

The influence of temperature on brood development in the incipient colonies of the ants *Camponotus herculeanus* (L.) and *Camponotus xerxes* Forel (Hymenoptera, Formicidae)

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Abstract - *Dealated queens of Camponotus herculeanus from the White Sea region and C. xerxes from Karakum desert (Turkmenistan) just after their nuptial flight were kept singly in Petri dishes with damp cotton wool at long days (20 h) and constant temperature from 23 to 30 °C or 12-hours thermoperiods 14/32, 16/30 and 20/30 °C. The food (sugar syrup and crushed cockroaches) was added only after the first worker emergence. Queens were inspected every other day with the full brood census. After the laying of initial egg batch queens ceased oviposition and reared the first brood larvae. The second maximum of egg number coincided with the emergence of first brood workers. Nearly all first brood larvae of C. herculeanus pupated independently of temperature but in the second brood only a few larvae completed their development and exclusively at 25 and 30 °C and thermoperiods; the rest entered diapause. The mean developmental time of the second brood larvae was about twice greater than in the first brood larvae. The total number of pupae reared was clearly temperature dependent being the greatest at 30 °C and at thermoperiods. In contrast to C. herculeanus the successful development of C. xerxes first brood was possible in an extremely restricted temperature diapason (between 26 and 30 °C) and appeared to be much more temperature dependent. Thermoperiods were proved to be much more favourable for the development of both species. They accelerated development (by 14-20%), increased queen productivity and brood survival, promoted more prolonged development without diapause in comparison with constant temperatures that were equal to the mean daily temperatures of the respective thermoperiods. There are apparent differences between two species studied in the temperature adjustment of their development. C. herculeanus has much lesser temperature thresholds (theoretical minimums) of development for all ontogenetic stages and is able to develop much more rapidly and at the inferior temperature. These differences are in good agreement with geographical distribution of the two species and could, therefore, be considered as adaptations to different climates. The extremely elevated temperature thresholds of C. xerxes brood stages are similar to the thresholds of other ants from Turkmenistan.*

Keywords: Formicinae, oviposition, pupation, developmental rates, diapause, thermoperiod, temperature thresholds, distribution.

Introduction

The influence of temperature on the development of ants remains insufficiently investigated despite of the obvious importance of such studies for more thorough understanding of ecology, geographical distribution and site preferences of various ant species. Temperature is one of the most significant factors also in the regulation of annual cycles in ants (Kipyatkov, 1990, 1993).

The data on this subject existing in ant literature are very scarce. Many authors usually report on the duration of development of some brood stages under any temperature that is not sure to be even stable or accurately measured at all (Bruder and Gupta, 1972; O'Neal and Markin, 1975; Plateaux, 1980; Suzzoni et al., 1986; Basalingappa et al., 1989). Moreover, it is even impossible to find an indication of a temperature used by authors in some papers (Onoyama, 1981; Ulloa Chacón and Cherix, 1988; Nuhn et al., 1992; Chang-Lu and Jian Wu, 1992).

Besides our three papers (Lopatina and Kipyatkov, 1990a,b; Kipyatkov and Lopatina, 1993) we are aware of only two works in which the influence of temperature on ant developmental rates was investigated in detail and with the use of adequate technic. G. Elmes and J. Wardlaw (1983) detected the rates of development of large overwintered larvae in four species of the genus *Myrmica* (*ruginodis*, *rubra*, *scabrinodis*, *sabuleti*) under 16, 18, 20, 22.5 and 25 °C. The rate of larval development was shown to decrease in a row of species *M. ruginodis* - *M. rubra* - *M. scabrinodis* - *M. sabuleti*. The results agree with the ecological distribution of these species in the South of England: *M. ruginodis* prefers the most cool biotopes and *M. sabuleti* chooses the most warm sites.

The impact of temperature on incipient colony growth and developmental rates in the fire ant *Solenopsis invicta* was thoroughly studied by S. D. Porter (1988) across a broad range of constant temperatures. The development of the brood is possible between 24 and 36 °C, the optimum being around 32 °C. The theoretical minimum for brood development (i.e. the lower temperature threshold) is shown to be at 17 °C.

The temperature in natural ant nests is not, however, constant but fluctuates according to daily climatic rhythms especially expressed in spring time and in the open nest sites. In spite of the apparent significance of the phenomenon the role of daily temperature rhythms in ant ecology and development regulation scarcely investigated (Buschinger, 1973; Elmes and Wardlaw, 1983; Lopatina and Kipyatkov, 1990a,b; Kipyatkov and Lopatina, 1993).

The aim of this work was to study the influence of temperature conditions including daily thermoperiods on brood development and survival during the incipient colonies establishment by the young queens of *Camponotus herculeanus* (L.) and *Camponotus xerxes* Forel. The analogous work carried out by Z. A. Zhigul'skaya (1987) on *C. herculeanus* could not be compared with our results because of the lack of elementary statistical data treatment in her paper.

The ants of the genus *Camponotus* have greatest species diversity in tropical regions. *C. herculeanus* belongs to the subgenus *Camponotus s. str.* It is the only species in this large genus that has penetrated to the North up to the forest-tundra zone - the northern border of ant occurrence (Arnoldi, 1967). The study of temperature parameters of *C. herculeanus* development and its ecological comparison with more southerly distributed *Camponotus* species seems, therefore, to be of exceptional interest. One of such southern species is *C. xerxes* occurring in arid regions of Turkmenistan (Karakum desert), Afghanistan and Iran; it belongs to another subgenus *Tanaemyrmex* (Dlusskii and Soyunov, 1989). All species of *Camponotus s. str.* subgenus are found in forest and forest-steppe zones whereas *Tanaemyrmex* species are confined to arid regions - steppes and deserts (Arnoldi, 1967; Dlusskii and Soyunov, 1989).

According to our earlier investigations (Kipyatkov, 1990, 1993) *C. herculeanus* is characterized by endogenously heterodynamous annual cycle: the duration of the period of oviposition and larval development is limited, diapause is obligate and development ceases sooner or later even under optimal circumstances; the hibernation is indispensable for diapause termination and development renewal. In *C. xerxes*

at optimal temperature (26-27°C) oviposition and development go on continuously and unlimitedly only with some variation of eggs and larvae numbers. The decrease of temperature results in a break of development but it can be easily resumed after the rise of temperature. This is so-cold exogenously heterodynamous annual cycle (Kipyatkov, 1990, 1993).

Material and Methods

Dealated queens of *C. xerxes* were collected just after their nuptial flight in the end of April 1990 in Central Karakum desert (the field station of the Institute of Deserts, Academy of Sciences of Turkmenistan). In the laboratory they were maintained in photothermostats under long days (20 h.) and constant temperatures of 23, 25, 26.5 and 30°C or at 12-hours thermoperiods 16/30°C and 20/30°C with mean daily temperatures of 23 and 25°C respectively.

Young queens of *C. herculeanus* were collected by I. R. Pozdnyakov after their mating flight in July 1991 on Srednii Island in the White Sea (Marine Biological Station of the St. Petersburg University). During their first summer queens were kept at room temperature that was inadequate for normal development. Queens have, therefore, reared only 2-3 larvae per capita. After the hibernation in a refrigerator queens were maintained without larvae in photothermostats under 20-hours days and constant temperatures of 23, 25, 28 and 30°C or at 12-hours thermoperiods 16/30°C and 14/32°C with mean daily temperatures of 23°C.

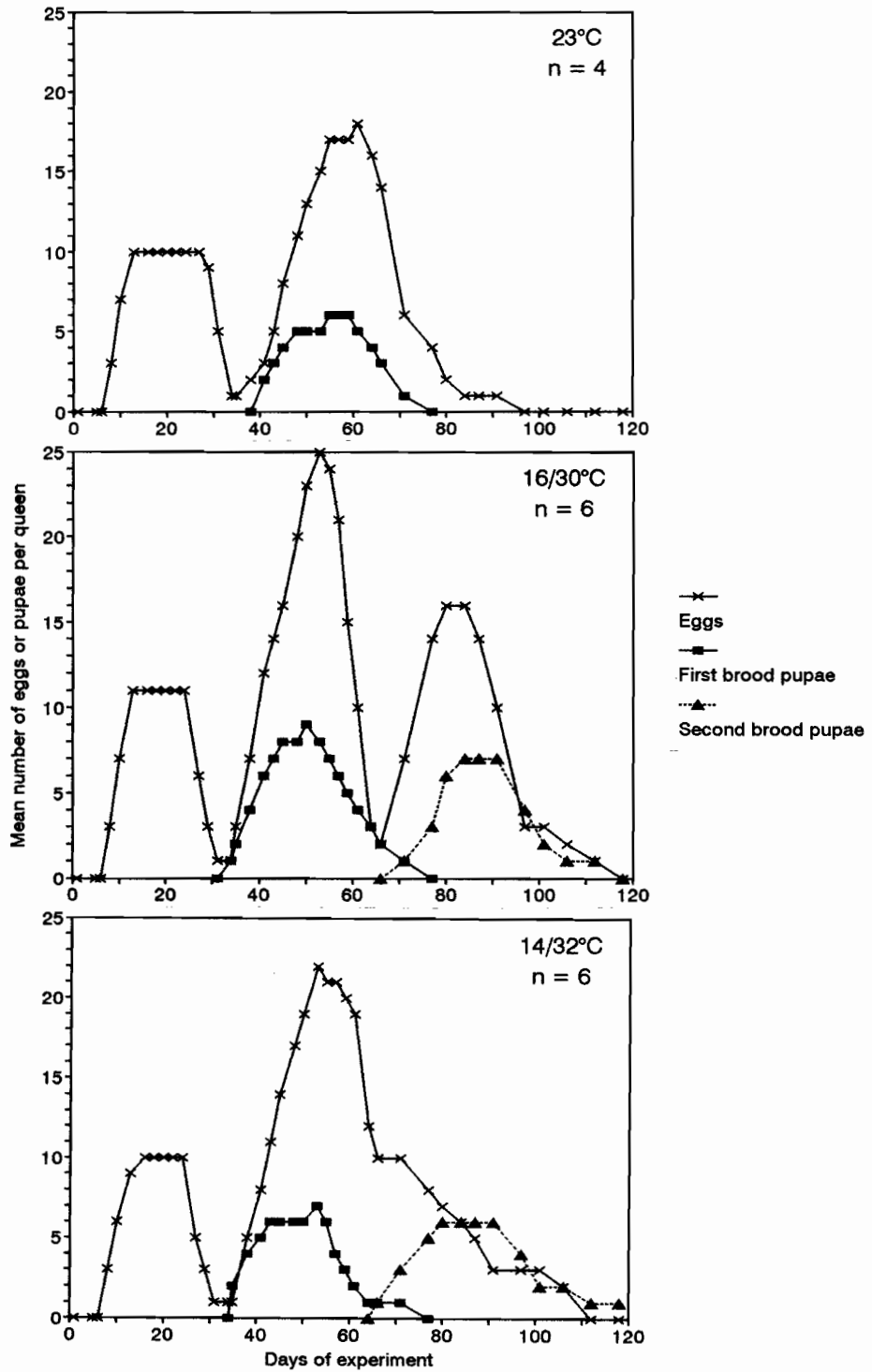
All queens were kept singly in Petri dishes (d. 90 mm) with damp cotton wool and without food. After the emergence of the first worker ants were fed with sugar syrup and crushed cockroaches. Queens were inspected every other day with the full census of eggs, larvae, pupae and workers. From these counts the durations of all ontogenetic stages were obtained.

Results and Discussion

In all experimental regimes regular variations of oviposition rate and corresponding changes in egg number were observed in *C. herculeanus* queens (Fig. 1). After the first amounts of eggs were laid queens ceased oviposition and the egg number gradually fell almost to zero. The second maximum of egg number coincided with first workers emergence. Because of this egg-laying periodicity all the brood was normally segregated into two parts: (1) *first brood* developing from the initial egg batch, and (2) *second brood* developing from the eggs laid after the renewal of oviposition.

The larvae in the first brood have pupated almost completely under all experimental regimes. In the second brood only a few larvae finished their development at 28 and 30°C exclusively; the rest of larvae entered diapause (Tab. 1). The beginning of the second brood larvae pupation coincided with the emergence of the last workers from the first brood pupae (Fig. 1).

The quantity of the brood reared by queens in different regimes was explicitly dependent upon temperature conditions (Tab. 1). The higher was the temperature, the more pupae and workers were raised. The mean number of first brood pupae reared per queen was the greatest (11.2) at 28°C and the least (5.8) at 23°C. Under thermoperiods queens reared more first brood pupae than at 23°C. The total number of pupae (first and second broods together) was much more temperature dependent: it increased from 5.8 per queen at 23°C to 15.2 at 30°C and was the greatest (18.3) under 16/30°C. The lesser mean pupae production under 14/32°C (15.7) is most probably connected with unfavourable influence of too high temperature of 32°C. The number of diapausing larvae did not change so significantly in connection with temperature variation. It was on average the greatest (21.5-22.7) under thermoperiods and the least (10.2) at constant 30°C.



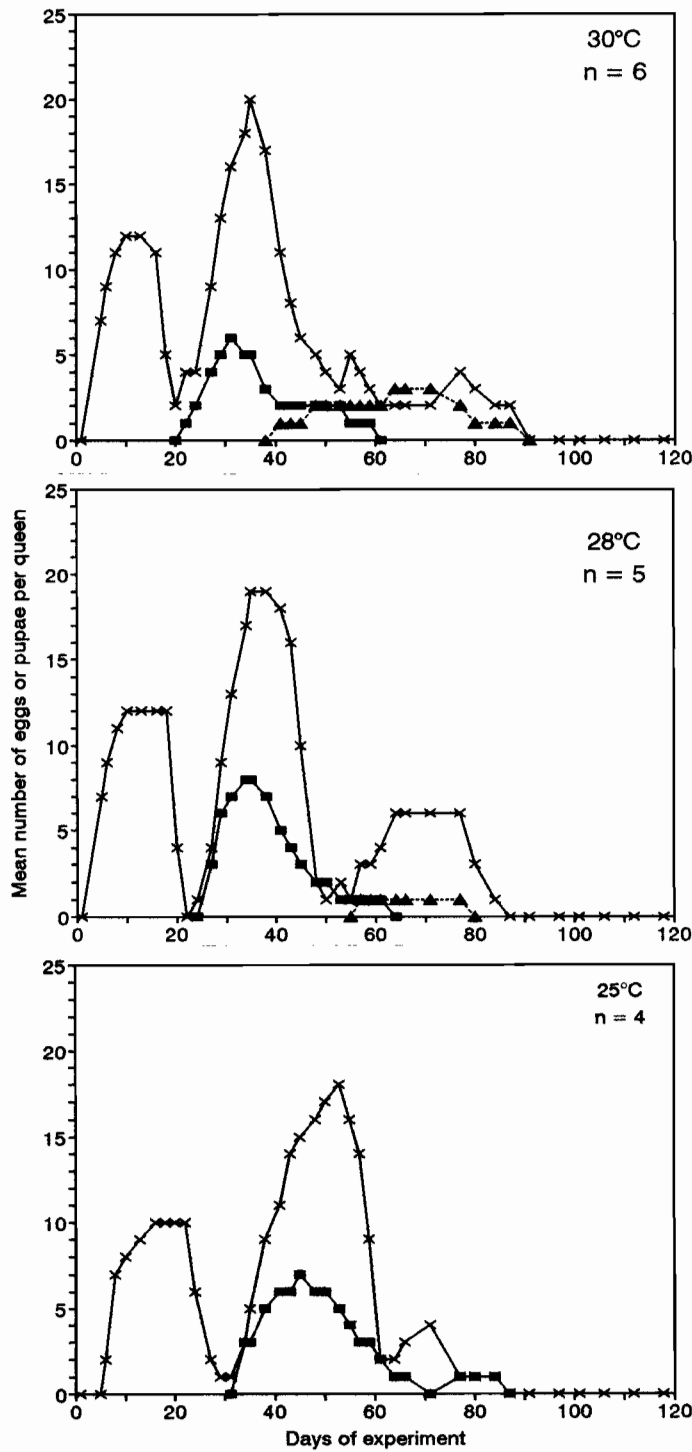


Figure 1. Brood rearing dynamics in the incipient colonies of *Camponotus herculeanus* under different temperature regimes.

The total queen productivity (pupae and diapausing larvae in sum) appeared to be on average almost equal at all constant temperatures but significantly higher under thermoperiods (Tab. 1). It may be concluded that queens laid similar numbers of eggs at all constant temperatures but the higher was the temperature, the greater became the portion of the brood attained the pupal stage. Thermoperiods are found, however, to be most advantageous for queen productivity and brood development.

Table 1. Productivity of nest-founding queens of *Camponotus herculeanus* at different temperature regimes (the number of larvae and pupae reared per queen).

Temperature °C		30	28	25	23	16/30	14/32
Number of queens		6	5	4	4	6	6
Number of the first brood pupae	min	4	10	4	3	5	3
	max	13	12	11	7	11	10
	mean	8.5	11.2 ^{ab}	7.8	5.8 ^{ac}	9.5 ^c	6.8 ^b
	s.d.	3.62	1.10	3.00	1.90	2.4	2.79
Number of the second brood pupae	min	2	0	-	-	1	1
	max	9	3	-	-	18	16
	mean	7.0	1.0	-	-	8.8	8.8
	s.d.	3.16	1.22	-	-	8.33	5.12
Total number of pupae	min	13	11	4	3	11	10
	max	18	13	11	7	26	21
	mean	15.2 ^{ab}	12.2 ^{ab}	7.8 ^{aef}	5.8 ^{bcd}	18.3 ^{ce}	15.7 ^{df}
	s.d.	1.60	0.84	3.00	1.90	7.03	4.27
Number of diapausing larvae	min	4	12	12	11	11	15
	max	17	22	14	23	40	34
	mean	10.2 ^{ab}	16.2	13.0 ^{cd}	16.8	22.7 ^{ac}	21.5 ^{bd}
	s.d.	4.71	4.26	0.82	4.92	9.93	7.66
Total number of larvae and pupae	min	19	24	17	17	22	25
	max	32	34	25	26	66	51
	mean	25.3 ^{ab}	28.4 ^c	20.8 ^{cde}	22.5 ^{fg}	41.0 ^{adf}	37.2 ^{beg}
	s.d.	4.56	4.16	3.50	3.87	14.81	10.63

In parentheses - mean number of the first brood larvae among the diapausing ones.

The identical letters in the same line denote the means that differ significantly ($P \geq 0.95$) from each other.

Relying on our regular brood counts we determined mean developmental times for all brood stages at all temperatures and mean duration of eggs and pupae presence in ant nests for each experimental regime. Then by a subtraction of the mean developmental time from the mean duration of a given brood stage presence we calculated the mean durations of oviposition and pupation periods for each experimental regime (Tab. 2).

The mean duration of oviposition period appeared to be quite similar at all constant temperatures but substantially higher under both thermoperiods where this parameter (70.7-73.1 d.) significantly

differed from the duration of oviposition under constant 23 °C (55.5 d.) which is equal to mean daily temperature of both thermoperiods. The mean duration of pupation period is found to be even more dependent on temperature conditions: it increased from 11.9 d. at 23 °C to 47.4 d. at 30 °C. Under thermoperiods larvae have been pupating considerably longer (55.0-63.7 d. on average) than even at 30 °C. Individual variability of both oviposition and pupation periods in all experimental regimes was rather high (Tab. 2).

Table 2. Influence of temperature on the duration of oviposition and pupation in the incipient colonies of *Camponotus herculeanus*.

Temperature °C		30	28	25	23	16/30	14/32
Number of queens		6	5	4	4	6	6
Duration of oviposition (days)	min	36.8	50.6	35.1	39.9	63.6	56.4
	max	77.3	67.6	62.6	65.4	89.6	83.4
	mean	61.1 ^a	63.8 ^b	42.8 ^{abcd}	55.5 ^e	73.1 ^{ce}	70.7 ^d
	s.d.	14.75	7.40	13.28	11.97	8.80	10.69
Duration of pupation (days)	min	39.0	20.0	9.7	7.5	43.2	44.9
	max	54.0	47.5	43.7	14.0	72.2	82.9
	mean	47.4 ^{abc}	37.5 ^{def}	26.5 ^{agh}	11.9 ^{bdi j}	55.0 ^{egi}	63.7 ^{cfh}
	s.d.	6.36	10.65	14.72	2.95	10.65	13.44

The identical letters in the same line denote the means that differ significantly ($P \geq 0.95$) from each other.

The constant temperature of 23 °C appeared to be near to the lower temperature threshold for the larvae of *C. xerxes* (22.0 °C) and so the night temperature of thermoperiod 16/30 °C was notably below this threshold. Both these regimes (23 °C and 16/30 °C) proved to be, therefore, unfavourable for the development of *C. xerxes*. Consequently, we do not include here the data for 23 and 16/30 °C as graphics (Fig. 2).

The initial period of colony founding in *C. xerxes* is characterized by the changes of brood stage numbers analogous to described above for *C. herculeanus* (Fig. 2). Under 26.5 and 20/30 °C the first peak of eggs was followed by a decrease of their number up to the minimum associated with the time of the first worker emergence. The constant temperature of 30 °C was inadequate for normal development and caused high brood mortality and gradual decline of brood quantity. At 25 °C brood development was quite prolonged and rather weak but proceeded continuously without any break. *C. xerxes* queens in contrast to *C. herculeanus* ones evidently have extremely narrow temperature optimum: the successful development of their first brood is possible in a restricted diapason between 26 and 30 °C.

Thermoperiod 20/30 °C exerted a profound effect on queen productivity and brood development comparing with constant 25 °C corresponding to daily mean temperature of this thermoperiod. Queens have reared on average 7.0 pupae each at thermoperiod (so many as at 30 and 26.5 °C) but only 2.0 pupae each at 25 °C (Tab. 3).

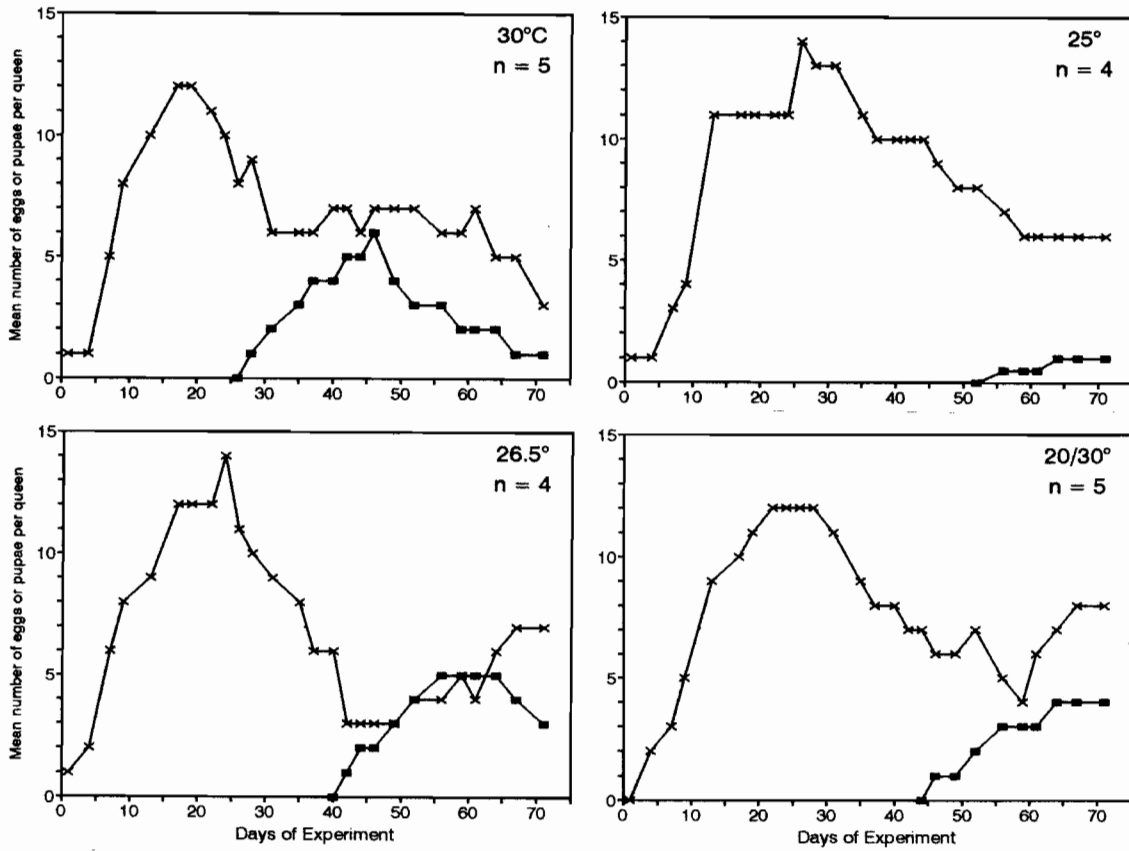


Figure 2. Brood rearing dynamics in the incipient colonies of *Camponotus xerxes* under different temperature regimes.

—x— Eggs —■— Pupae

The dependence of brood development on temperature proved to be quite different in two ant species studied. First, the durations of development of all ontogenetic stages are significantly greater in *C. xerxes* in comparison with *C. herculeanus* (compare Tab. 4 with Tab. 5). Total developmental time (from egg to adult) of *C. herculeanus* at 25°C is not less than in *C. xerxes* at 30°C. In the second place, the lower temperature thresholds (LTT) of development are lesser in *C. herculeanus* than in *C. xerxes*, this difference being most expressed between the thresholds of larvae: 22.0 and 7.7°C respectively (Fig. 3). And thirdly, the development of *C. xerxes* is much more temperature dependent comparing with *C. herculeanus*: the decrease of temperature leads to a considerable augmentation of developmental times in the first species but only to a moderate rise in the second one (Tab. 4, 5; Fig. 3). The most temperature labile development is found in *C. xerxes* larvae; they also have the highest temperature threshold - 22°C (Fig. 3B). Thus, it may be suggested that when the temperature falls in autumn the eggs and pupae of *C. xerxes* manage to complete their development but the larvae are compelled to hibernate.

The apparent differences between two species of *Camponotus* in temperature adjustment of development revealed by our experiments are in a good agreement with above described geographical distribution of these ants. The lesser temperature thresholds of development, the ability to develop much more rapidly and at the inferior temperature - all these traits obviously have great adaptive value for *C. herculeanus*

and enable this ant to populate territories in the Extreme North with severe cold climate and very short summer. It is also evident that *C. xerxes* could not advance farther to the North because of the lack of such adaptations. The extremely elevated temperature thresholds of *C. xerxes* brood stages are similar to the thresholds of other ants from Turkmenistan studied in our earlier works (Lopatina and Kipyatkov, 1990a).

Table 3. - Productivity of nest-founding queens of *Camponotus xerxes* during first 12 weeks of experiment

Temperature °C		30	26.5	25	23	20/30	16/30
Queen number		5	4	4	5	5	3
The number of pupae reared per queen	min	6	5	1	0	4	0
	max	9	9	3	3	10	4
	mean	7.8	6.8	2.0 ^a	0.6 ^b	7.0 ^{abc}	2.3 ^c
	s.d.	1.30	1.71	0.82	1.34	2.24	2.08

The identical letters in the same line denote the means that differ significantly ($P \geq 0.95$) from each other.

The lower temperature thresholds, or threshold temperatures (T_{thr}), for all brood stages of *C. xerxes* and for the pupal stage of *C. herculeanus* appeared to be higher than night temperatures of certain thermoperiods (Tab. 6, 7). It needs, therefore, to calculate the effective temperatures (T_{ef}) of these thermoperiods for each ontogenetic stage in order to evaluate more precisely the impact of thermoperiods on the developmental rates in comparison with constant temperature. For example, if LTT is equal to 22°C as in larvae of *C. xerxes*, then under thermoperiod 20/30°C development could not continue at night temperature at all because $T_{ef} = T - T_{thr} = 20^\circ - 22^\circ = -2^\circ$, i.e. $T_{ef} < 0$. Development is, however, possible at day temperature because $T_{ef} = 30^\circ - 22^\circ = 8^\circ$, i.e. $T_{ef} > 0$. On average for day and night together $T_{ef} = (0^\circ + 8^\circ)/2 = 4^\circ$. At the same time under constant 25°C, which is equal to the mean daily temperature of thermoperiod 20/30°C, effective temperature is only 3°C ($25^\circ - 22^\circ$), i.e. lesser than at 20/30°C. It is necessary, therefore, to compare the rates of development under thermoperiod 20/30°C not with the rates at constant 25°C but with rates estimated by linear regression equation (Fig. 3) for constant temperature of 26°C because it is at this regime effective temperature is equal to 4°C. The constant temperature of 26°C is thus equivalent to thermoperiod 20/30°C in respect of effective temperature (and only for *C. xerxes* larvae). Analogous calculations of the equivalent temperatures (T_{eq}) were fulfilled in all cases where it was required (Tab. 6, 7).

The results of this analysis made it apparent that at all thermoperiods development is always faster than at constant temperature equal to the mean effective temperature of corresponding thermoperiod. Such acceleration was quite small (4-9%) when the night temperatures of thermoperiods were lesser than LTT and rather significant (up to 20-25%) in all other cases (Tab. 6, 7). It is likely that temperature fall during the nights below the threshold of development exerts too harmful influence on metabolism and growth processes and thus diminishes the beneficial effect of thermoperiod.

Obtained results confirm again the exceptional significance of daily rhythms of temperature in ant ecology (Buschinger, 1973; Lopatina and Kipyatkov, 1990a,b). Many ants have nests exposed to daily changes of environmental temperature that became a constant and indispensable factor for their brood development. In spring when thermoperiods in ant nests are most apparent they make the development

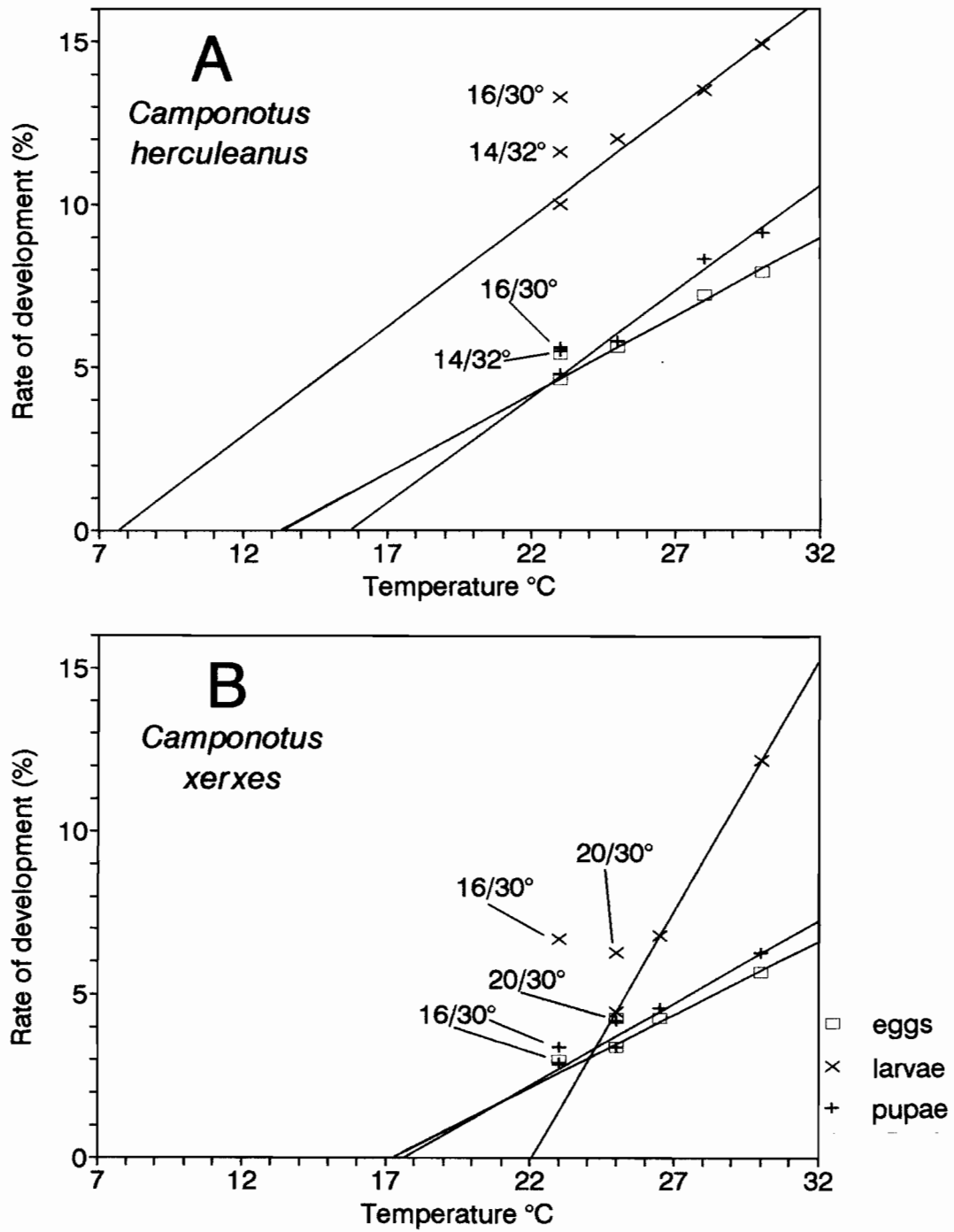


Figure 3. Regression of the brood stages developmental rates on temperature in two species of *Camponotus*.

Table 4. Duration of development (in days) of *Camponotus herculeanus* brood stages at different temperature regimes.

Temperature °C		30	28	25	23	16/30	14/32
E g g s	n	10	10	7	8	11	11
	min	12	13	17	19	17	17
	max	13	15	19	23	19	20
	mean	12.7	13.9	17.9	21.6 ^{ab}	18.4 ^a	18.6 ^b
	s.d.	0.47	0.78	0.90	1.19	0.67	0.92
L a r v a e of the first brood	n	7	5	3	4	6	6
	min	6	7	8	10	7	8
	max	8	8	9	10	8	10
	mean	6.7	7.4	8.3	10.0 ^{ab}	7.5 ^{ac}	8.6 ^{bc}
	s.d.	0.76	0.55	0.58	0	0.55	0.82
L a r v a e of the second brood	n	6	3	0	0	6	6
	min	7	14	-	-	9	7
	max	20	24	-	-	32	21
	mean	13.5	19.7	-	-	21.8	14.7
	s.d.	5.82	5.13	-	-	8.18	5.24
P u p a e	n	6	5	4	4	6	6
	min	10	12	16	21	17	17
	max	12	13	18	21	19	19
	mean	11.0	12.0	17.3	21.0 ^{ab}	17.8 ^a	18.2 ^b
	s.d.	0.63	0.71	0.96	0	0.75	0.98
Full developmental time of the first brood	n	6	5	3	4	6	6
	min	29	32	42	53	42	45
	max	32	34	44	54	45	46
	mean	30.3	33.2	43.0	53.3 ^{ab}	43.8 ^{ac}	46.7 ^{bc}
	s.d.	1.21	1.30	1.00	0.50	0.98	0.52

The identical letters in the same line denote the means that differ significantly ($P \geq 0.95$) from each other (the comparison was fulfilled only between thermoperiods and constant temperatures that were equal to the mean daily temperatures of these thermoperiods).

of overwintered larvae possible despite of too low mean daily temperature. Thermoperiods extend, therefore, the period of a year suitable for development.

It should be mentioned also that the developmental rates of the first brood larvae in *C. herculeanus* proved to be about twice greater on average in comparison with the development of the second brood larvae (Tab. 4). The first brood larvae developed very concurrently and had quite similar developmental times (for example 7-8 d. at 16/30 °C). On the contrary the larvae of the second brood exhibited significant variability of developmental times (9-32 d. at the same regime). This feature is possibly linked with the apparent predisposition of the second brood larvae to diapause whereas the larvae in the first brood

have a strong tendency to non-diapause development. It is thus reasonable to conclude that in nature the outcome of queens' brood-rearing efforts is under a strong environmental control: the occurrence of diapause among second brood larvae will vary within broad limits depending on climate conditions at the end of summer. The stimulation of non-diapause development by daily rhythm of temperature existing in natural ant nests could be of great significance in this situation.

Table 5. Duration of development (in days) of *Camponotus xerxes* brood stages at different temperature regimes.

Temperature °C		30	26,5	25	23	20/30	16/30
E g g s	n	9	8	3	-	8	10
	min	17.0	20.5	28.5	-	21.5	29
	max	18.0	24.5	29.5	-	24.5	37.5
	mean	17.5	23.2	29.2 ^{ab}	?	23.4 ^{ac}	32.7 ^{bc}
	s.d.	0.35	1.51	0.58	-	1.17	3.02
L a r v a e	n	8	9	6	1	8	3
	min	6.5	13.0	18.0	-	13.0	14.0
	max	9.5	17.0	25.5	-	18.5	16.0
	mean	8.2	14.6	22.0 ^{ab}	34	15.9 ^b	15.0 ^b
	s.d.	1.07	1.45	3.49	-	1.79	1.00
P u p a e	n	8	7	1	1	8	2
	min	15.0	21.0	-	-	22.0	29.0
	max	17.5	24.0	-	-	25.5	30.0
	mean	15.9	21.9	29.5	35	23.6 ^a	29.5 ^a
	s.d.	0.98	1.00	-	-	1.08	0.70
Full developmental time of the first brood	n	4	4	-	-	-	-
	min	40.5	55.5	-	-	-	-
	max	44.0	65.0	-	-	-	-
	mean	41.9	60.3	80.7*	-	-	77.2*
	s.d.	1.55	4.30	-	-	-	-

The identical letters in the same line denote the means that differ significantly ($P \geq 0.95$) from each other (the comparison was fulfilled only between thermoperiods and constant temperatures that were equal to the mean daily temperatures of these thermoperiods);

? - All the eggs perished, so the data on the duration of their development are not available;

* - Full developmental time calculated by the summing up the mean developmental times of all ontogenetic stages.

It is worthy to note the similar results reported by K. Bruder and A. Gupta (1972) for *Tetramorium caespitum*. The larvae reared by nest-founding queens of this species from the second batch of eggs developed at 21-24 °C 2.5 times longer than the larvae hatched from the first batch eggs. Their data could also be explained if we consider the fact that according to our unpublished results at the end of summer most of *T. caespitum* larvae fall in diapause at 20-23 °C.

Table 6. Influence of daily temperature rhythms on the duration of brood development in *Camponotus xerxes*.

Brood stage	E g g		L a r v a		P u p a		
Lower temperature threshold (°C)	17.2		22.0		17.6		
Thermoperiod [Thr] (°C)	16/30	20/30	16/30	20/30	16/30	20/30	
Equivalent temperature [Teq] (°C)	23.6*	25.0	26.0*	26.0*	23.9*	25.0	
Mean developmental time (days) at:	thermoperiod [DT(Thr)]	32.7	23.2	15.0	15.9	30.0	23.6
	equivalent temp. [DT(Teq)]	35.0*	29.2	16.6*	16.6*	31.7*	29.5
Acceleration of development at thermoperiod (%)	6.6	20.5	9.6	4.2	5.4	20.0	

T_{eq} - temperature that is equal to the mean effective temperature of the corresponding thermoperiod (see more in the text); The asterisks denote calculated values of T_{eq} and DT for the cases when temperature threshold was higher than the night temperature of the thermoperiod (see more in the text); The acceleration of development was calculated as $[1 - DT(Thr) : DT(Teq)] \times 100\%$.

Table 7. Influence of daily temperature rhythms on the duration of brood development in *Camponotus herculeanus*.

Brood stage	E g g		L a r v a		P u p a		
Lower temperature threshold (°C)	13.3		7.7		15.7		
Thermoperiod [Thr] (°C)	16/30	14/32	16/30	14/32	16/30	14/32	
Equivalent temperature [Teq] (°C)	23.0	23.0	23.0	23.0	23.0	23.0	
Mean developmental time (days) at:	thermoperiod [DT(Thr)]	18.4	18.6	7.5	8.6	17.8	18.2
	equivalent temp. [DT(Teq)]	21.6	21.6	10.0	10.0	21.0	18.9*
Acceleration of development at thermoperiod (%)	14.8	13.9	25.0	14.0	15.2	3.7	

See Table 6 for comments.

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