The evolution of seasonal cycles in cold-temperate and boreal ants: Patterns and constraints

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Abstract – *The paper is an introduction to the research programme on physiological, ecological and behavioural adaptation of ants to cold-climate environments developed over the past two decades by the research group at St. Petersburg State University. Temperate and cold-climate ants use two main seasonal strategies: the* strategy of concentrated brood-rearing *(no dormancy in larvae, queens and workers pass the winter in diapause without brood) and the* strategy of prolonged brood-rearing *(overwintering with larvae in diapause, larvae of rapid brood develop from egg to pupa within the same summer season,* slow brood *larvae overwinter and pupate the next summer). Most temperate ants depart from the bang-bang strategy of worker and sexual production predicted by Oster and Wilson (1978) and use the* strategy of two separated bangs, *or else the* strategy of spring rearing of sexuals. *This strategy has several modifications differing mainly in the* time of resource acquisition and allocation in sexuals *(autumn or spring). It is proposed that the success of the founding queens can be the main determinant of the seasonal pattern of sexual production observed in temperate climate ants.*

Simple graphic and mathematical models demonstrate that total annual brood production per colony and per worker should decrease as one goes north. Our field and experimental data on Myrmica *confirm a gradual decrease in annual production of new adults and in the quantity of rapid brood from 50° and 66° N , with this type of brood disappearing entirely at about the level of the Arctic Circle. The model is developed that predicts that the main consequence of the decreasing annual brood production as one proceeds northward is a diminished mature colony size. Our field studies of* M. ruginodis *show a significant decrease in the number of workers per nest between 56 and 69° N. Beyond the latitude at which some larvae are forced to hibernate twice or more, a much sharper decrease in the annual production of new adults and an abrupt decrease in the size of mature colonies are expected. This should result in a two-fold dependence of colony size on latitude. Since too small colonies seem to be unable to survive and reproduce, this will set a northern limit to distribution. The change from monogyny to polygyny and the decrease in the development time from egg to adult are the most plausible adaptation that might buffer the decrease in mature colony size in far-northern ant populations.*

Keywords: ants, cold-temperate, boreal, climates, seasonal cycles, life-history, evolution, constraints, seasonal strategies, sexual production, colony size, latitudinal variation, northern distribution limit.

Introduction

In the most fruitful theoretical study to date of the colony cycle in social insects, Oster and Wilson (1978) focussed on the scale and timing of the resource allocation between worker and sexual production. For annual species such as vespine wasps or bumble bees, they distinguished three main stages in a colony's life cycle: *founding stage* in which the queen initiates the colony and rears the first brood of workers, *ergonomic stage* in which the colony grows rapidly by producing more workers, and *reproductive stage* in which the colony completely switches to production of sexuals. This latter switch is the key to the *bang-bang strategy* of maximizing the colony's fitness, measured as production of sexuals.

In perennial species, such as ants and termites, the founding stage (or phase) is also followed by an ergonomic stage. However, this latter may last for a number of years, during which the colony grows by producing all-worker broods. When it finally comes, the reproductive stage is typically not the last part of the colony cycle, as in following years the colony again produces a mixture of workers and sexuals. For species with perennial colonies, Oster and Wilson likewise predicted a bang-bang strategy, with a strict alteration of ergonomic and reproductive stages each year after the first reproductive stage. The ergonomic stage within each season should be as long as possible, so that more workers are available to raise sexuals during the second part of the year. Such seasonal switches from worker to sexual production, predicted by Oster and Wilson's model, were indeed observed in several tropical and subtropical ants (Bourke and Franks, 1995). For example, in *Solenopsis invicta* this alternation results in clear oscillations in numbers of worker present in a colony (Tschinkel, 1993).

However, perennial colonies living in cold-temperate and boreal climates – henceforth collectively termed "cold climates" – face some special constraints arising from seasonality. In particular, as one proceeds toward either pole the winter becomes more severe, and the warm season during which the colony can grow becomes shorter. The colony must thus invest more resources in workers in order to promote winter survival and subsequent reproduction, yet it has less time in which to amass those resources. Considering this constraint, Oster and Wilson (1978) only predicted that the switch to producing sexuals should occur later in the growing season as the colony overwintering survival rise. They did not go farther in their analysis.

Little attention has been paid to the role of seasonality in life history evolution in ants. For example, in Hölldobler and Wilson's (1990) definitive review "The Ants", seasonality is not even mentioned as a factor shaping the colony cycle. In "Social Evolution in Ants", Bourke and Franks (1995: 336) emphasized the role of seasonality as follows: "*Myrmica* seasonality is therefore a central feature of life history strategy within the genus. However, ant biologists simply do not know if the complex response to seasonality shown by *Myrmica* ants occurs in other ant species, ... because there are few detailed studies of the social physiology of other ants genera." (Bourke and Franks, 1995:336).

Our group at St. Petersburg State University developed a research programme to eliminate this gap in the ecophysiology and social biology of ants. Over the past two decades we have studied the seasonal cycles in more than 80 species belonging to more than 20 genera from different regions of Russia and the former USSR, ranging from warm-temperate to cold-temperate and boreal climate zones. Special attention has been given to the ecophysiology of cold-climates and boreal ants in European Russia between 50°–69° N. Our

field and laboratory studies have allowed us to map the diversity of annual cycles, to reveal the underlying ecophysiological and social mechanisms of control, and to develop ideas on possible pathways in the evolution of the seasonal cycle in ants (Kipyatkov, 1993, 1994, 1996, 2001; Kipyatkov and Lopatina, 2006). To date, our results have been published mainly in Russian.

The following is an introduction to our research programme on physiological, ecological and behavioural adaptation of ants to cold-climate environments over the past two decades. My purpose here is to present a more broadly accessible review and synthesis of our research program around five questions:

1. What seasonal strategies are available to ants use in cold climates?
2. Do the main patterns of seasonal cycles in temperate and boreal climate ants conform to the predictions of Oster and Wilson's model (1978)?
3. How do seasonal cycles change with latitude, especially toward the far north?
4. Do particular social factors constrain such changes and set a limit to northward extension?
5. Are there identifiable physiological and/or ecological adaptations to overcome these constraints?

Two seasonal strategies of brood-rearing in cold-climate ants

Most temperate and all boreal climate ants are heterodynamic, with a period of dormancy (winter diapause) in their annual life cycle (Kipyatkov, 1993, 1996, 2001; Kipyatkov and Lopatina, 2006). All cold-climate ants have adult diapause, so that their queens and workers are capable for overwintering, as are alates in some species. Queens and some workers experience diapause several times in their life. On the contrary, the ability of larvae to undergo diapause is not universal in ants. This is a major factor in seasonal-cycle evolution in these insects.
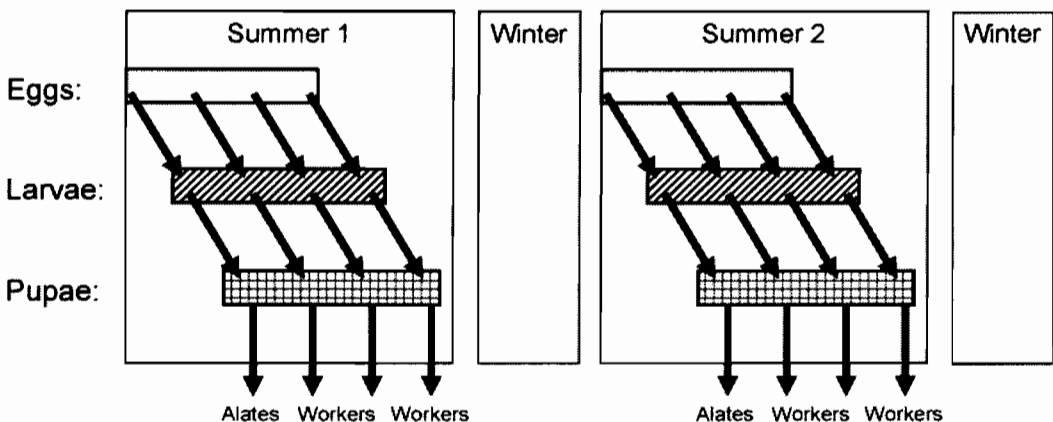

Figure 1. *The strategy of concentrated brood-rearing. Further explanation in text.*

Our own data, as well as those from the literature, support the hypothesis that temperate and cold-climate ants use two main seasonal strategies with respect to brood rearing. The simpler of these is termed the *strategy of concentrated brood-rearing* (Fig. 1). It can be thought

of as a quantitative response to the shorter growing season, or summer, distinguished by the following features:

1. Larvae have no dormancy and complete their development during the summer.
2. The development of all brood stages is thus restricted to the growing season.
3. Only queens and workers are able to undergo diapause and to overwinter.
4. The colony thus passes the winter without brood or adult males.
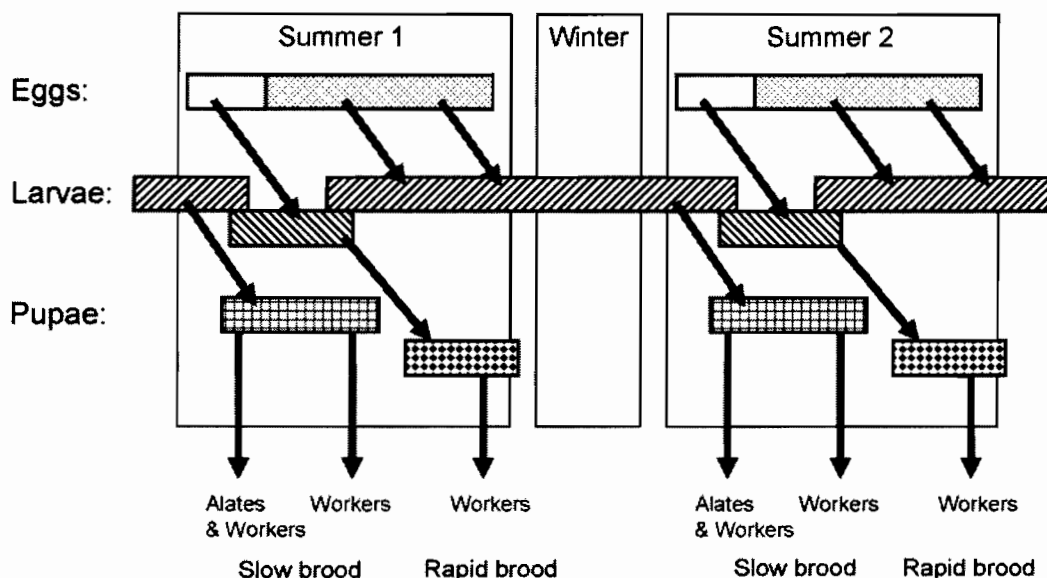
Figure 2. *The strategy of prolonged brood-rearing. Further explanation in text.*

This strategy, however, is not the most common. Rather, temperate and cold-climate ants are more likely to follow the *strategy of prolonged brood-rearing* (Fig. 2), distinguished by the following features:

1. Larval diapause is facultative and controlled by environmental (temperature, photoperiod) and social (worker care, queen influence, pheromones, etc.) factors.
2. Only some larvae develop from egg to pupa within the same summer season without overwintering. This *rapid brood*, or summer brood, yields only workers.
3. A large proportion of larvae delay their development, continue to grow in autumn, overwinter in diapause and pupate the next summer. This *slow brood*, or winter brood, yields both workers and alates.

According to our observations and published data, concentrated brood rearing is characteristic of the tribe Formicini (*Alloformica, Cataglyphis, Formica, Proformica*) and some species of *Dolichoderus, Pogonomyrmex, Ponera* and *Prenolepis* (Kipyatkov 1993, 1996, 2001; Kipyatkov and Lopatina, 2006). The onset of diapause in queens is a central point in the cycles of the *Formica* type, as 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, as this would effectively waste a part of the growing season. At the same time, if diapause ensues too late many larvae and pupae will be caught by the onset of winter and perish. Evidently, concentrated brood-rearing is only adaptive in

cold climates where development times are very short. Among temperate ants, *Formica* species have the shortest developmental times. Furthermore, development is more temperature dependent, which allows *Formica* workers to rear the brood very rapidly when temperatures are high (Kipyatkov and Lopatina, 1993, in press).

The strategy of prolonged brood-rearing, in contrast, has two evident advantages in cold climates (Kipyatkov, 1993): (1) the larvae can be reared from early spring up to late autumn, thus utilizing the entire growing season, (2) the quantity of rapid brood can be changed to adapt to long-term and short-term climatic variations and to the duration of the warm season (see Fig. 5).

The larval stages at which diapause can ensue are extremely variable among ants (Kipyatkov, 1996; Kipyatkov and Lopatina, 2006). We distinguish five species-characteristic patterns: (1) diapause in early (1st–3rd of 5) instars (*Lepisiota, Plagiolepis, Tapinoma*, some *Camponotus*), (2) diapause in middle (2nd–4th of 5) instars (*Camponotus s. str.*), (3) diapause in the late (3rd–4th of 4) instars (*Harpagoxenus, Leptothorax, Temnothorax, Messor*), (4) diapause in the last (usually 3rd) instar (*Manica, Diplorhoptrum, Leptanilla, Monomorium, Myrmica, Tetramorium*), and (5) diapause in all (of 3–6) instars (*Aphaenogaster, Crematogaster, Lasius, Paratrechina, Camponotus (Tanaemyrmex)*).

Seasonal strategies of sexual production

Our field and laboratory data, together with data from the literature, indicate that most temperate ants depart from Oster and Wilson's (1978) predictions regarding seasonal timing of worker and sexual production in two main aspects (Kipyatkov, 1996; Kipyatkov and Lopatina, 2006):

1. Most species raise their alate reproductives not in late summer after the worker brood but quite the contrary, just after overwintering. In a few species the sexuals may develop from the first eggs laid in spring or in most others they originate from the overwintered larvae. In either case, the rearing of alates precedes the main period of worker production in a growing season.

2. The production of sexuals is always accompanied by rearing of workers, often in greater numbers than the sexuals. That is, there is no sharp switch from alate to worker production (see Fig. 5 as an example).

These conclusions are consistent with the two brood-rearing strategies described above (Fig. 1–2), in each of which sexual production precedes production of workers within each growing season (Kipyatkov, 1996, 2001; Kipyatkov and Lopatina, 2006). Since the ergonomic stage is always followed by a long overwintering period which delays the reproductive stage until the beginning of the next growing season, we propose to term such seasonal pattern of sexual production as the *strategy of two separated bangs*, or else the *strategy of spring rearing of sexuals* (Kipyatkov and Lopatina, 2006).

This strategy has been realized in several modifications (Kipyatkov and Lopatina, 2006). In some species, sexuals arise from the first eggs laid by the queen in early spring. This is the case in the tribe Formicini (*Alloformica, Cataglyphis, Formica* and *Proformica*) and the genera *Dolichoderus* and *Pogonomyrmex*. Consequently, the *spring resource acquisition and allocation in sexuals* is characteristic of all these species. However, the species of red wood ants (*Formica s. str.*) also follow the strategy of spring rearing of sexuals but it is based on the *resource acquisition in autumn*. This is because the workers accumulate food reserves in their

fat bodies during the late summer and autumn and use them for the rearing of sexuals in early spring when there is no food sources in the environment (Otto, 1962; Dlussky, 1967; Schmidt, 1974).

Another, much larger group consists of those ant species in which alates develop from overwintered larvae, in most cases from the largest among them (Kipyatkov and Lopatina, 2006). Therefore, these ants also invest in the growth of alates mainly in spring. At the same time, *Leptothorax acervorum*, and probably other species of *Leptothorax*, significantly differ from other ants in that their sexual larvae grow up to the full size in late summer so that they are able to pupate just after temperature rise in spring without any additional feeding. In fact these ants invest in sexuals mainly at the end of growing season. Only pupation and the development of sexual pupae are postponed until the next spring. Thus, this modification of the strategy of spring rearing of sexuals is distinguished by the *resource acquisition and allocation in autumn* (Kipyatkov and Lopatina, 2006).

The strategy of spring rearing of sexuals demands that the colony's annual cycle should be organized to maximize the quantity of diapausing larvae and new workers produced by the end of each growing season. These new workers will aid in the colony's winter survival and will rear alate females and males from eggs or overwintered larvae the next spring. To this end, brood-rearing should start as early as possible and continue as long as possible in the growing season. At the same time, the brood stages and adults present in the nest at the start of winter should be capable of overwintering. Temperate climate ants have solved this problem by evolving appropriate forms of winter dormancy and efficient mechanisms to control its onset and completion (Kipyatkov, 1993). The forms of winter dormancy and diapause in ants, and the physiological and social mechanisms of their control are treated at greater length by Kipyatkov (2001).

The apparent departure of the seasonal patterns of worker and sexual production in temperate climate ants from Oster and Wilson's (1978) predictions might be explained if we consider not only the optimal allocation of resources within the colony but also the reproductive success of sexuals produced. In temperate and particularly cold-temperate climates the colony-founding by queens after the nuptial flight seems to be more successful if it occurs as earlier in the growing season as possible in most ant species. Earlier founding allows the incipient colonies to attain lager size before the winter and thus increases their overwintering survival. The food resources available for new colonies might also be more abundant in the middle of growing season as compared to its end. Consequently, the success of the founding queens can be the main determinant of the seasonal pattern of sexual production observed in temperate climate ants.

Nevertheless, Oster and Wilson's (1978) model seems to be acceptable in general. It should be only corrected a little taking the colony's responses to seasonality into account. The rearing of new workers in summer and autumn really precedes the production of sexuals in spring, but these two "bangs" are separated by the winter in all temperate climate ants. Although the bang-bang strategy might be optimal in the tropical regions, the strategy of two separated bangs appears more appropriate for temperate and cold climate ants due to the increased fitness of early founding queens and other seasonal factors.

Latitudinal variation in the seasonal cycle: Ecological constraints

How do seasonal cycles of ants change as we look further north? A simple graphic model of the strategy of concentrated brood-rearing demonstrates that total annual brood production per worker should decrease as one goes north (Fig. 3). The same is evident from an elementary mathematical model developed below.

Let D be the development time from an egg to an adult ant, S the duration of the growing season during which brood can be reared, N_W the mean number of workers in a colony during the growing season, q_{NW} the proportion of nurses (N_{NW}) among all workers (i.e. N_{NW}/N_W), and L the maximum number of larvae a nurse worker is able to care for simultaneously. Then $q_{NW} N_W$ will be the mean number of nurses per colony, and S/D will be the number of brood periods (i.e. periods from egg to adult) per season. The maximum total annual production of new adults per colony will therefore be (we do not account here for possible mortality of pupae and callows):

$$P_A = q_{NW} N_W L \frac{S}{D} \tag{1}$$

The same value per nurse worker will be:

$$p_A = \frac{P_A}{q_{NW} N_W} = \frac{LS}{D} \tag{2}$$

Let us assume that natural selection favours workers caring for as much brood as they can rear successfully. This sets a limit to the number of larvae that a colony can rear at one time, given the size of its workforce, so that the parameter L is more or less constant. Let us further assume for a certain time that the development time from egg to adult D is also constant within a species, regardless of climate or habitat. Then only the duration of the growing season S varies with latitude in equation 2. Given these assumptions, the mean annual production of new adults per nurse worker p_A must decrease as we go further north. Shortening the growing season results in decreased total annual production of new adults per worker simply because a colony cannot increase the work load of an individual nurse worker. In exactly the same way the work loads could not be increased for foragers and the workers carrying other social functions in a colony.

Species employing the strategy of prolonged brood-rearing face the same constraint. The mathematical description of the colony cycle becomes more complicated if some larvae extend their development into the next year. However, the same conclusion is seen in a simple graphic model, which also serves to illustrate the main patterns of variation in the seasonal cycle according to latitude (Fig. 4).

This graphic model supports the conclusion that species using the strategy of prolonged brood-rearing should see the following changes in the seasonal cycle structure and brood production as one proceeds northward: (1) a decrease in the annual production of new adults per worker, (2) a decrease in the quantity of rapid brood and thus in the proportion of new adults developing from egg to adult during a single growing season, and (3) above a critical latitude, the entire absence of rapid brood.

A

B

C
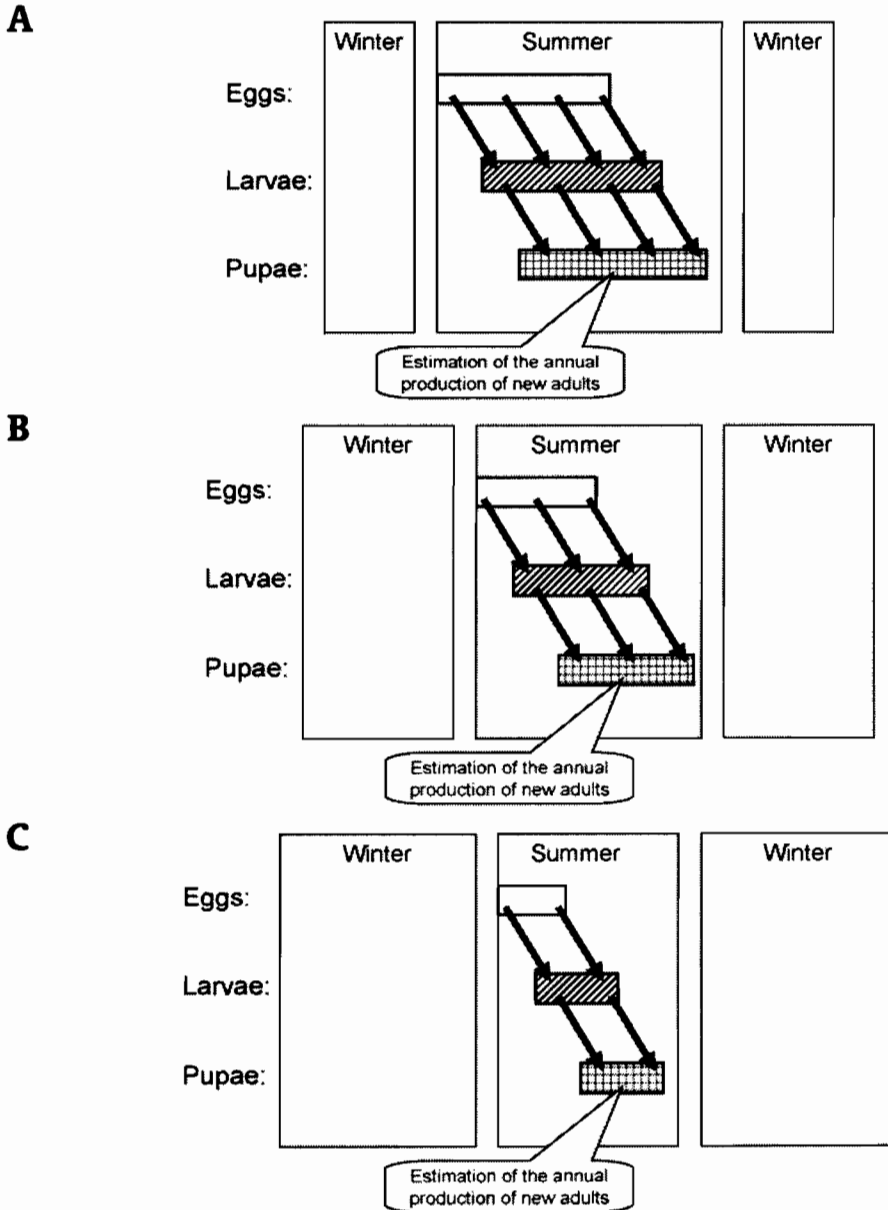
Figure 3. *Effects of a shortened growing season on the total annual production by the colony under the strategy of concentrated brood-rearing.*

The width of the rectangles is proportional to the quantity of the respective brood stages in the colony at any moment, so that their area is proportional to total annual production of the respective brood stages. As a species extends its range to the north and the growing season is progressively shortened (from A to C), the total annual production of new adults decreases, as the colony cannot increase the quantity of larvae that the workers simultaneously take care of.

The literature does not provide field data on intraspecific latitudinal variation in brood production in ants. We first studied the phenology of brood development in three *Myrmica* species at different latitudes. These studies confirmed the three predictions stated above. Our data for *M. ruginodis* – the *Myrmica* species that extends furthest north in the western Palearctic Region – provide estimates of the annual production of pupae in colonies at the latitudes of Vladimir, St. Petersburg and near the Arctic Circle. As seen in Table 1, St. Petersburg colonies produced about twice as many pupae per colony and 25–30% more per worker as did colonies further north. This difference was even greater between colonies at the latitudes of the Arctic Circle and Vladimir: nearly twice as more pupae per worker in Vladimir. Thus, a significant decrease in annual production of new adults between 56° and 66° N is evident in our field data.

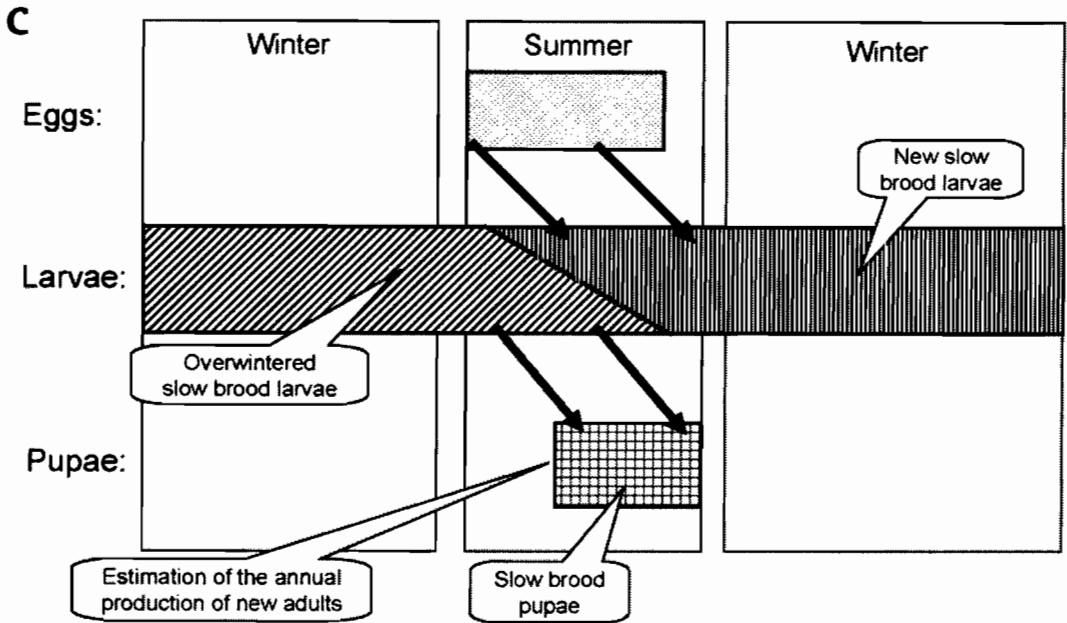**Table 1.** *Annual production of pupae in* Myrmica ruginodis *colonies at different latitudes.*

Latitude	Region and Year	Sample size (number of colonies)	Estimated annual production of pupae	
			per colony (mean ± SE)	per worker
56° 15' N	Vladimir, 1996	27	1504 ± 138 [a,b]	2.45 ± 0.23 [a,b]
59° 20' N	St. Petersburg, 1996	42	1269 ± 347 [c]	1.59 ± 0.43 [c]
	St. Petersburg, 1997	49	1299 ± 343	1.63 ± 0.43
66° 15' N	Chupa, 1997	41	595 ± 111 [a,c]	1.27 ± 0.43 [a,c]
66° 33' N	Poyakonda, 1996	56	715 ± 244 [b]	1.27 ± 0.24 [b]

The mean numbers of pupae produced per colony and per worker are significantly (p<0.05) different according to t-test if are marked by the same letter (p<0.05). Based on the results of unpublished study.

Predictions 2 and 3 are also upheld by our studies of brood-rearing phenology in *M. rubra*, *M. ruginodis* and *M. scabrinodis* at different latitudes. As an example, let us consider the annual brood-rearing cycle of *M. ruginodis* colonies in four regions near Kiev (50° 30' N), Vladimir (56° 15' N), St. Petersburg (59° 20' N) and Poyakonda (66° 33' N) (Fig. 5). Only the larvae of the third (last) instar overwinter. Near Kiev (Fig. 5a) overwintered larvae begin to pupate at the beginning of June, and both workers and alate larvae have all pupated by 10 July. At this time new third-instar larvae (i.e. from eggs laid by queens earlier in spring, not from the previous season) begin to appear in the colony. They develop rapidly, and many pupate during July and August to yield a rapid brood of workers. However, the majority of new third-instar larvae do not pupate in this season. Rather, they enter diapause and overwinter. By the end of September the brood consists entirely of third-instar larvae in diapause.
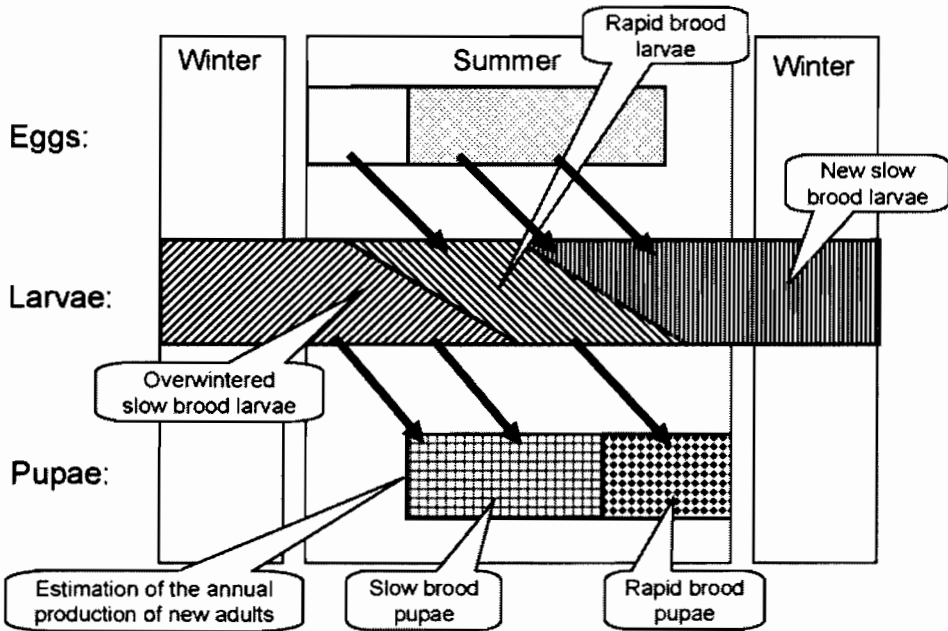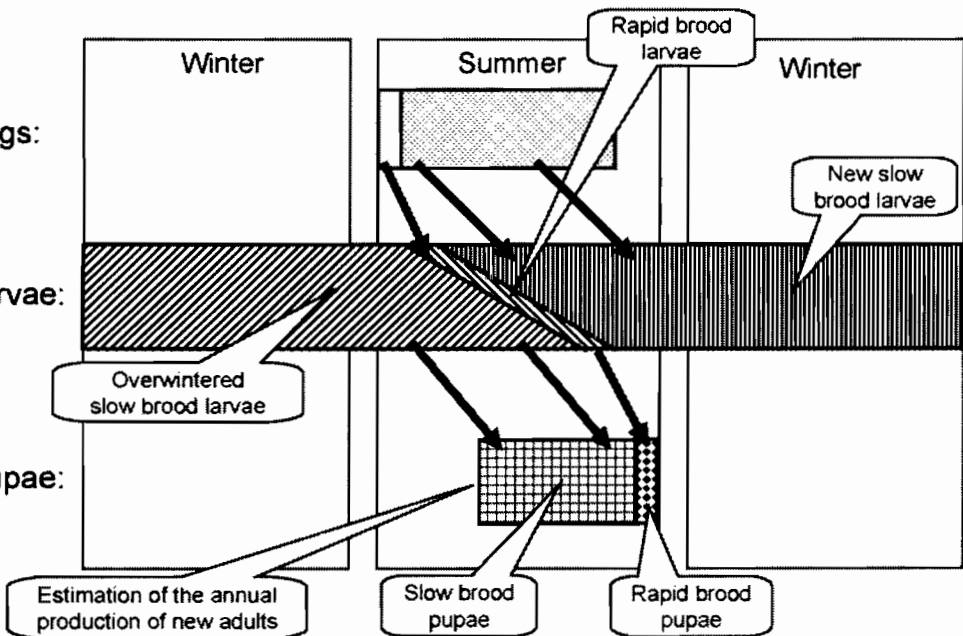
Figure 4. *Effects of a shortened growing season on the total annual production by the colony under the strategy of prolonged brood-rearing.*

C

Winter	Summer	Winter

Eggs:

New slow brood larvae

Larvae:

Overwintered slow brood larvae

Pupae:

Estimation of the annual production of new adults

Slow brood pupae

Figure 4. *Continued.*

As in Figure 3, the width of the rectangles is proportional to the quantity of the respective brood stages in the colony at any moment, and their area is proportional to total annual production of the respective brood stages. Thus, as the growing season becomes shorter (from A to C), the total annual production of new adults and the quantity of rapid brood decreases. Rapid brood disappears completely (C) beyond a certain latitude.

The brood-rearing cycle in colonies near Vladimir and near St. Petersburg (Fig. 5b,c) is similar, but in St. Petersburg overwintered larvae begin pupating a week or more later, and all have pupated by mid-July. The major difference is that near Vladimir and near St. Petersburg pupation of new third-instar larvae stops earlier in August, and the quantity of rapid brood is less. Near the Arctic Circle brood-rearing cycle is even shorter (Fig. 5d). Overwintered larvae begin to pupate only after mid-June, and all have pupated well before mid-July. However, the key difference is that new third-instar larvae do not pupate at all, so that rapid brood is entirely absent.

Our experimental studies upheld field observations (Kipyatkov and Lopatina, 1997a,b; Kipyatkov *et al.*, 2003). One could suggest that the significant differences in rapid brood quantity between *Myrmica* colonies from south and north are due to direct influence of very different local climatic conditions on brood development. To investigate this assumption experimentally we used natural colonies of both *Myrmica rubra* and *M. ruginodis* collected near Belgorod (50.5°N) and near St Peterburg (59° 20' N), in spring before the commencement of oviposition. Experimental cultures were maintained at long (20 h light) or short (12 h) days and 17, 20 or 25°C and the workers were allowed to rear the eggs laid by queens, into either rapid brood pupae or diapausing larvae.

A

B

C

D

□ Larvae 1st & 2nd instar ▨ Larvae 3rd instar ▨ Prepupae ▨ Worker pupae ▨ Pupae of alates
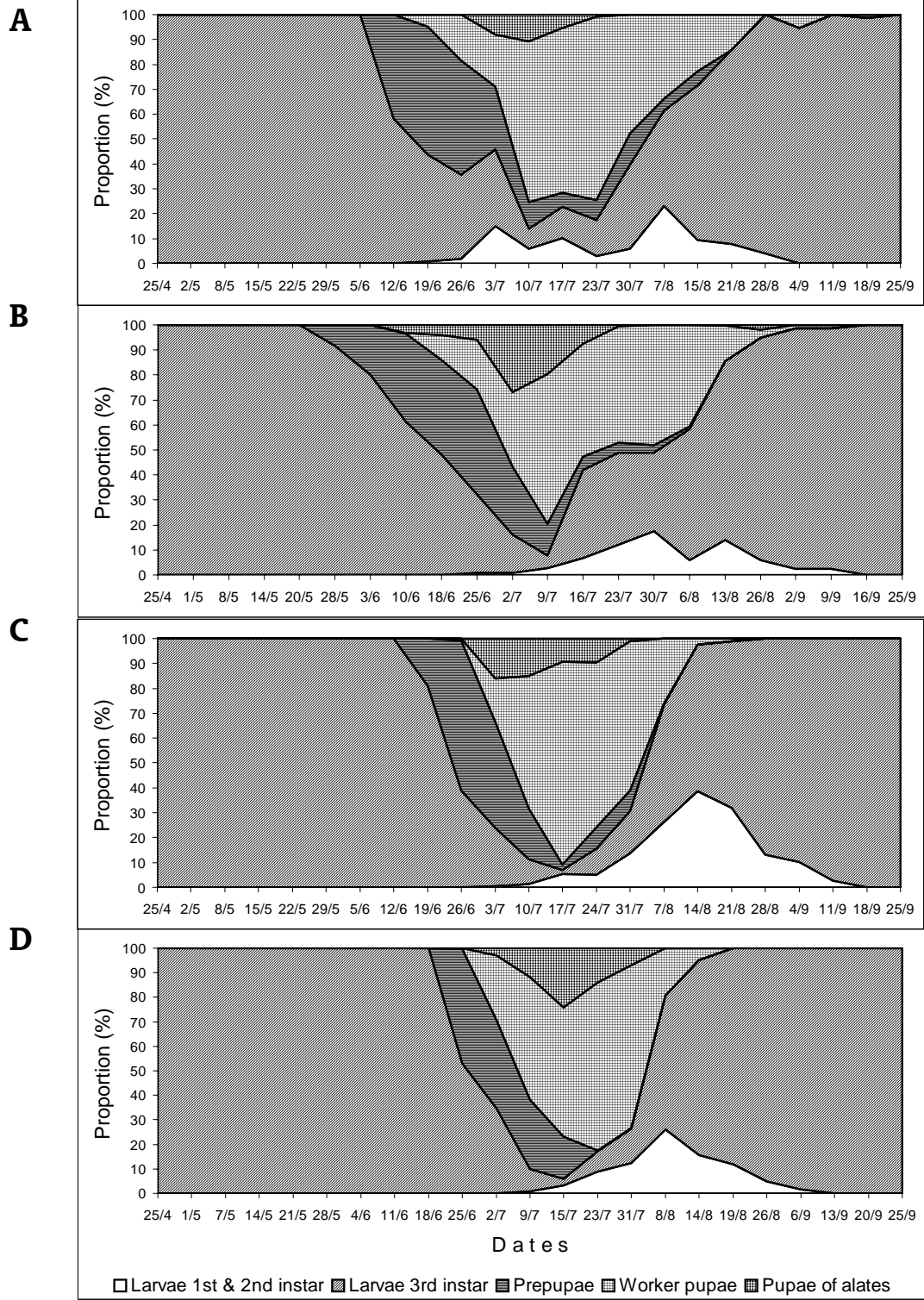
Both queen oviposition and brood pupation eventually ceased under all regimes, but short days and low temperature significantly reduced the periods of oviposition and pupation, and consequently the numbers of rapid brood. The most interesting result was, however, that St. Petersburg colonies differed from those from Belgorod by having far shorter oviposition and pupation periods, and much weaker rapid brood production, at the same temperature and photoperiod. Thus, we concluded (Kipyatkov and Lopatina, 1997a) that the dramatic differences in the colony life cycles between Belgorod and St. Petersburg *Myrmica* populations, are not only the results of responses to distinct local climates, but is also due to local adaptation of the innate endogenous mechanisms which exist in ant colonies (Kipyatkov, 1994, 2001).

In another study (Kipyatkov and Lopatina, 1997b) colonies of *Myrmica lobicornis, M. rubra, M. ruginodis, M. scabrinodis*, and *M. sulcinodis* collected near Poyakonda (66° 33' N) at the end of June were maintained at 22.5 or 25°C and the day-lengths of 24, 17 and 12 h. All or almost all larvae pupated regardless of photoperiod and temperature. New larvae emerging from the eggs laid by queens developed up to the final instar and fell in diapause independently of the day-length and temperature. Thus, *Myrmica* colonies from the latitude of the Arctic Circle failed to produce rapid brood even under long days and optimal temperature.

In summary, our field and experimental data confirm a gradual decrease in the quantity of rapid brood in *Myrmica* along a latitudinal gradient from south to north, with this type of brood disappearing entirely at about the level of the Arctic Circle.

Latitudinal variation in the seasonal cycle: Social constraints

The main consequence of the decreasing annual brood production as one proceeds northward is a diminished mature colony size and this may set the northern distribution limit of cold-climate ants. To show this let us consider the growth of a colony up to its mature, i.e. maximal size. As an incipient colony grows in size it passes through the three periods characterised by increasing, constant, and decreasing returns to scale (Oster and Wilson, 1978). The causes of this final decrease in growth rate have been considered by Oster and Wilson (1978) at greater length. Here it is most important that, ultimately, net colony growth should fall to zero. It means that the colony reaches its mature and maximal size, and is in a balanced state when the annual increase in worker number is approximately equal to their loss due to death, predation and other causes. A lot of factors, including queen's egg-laying capacity (for monogynous colonies), resource abundance, competition, and predation, are determinants of the mature colony size (Oster and Wilson, 1978). However, my purpose here is to consider the possible role of seasonal factors as determinants of colony size. Therefore, let us assume for a certain time that all other factors are fixed except seasonality.

Figure 5. *Field data on brood-rearing phenology in* Myrmica ruginodis *colonies living at four latitudes.*
A. *Near Kiev (50° 30' N)*; B. *Near Vladimir (56° 15' N)*; C. *Near St. Petersburg (59° 20' N)*;
D. *Poyakonda, near the Arctic Circle (66° 33' N). The vertical width of each zone denotes the proportion of the respective brood stage in the whole colony brood (except eggs) at the moment. Rapid brood is less numerous in St. Petersburg and completely absent in Poyakonda. However, even in Poyakonda all overwintered larvae pupate during the next growing season. Based on the results of unpublished study.*

We should consider a mature colony in a balanced state. Let T_H be the half-life of adult workers, and P_W the annual production of new workers in a colony. The mean number of workers in a colony at equilibrium is therefore

$$N_W^* = 2T_H P_W \tag{3}$$

Evidently, if P_W decreases for some reason, then colony size would decrease as well, and vice versa, *other circumstances being unchanged*.

The annual production of workers is a part of the total production of new adults in a colony,

$$P_A = P_W + P_R \tag{4},$$

where P_A is total production of new adults and P_R is production of reproductives (queens and males). If q_W is the proportion of workers in the total annual production of new adults (i.e. $q_W = P_W/P_A$), then

$$P_W = q_W P_A \tag{5}$$

If we know the annual production of new adults per nurse worker p_A and the proportion of nurses among all workers in a colony q_{NW}, we can calculate the total annual production of new adults as

$$P_A = q_{NW} N_W p_A \tag{6}$$

Then the substitution of P_A in 5 by equation 6 gives us

$$P_W = q_W q_{NW} N_W p_A \tag{7}$$

According to equation 2, the annual production of new adults per nurse worker p_A is equal to LS/D. Accordingly,

$$P_W = q_W q_{NW} N_W \frac{LS}{D} = \frac{q_W q_{NW} N_W LS}{D} \tag{8}$$

The main consequences of this equation are analysed in the next section. For now, let us note that when the length of the growing season S decreases, the annual production of new workers in a colony P_W should decline, which according to equation 3 should result in a reduction of the mean equilibrium number of workers in a colony N_W^* if all other parameters are held constant. This prediction needs to be tested in the field.

We have not found data in the literature on intraspecific variation in colony size according to latitude. However, our own studies of M. ruginodis show a significant decrease in the number of workers per nest between 56 and 69° N (Table 2). These are consistent with the prediction from the equations 8 and 3.

Kaspari and Vargo (1995) found a positive correlation between colony size and latitude by a broad comparison of ant species from tropical to cold-temperate region. These authors argued that Bergmann's rule holds true for social insects when colony size is regarded as the body size of a superorganism. They suggested that colony size in all social insects should be generally smaller in the tropics than in temperate regions and put forward the hypothesis that larger colony size can buffer harsh seasonal environments of colder regions.

Table 2. *Latitudinal variation of worker number in* Myrmica ruginodis *colonies at different latitudes.*

Latitude	Region and Year	Sample size	Number of workers per colony			
			Min	Max	Mean	SE
56° 15' N	Vladimir, 1996	27	137	2333	613 [a]	86
59° 20' N	St. Petersburg, 1996	42	240	1961	799 [b]	63
	St. Petersburg, 1997	49	151	1830	798 [c]	58
66° 15' N	Chupa, 1997	53	41	4596	469 [b,c]	87
66° 33' N	Poyakonda, 1996	27	56	1844	565 [b,c,d]	76
68° 47' N	Murmansk (Fregat), 2001	32	135	867	398 [a,b,c]	46
69° 11' N	Murmansk (Polyarny), 2001	15	143	956	332 [a,b,c,d]	40

The mean numbers of workers per colony are significantly ($p < 0.05$) different according to t-test between Vladimir (a), St. Petersburg 1996 (b), St. Petersburg 1997 (c) and the sites marked by the same letters. The means for Poyakonda and Polyarny are also significantly different (d). Based on the results of unpublished study.

This conclusion seems somewhat opposing to the prediction from the model and field observations discussed above. However, simple comparison between the two approaches might not be possible for two reasons. First, Kaspari and Vargo made interspecific comparison of colony size in relation to latitude. They did not consider intraspecific variation which was the subject of our study. However, the intraspecific variation may not obligatory follow the interspecific patterns and vice versa. Second, Kaspari and Vargo mainly compared between tropics and temperate regions, whereas our research was made in much colder regions, beyond 56° N. We suppose that in the warmer regions the duration of growing season may not be so limiting as in cold-temperate and boreal zones so that colony size mostly depends on other factors.

How is the seasonal cycle expected to evolve in any ant species that extend their range beyond the point at which rapid brood disappears entirely, so that the development of individual larvae continues into a second or even further growing seasons? Such life cycles are common among Arctic and Antarctic arthropods, which may continue growth and development over several years (e.g. Danks, 1981). Larvae of several ant species were experimentally shown to be capable of diapausing yet again after overwintering if faced with low temperature, food shortage and/or inadequate worker care (Kipyatkov *et al.*, 1996, 1997; Kipyatkov and Lopatina, 1999). However, do boreal and subarctic ants really use the opportunistic strategy of extending larval development for more than one year? It is our hypothesis that such a strategy is unavailable to them on account of social constraints, which therefore set a northern limit to the distribution of ants.
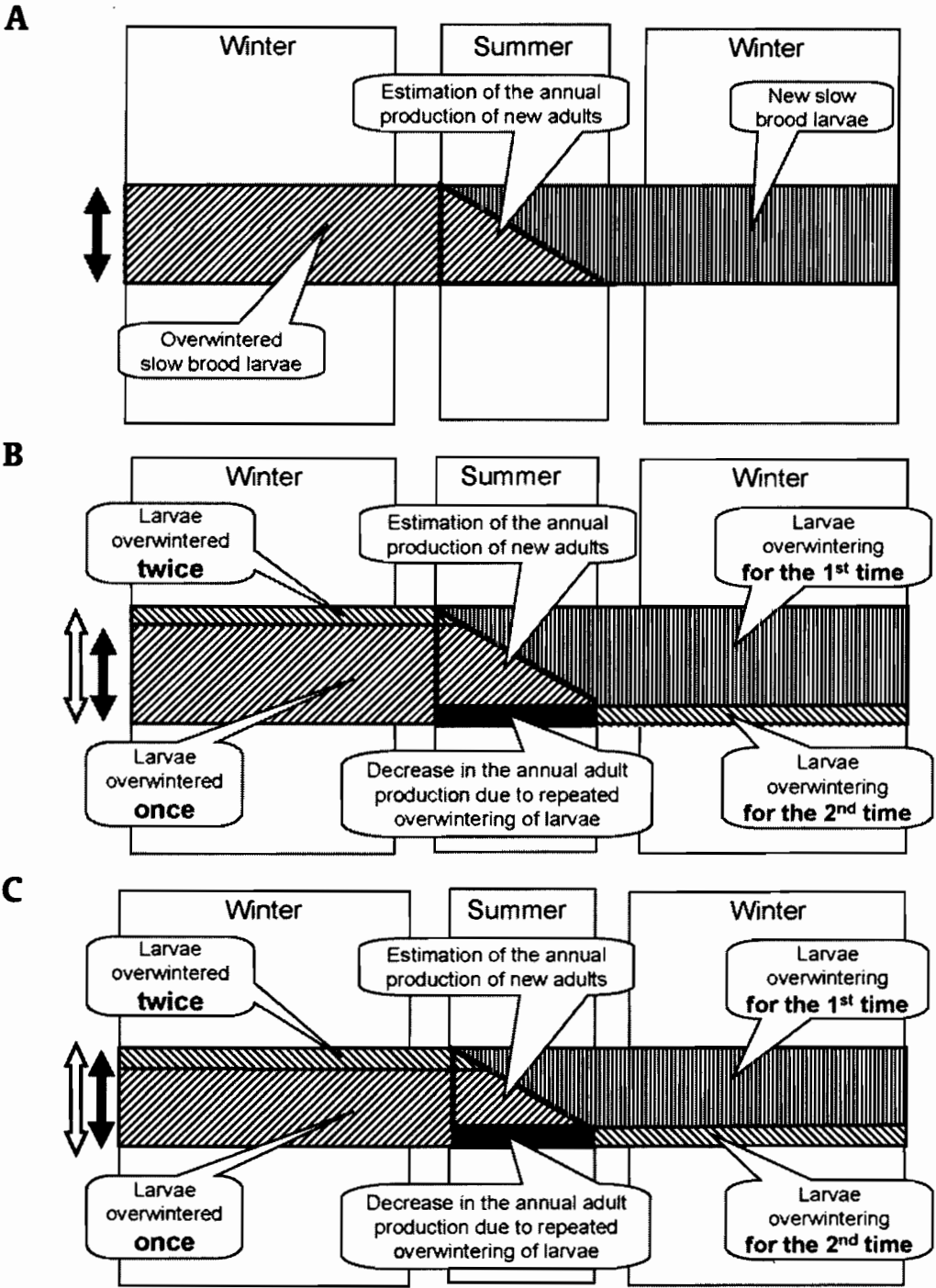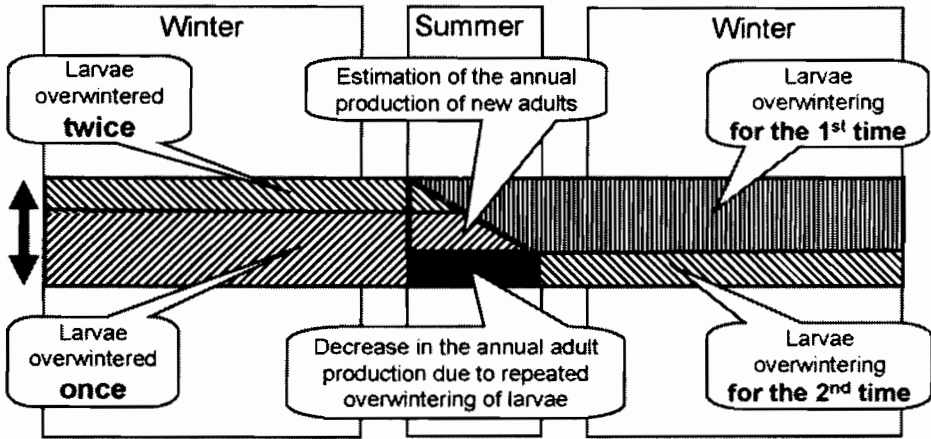
A

B

C

Figure 6. *Graphic model of a seasonal cycle with repeated overwintering of some larvae.*

D

Winter	Summer	Winter

Larvae overwintered **twice**

Estimation of the annual production of new adults

Larvae overwintering **for the 1st time**

Larvae overwintered **once**

Decrease in the annual adult production due to repeated overwintering of larvae

Larvae overwintering **for the 2nd time**

Figure 6. *Continued.*
The width of the rectangle is proportional to the quantity of larvae in the colony at any moment. An arrow on the left denotes the maximum number of larvae in the colony where this is limited by the nurse workers' capacity to rear them.
A. All larvae overwinter once. B. If some larvae overwinter a second time, this leads to an increase in the total number of larvae (white arrow). C. Repeated overwintering of some proportion of larvae is only possible at the expense of the total quantity of larvae that pupate during summer (a triangle), hence of the annual production of new adults. D. The decrease in annual production of new adults when the growing season shortens further.

This hypothesis, again, is illustrated by means of a graphic model (Fig. 6). The main assumption of this model is that the maximum quantity of larvae in a colony is limited by the nurse workers' capacity to rear them. Thus, the maximum quantity of larvae per worker is fixed (Fig. 6a). If the growing season is shortened, there comes a point where some overwintered larvae cannot complete their development during the second season. If they overwinter a second time, the total number of larvae in the colony is increased (Fig. 6b). Such an increase is maladaptive, however, as the workers are presumably already rearing as many larvae as they are able. A second or further diapause of some proportion of the larvae is only possible at the expense of a decrease in the total quantity of larvae that pupate each year, that is, in the annual production of new adults (Fig. 6c). In such a situation the annual production of new adults decreases not only because fewer larvae can complete their development during the shorter growing season but also due to the increase of the proportion of larvae that overwinter twice or more (Fig. 6d, 7).

Consequently, when an ant species extends into the far north the annual production of brood and new adults gradually decreases, leading to smaller colony size. Beyond the latitude at which some larvae are forced to hibernate twice or more, a much sharper decrease in the annual production of new adults and an abrupt decrease in the size of mature colonies are expected. This should result in a two-fold dependence of colony size on latitude in species using the strategy of prolonged brood-rearing (Fig. 8).

Since too small colonies seem to be unable to survive and reproduce, this will set a northern limit to distribution. In such a way, the social mode of life and the dependence of

brood on the worker care hinder the repeated hibernation of a noticeable proportion of larvae and thus make an opportunistic seasonal strategy unfeasible for ants.
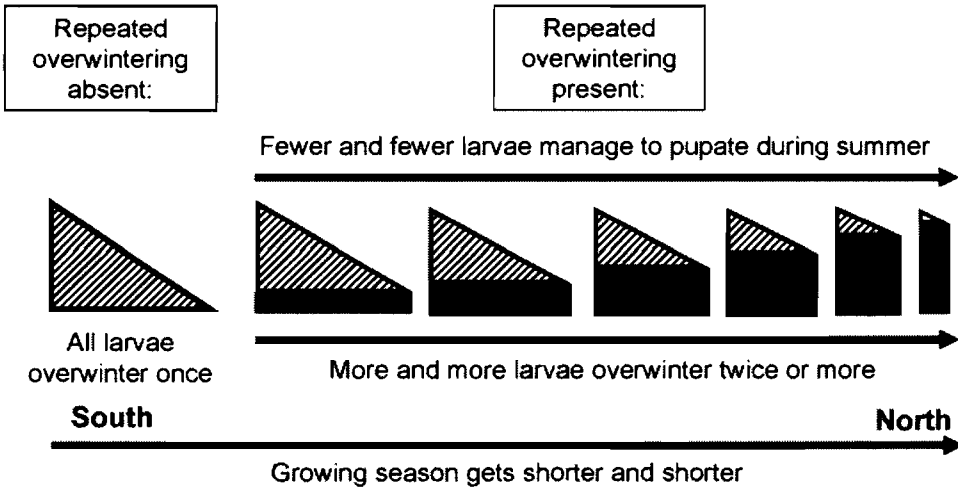
Figure 7. *Effects on the annual production of new adults of the proportion of larvae that overwinter more than once.*

Here the annual production of new adults decreases not only because fewer larvae can complete their development during shorter growing season but also due to the increase of the proportion of larvae that overwinter twice or more.
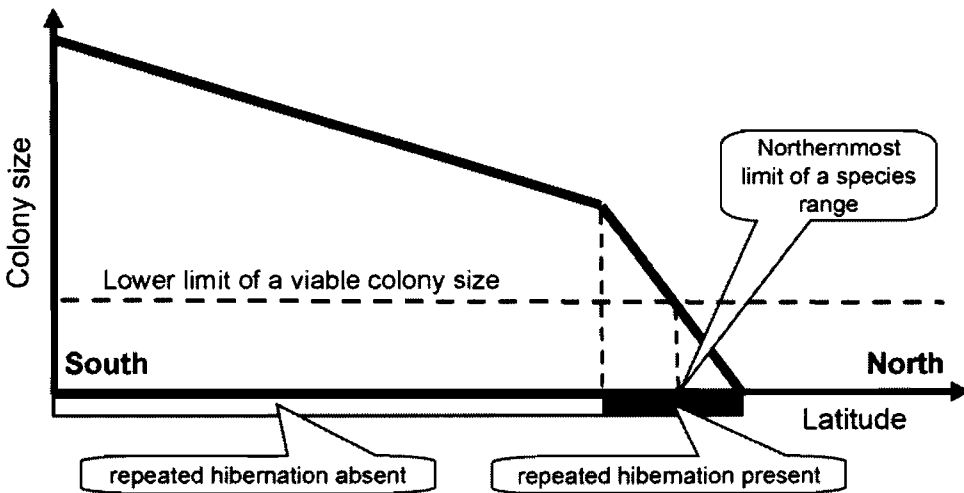
Figure 8. *Two-fold dependence of colony size on latitude under the strategy of prolonged brood-rearing.*

As a species extends north of the latitude at which some larvae are forced to hibernate twice, the annual production of new adults is sharply decreased, leading to an abrupt decrease of the mature colony size. This is expected to set the northern distribution limit of cold-climate ants.

From this we can predict that most larvae should finish development and pupate during the second summer of their life even in the northernmost ant populations. Our field studies on *M. ruginodis* appear to uphold this prediction (Kipyatkov and Lopatina, 1997b; Kipyatkov *et al.*, 2003). In the Arctic Circle region all overwintered larvae in *M. ruginodis* colonies pupate during the growing season, as it is seen on Figure 5d. However, we have not yet examined more northern populations of this species, so that our hypothesis is only partly tested.

Possible adaptations to overcome ecological and social constraints

What factors might buffer the decrease in mature colony size in far-northern ant populations? Returning to equations 8 and 3, a decrease in N_w^* due to a shortening of the growing season S could be compensated for by changing other parameters that we have held constant up to now:

1. Increase in the lifespan of workers, i.e. in their half-life (T_H). Unfortunately, no data exist on the intraspecific latitudinal variation in worker lifespan in ants. An extension of worker lifespan might be possible if senescence happens mainly in summer due to the low metabolic load in winter. For example, honeybee workers live longer when they experience winter hibernation. It seems unlikely, however, that worker longevity would substantially increase under the harsh far-northern conditions of relatively cool summers and very long, cold winters. Much higher mortality due to the adverse abiotic environments might compensate for increased worker longevity in far northern habitats.

2. Increase in the proportion of workers in the annual production of new adults (q_w). Colonies are certainly capable of altering this proportion. However, increasing worker production at the expense of alate production appears maladaptive, as it represents a decrease in the colony-level reproductive success.

3. Increase in the number of larvae that a nurse worker can care for simultaneously (L). It is hard to see how this parameter could be increased, as one assumes that natural selection has already brought it to its maximum level.

4. Increase in the proportion of nurse workers in the colony (q_{NW}). This is an unlikely candidate, as there is a necessary trade-off in the allocation of worker force to brood rearing and other social functions that are vital to the colony's survival and reproduction. For example, it seems hardly possible to increase the forager efficiency in order to reduce their number because the food resources are not more abundant and the foraging is more limited daily and seasonally by unfavourable climatic conditions in the far northern habitats.

5. Change from monogyny to polygyny and/or the increase of queen number in polygynous colonies in northern habitats. Simultaneously, colonies may become seasonally polydomous and experience the fission during summer and the fusion before the winter to make larger groups more capable of overwintering. This could really be an appropriate way of adaptation in some species. We found extremely polygynous and large colonies of *Leptothorax acervorum* near Poyakonda (66° 33' N) and *Myrmica rubra* near Umba (Kola Peninsula, 66° 42' N). Some colonies included several thousands of workers and dozens or even hundreds of queens. Moreover, sometimes there were no distinct boundaries between numerous colonies of *L. acervorum* nesting in the wood under the bark along a long dead tree trunk, which is a sign of possible unicoloniality. However, this is not the case in *M. ruginodis*. According to our observations the colonies of this species are monogynous or weakly polygynous in all habitats studied from Belgorod and Kiev (50° 30' N) to Murmansk (68° 47' N).

6. Decrease in the development time from egg to adult (*D*). Curiously enough, this seems like the only plausible adaptation to this end that is experimentally studied in far-northern ants. According to our data a decrease in the average development time from egg to adult could evolve through: (a) an increase in the development rate, (b) the preference for warmer nest sites, and/or (c) special design features of nests destined to concentrate incident sunlight.

The most surprising general result, perhaps, is that brood development in far-northern populations is more rapid over a rather broad temperature range than it is in more southern populations. In other words, given the same temperature conditions, northern ants are able to rear their brood in a shorter time (Elmes *et al.*, 1999; Kipyatkov and Lopatina, 2002; Lopatina *et al.*, 2002; Kipyatkov *et al.*, 2004). This is because brood development in northern populations is more temperature dependent, i.e. characterised by higher slopes of regression lines of development rate on temperature. The sum of effective temperatures decreased with the advance to North. The higher slopes were always associated with higher thermal thresholds for development. This is mainly due to latitudinal variation in the thermal reaction norm for brood development. Thermal reaction norms of ant colonies usually change according to the local climate in such a way that metabolism (Nielsen *et al.*, 1999), egg production, brood rearing, and the growth and development of individuals become more temperature-dependent in more severe environments. As a result, the physiological response increases at higher temperatures but decreases within lower temperature ranges (Kipyatkov and Lopatina, 2002; Kipyatkov *et al.*, 2004, 2005). It means that northern *Myrmica* colonies rear brood under lower temperatures evidently worse in comparison with ants from southern regions. In fact *Myrmica* colonies from northern populations need on average higher temperatures in their nests for successful production of new adults as compared to southern ants.

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