sense that it ensues sooner or later under any circumstances (Tab. 1). Environmental cues, such as temperature and photoperiod (in some species), can only advance or delay the onset of diapause to some extent. In many ant species diapause in queens and workers is not stable and can easily be interrupted by the influence of above-optimum temperatures. These species are exactly the same as those listed above that have unstable larval diapause. In ants having a photoperiodic influence on the induction of diapause, the diapause can easily be broken by exposure to long photoperiods. This so-called *photoperiodic termination of diapause* is well known in many insects, especially in species with diapause in the adult stage (Danilevskii 1961, Müller 1965, 1970, Hodek 1983, Danks 1987), and was found in our experiments in all *Myrmica* species studied (Kipyatkov 1972, 1977b, 1981, 1996, Kipyatkov & Lopatina 1997b, 1999) and in *Aphaenogaster sinensis* (Kipyatkov & Lopatina 1990).

At the same time, in some species the adult diapause is extremely stable and cannot be easily terminated by high temperatures and long days. Hölldobler (1961) first observed such stable diapause in queens of *C. herculeanus* and *C. ligniperda* kept at high temperatures. In experiments of Passera (1969) queens and workers of *Plagiolepis pygmaea* that had ceased to lay eggs at optimal temperatures did not start oviposition again without winter chilling. We found very stable queen diapause in the same species that had similarly stable larval diapause (listed above) and also in those species that pass winter without brood, i.e. in species of *Formica* and *Cataglyphis*, and also in *Ponera coarctata* (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

Adult ants, including workers and queens, while in the state of diapause, retain the ability to move freely and actively, to collect food, to feed themselves and other individuals, i.e. to behave as they usually do. The changes in behaviour connected with diapause in adult ants might exist, but this problem has not yet been studied except for one instance: diapause workers of *Myrmica rubra* are less aggressive and disposed to collect food in comparison with non-diapause ants (Kipyatkov 1976b).

During overwintering the diapause adults of most temperate ants are also able to move slowly at above zero temperatures. According to our observations, the cold coma temperatures in most northern ants during overwintering are usually about or slightly below zero. When ants in a cold coma are warmed up they immediately resume normal activity. All this was first observed by Holmquist (1928) in *Formica ulkei*. At the same time, some ants fall into a state of complete stupor, even deep lethargy, during overwintering, and they need a rather long period at warm conditions to awake completely from this cataleptic state. Holmquist (1928) first described this phenomenon in

Camponotus pennsylvanicus workers. We observed the same lethargic dormancy only in *C. herculeanus*, *C. ligniperda* *Harpagoxenus sublaevis* and *Leptothorax acervorum*.

Diapause of adults in insects is primarily reproductive diapause and is characterized by an inactive state of the reproductive system and by the inability of females to lay eggs (Danks 1987). This statement is also correct for ant queens and workers. Diapause queens do not lay eggs and their ovaries contain no eggs and developing oocytes during this period (Kipyatkov & Shenderova 1990, Kipyatkov 1996, Kipyatkov & Lopatina 2002c). Workers in most ants are also able to lay eggs, either fertile haploid eggs developing into males (when the queen is absent in a colony), or infertile trophic eggs (in the presence of a queen) to be used as food for larvae and queens (Hölldobler & Wilson 1990). Following overwintering the workers in cultures without queens normally lay fertile eggs during some period but then stop oviposition and stay in that diapause state for a long time. This was shown in *Myrmica ruginodis* (Brian 1953), *Plagiolepis pygmaea* (Passera 1969), *Leptothorax nylanderi* (Plateaux 1970), *Cataglyphis cursor* (Cagniant 1979, 1980) and in our experiments in *Lasius niger*, *L. flavus*, *L. acervorum*, *Tapinoma karavaievi* and several species of *Formica* (Kipyatkov 1996, Kipyatkov & Lopatina 2002c). Kneitz (1970) described the seasonal cycle in the state of worker ovaries in *Formica polyctena* and found that the percentage of workers with well-developed ovaries attained a maximum in July, but by October the ovaries in all workers became completely undeveloped, which is a good indication of diapause onset. After an exposure to short days the workers of *M. rubra* in cultures without queens did not lay eggs whereas they still produced eggs under long days (Kipyatkov 1976b).

Ambient temperature evidently affects all adult ants in a colony directly. We know nothing about possible indirect effects of temperature cues. However, photoperiodic cues act both directly and indirectly, i.e. by means of some mediators. Evidently, forager ants exiting from the nest for food are able to perceive photoperiodic cues directly, but they do not feed larvae themselves. How can the queens and nurse workers which normally never leave the nest perceive photoperiods? Could the photoperiodic response be realized if there were constant darkness inside the nest? In order to test this situation a special laboratory formicarium with a completely light-insulated nest chamber was constructed, where only workers were allowed to get out to the illuminated section but queens were prevented from doing so by a wire mesh at the exit hole. A quite normal photoperiodic response both during induction and termination of diapause was obtained in colonies of *M. rubra* kept in such formicaria (Kipyatkov 1976b). This means that if only some workers regularly leave completely dark nests it is sufficient for the effective photoperiodic control of diapause both in larvae and queens. We then tested whether workers could control diapause in queens the same way as they govern the development of larvae (see above). It was found that *M. rubra* queens were able to respond to photoperiodic cues themselves but the workers also very strongly affected their queens: non-diapause workers quickly terminated diapause in queens kept under short days but diapause workers only succeeded in decreasing the number of eggs laid by queens under long photoperiods (Kipyatkov 1976b). The physiological state of the queens is, thus, only under partial control of the workers in this species.

This form of social control of diapause was later investigated in some other ant species lacking photoperiodic responses. We used the same four combinations as in experiments with larvae (see above): (1) overwintered workers with overwintered queen(s), (2) overwintered workers with diapause queen(s), (3) diapause workers with overwintered queen(s), (4) diapause workers with diapause queen(s). In three *Formica* species the induction and termination of queen diapause proved to be completely free from worker influence, whereas in other ants (*Lasius niger*, *Tetramorium*) it was under partial control of workers, similar to *Myrmica*: spring workers were able to interrupt the

diapause in queens but autumn workers could not prevent egg-laying by overwintered queens (Kipyatkov 1996).

An entirely new form of social control was also found in *L. acervorum*: spring larvae by unknown means affected queens and workers and terminated their diapause; as a result the workers activated by these larvae were able to provide adequate care and feeding not only for overwintered larvae but also for those larvae that originated from eggs laid by queens that had emerged from diapause; this response led to the unusual appearance of rapid-brood pupae in ant colonies without overwintering (Kipyatkov et al. 1997).

How do the forager workers in *M. rubra* colonies manage to transmit the information on photoperiodic cues from the outside of the nest to queens and nurse workers? Probably they use chemical mediators for this purpose. The existence of one such chemical signal was shown by Kipyatkov (1988, 2001). This substance was called *activator pheromone* since it terminated diapause in larvae and queens, i.e. exerted an activating effect on them. Unfortunately, no further experiments have been carried out in this very promising direction. In particular, we still do not know if there exists also an inhibitor pheromone causing the onset of diapause in larvae and queens.

Acknowledgments

I am very grateful to Elena Lopatina who participated in all field and experimental work as well as in discussion of their results starting in 1980. Several students and members of the Department of Entomology, St. Petersburg University, participated in these long-term investigations in different years. I am sincerely thankful to them all for their efforts and substantial help. I am also much obliged to an anonymous reviewer for his important advice and comments on the manuscript and his great help with the improvement of my English. This work was partially supported by European Union INTAS programme (grant No 94-2072) and Russian Foundation of Basic Research (grants No 94-04-12183, 97-04-48987 and 00-04-49003), as well as by The Council for Grants from the President of Russian Federation and for State Support of Leading Scientific Schools (grant No 00-15-97934).

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