Bull.Br.arachnol.Soc. (1979) 4 (8), 329-336

Silken chambers built by nymphal pseudoscorpions in laboratory culture

Paul A. Wood* and **Peter D. Gabbutt**
Department of Zoology, Williamson Building,
The University, Manchester M13 9PL

Summary

Attempts were made to rear laboratory bred nymphs of *Chthonius ischnocheles* (Hermann) in cultures over the range 5-25°C but these were only successful at 15, 20 and 25°C. Estimates are provided of the time spent (a) in the maternal breeding chamber by protonymphs, (b) in the protonymphal, deutonymphal and tritonymphal free-living stages and (c) in the moulting chambers of protonymphs, deutonymphs and tritonymphs. The data have been fitted to a regression of the form Log $Y = a + bX$ where Y is the duration (days) of a particular stage and X is the temperature (°C). Extrapolations from these regressions are consistent with observations made on a small number of nymphs collected in the field and maintained in 5 and 10°C cultures. Comparable but isolated observations were made on *Neobisium muscorum* (Leach) and *Roncus lubricus* L. Koch. The significance of these laboratory studies is discussed in relation to the difficulties encountered in earlier ecological work by Gabbutt (1967) and Wood & Gabbutt (1978).

Introduction

Several authors (Godfrey, 1910; Kew, 1929; Vachon, 1935; Levi, 1948; Gabbutt 1962, 1966) have reported from either field or laboratory observations that protonymphs, deutonymphs and tritonymphs normally construct a silken chamber prior to each moult. Ecdysis normally takes place within this moulting chamber. In addition, both Godfrey (1910) and Gabbutt (1966) infer that silken chambers are used by nymphs for hibernation; in the case of adults this has been demonstrated recently by Wood & Gabbutt (1979) in laboratory studies.

*Present address: c/o Waitaki Girls High School,
P.O. Box 42,
Oamaru,
New Zealand

The present paper records observations on the incidence of silken chamber construction and the duration of occupation of these by nymphs at various temperatures. These were made during an investigation of the gonadial cycle of pseudoscorpions by Wood (1971) when nymphs, either bred in the laboratory or collected in the field, were reared to maturity. The most complete set of data refers to *Chthonius ischnocheles* (Hermann) but isolated records are provided for both *Neobisium muscorum* (Leach) and *Roncus lubricus* L. Koch.

Materials and Methods

Adult pseudoscorpions, collected monthly during the period May-December 1969 from a beech wood site in Lambridge Wood, near Henley-on-Thames, Oxon. (Grid Ref. SU 746839), were cultured singly or in pairs in constant temperature cabinets at five different temperatures over the range 5-25°C (Wood & Gabbutt, 1979). At the higher temperatures, females constructed breeding chambers and within these produced eggs. Eventually the eggs hatched into protonymphs which emerged from the maternal silken chamber.

All the protonymphs from surviving broods (occasionally females ate their brood) were placed together in a single culture tube and subsequently transferred to other tubes, in smaller groups, as they moulted from one instar to the next. The culture methods were the same as those described for adults (Wood & Gabbutt, 1979). The 25 mm x 75 mm tubes containing 10 mm of acid-washed fine sand were kept in darkness in constant temperature cabinets maintained at 5, 10, 15, 20 and 25°C each to within ± 2°C. Nymphs kept in culture at 5 and 10°C came from broods produced at higher temperatures; those kept at 15, 20 and 25°C came from broods produced at the same temperatures.

In addition protonymphs, deutonymphs and tritonymphs were collected in the field at the same site during the same period. They were extracted from the beech litter by means of suitably modified Tullgren funnels (Wood & Gabbutt, 1979) or by a mechanical shaking device (Caplin, 1974) and cultured in the same way as laboratory bred nymphs. Few protonymphs were collected and even fewer survived to moult to deutonymphs.

It was impracticable to rear one nymph in each culture tube because of the limited space available in the constant temperature cabinets. Consequently the time spent by a particular nymph in each of its free-living stages (inter-moult) could not be measured directly. Since the protonymphs originated from laboratory cultured females, the time interval between the construction of the breeding chamber by the female and the eventual emergence of the protonymphal offspring could be measured. All the protonymphs emerged from the breeding chamber on the same day and thus the time could be measured from this emergence to the construction of protonymphal (time A), deutonymphal (time B) and tritonymphal (time C) moulting chambers. Moulting chambers were labelled and the time spent in the protonymphal (time D), deutonymphal (time E) and tritonymphal (time F) moulting chambers respectively was noted. Since these chambers were built in depresssions in the sand next to the glass wall of the culture tube it was possible to record the day on which each ecdysis took place. Subsequently the exuviae in each marked chamber were examined and the moulting chambers of protonymphs, deutonymphs and tritonymphs were distinguished without ambiguity.

Using the above data it was possible to estimate the duration of each of the free-living stages or intermoult periods. The duration of free-living protonymphs was measured directly (time A). The duration of free-living deutonymphs = the time from protonymphal emergence to the construction of the deutonymphal moulting chamber (time B) – (the duration of free-living protonymphs (time A) + the time spent in the protonymphal moulting chamber (time D)). The duration of the free-living tritonymphs = the time from protonymphal emergence to the construction of the tritonymphal moulting chamber (time C) – (the time from protonymphal emergence to the construction of the deutonymphal moulting chamber (time B) + the time spent in the deutonymphal moulting chamber (time E)).

Results

C. ischnocheles

Laboratory bred animals

It was not possible to rear protonymphs at 5 and 10°C although 31 and 33 protonymphs respectively were placed in cultures at these temperatures. All died before they built their first moulting chamber.

The numbers of protonymphs introduced into cultures at 15, 20 and 25°C and successfully reared as deutonymphs, tritonymphs and adults are shown in Table 1. Overall only 3% of the protonymphs were reared to adults. The success rate with tritonymphs was better (41% reared to adults) but the difficulties of culturing the younger nymphs are high-lighted by the fact that only one quarter (25%) of the protonymphs were reared to deutonymphs and only one quarter of these (28%) produced tritonymphs. Our observations suggest that perhaps the difficulty could be attributed to a higher rate of cannibalism in the more crowded protonymphal and deutonymphal cultures and partly to the presence of free water in tubes maintained at high humidity. Protonymphs, in particular, once caught in a droplet of water quickly succumbed.

The mean times between the emergence of protonymphs from the maternal breeding chamber and the construction of each of the protonymphal, deutonymphal and tritonymphal moulting chambers are

	15°C		20°C		25°C		Total	
	A	B	A	B	A	B	A	B
Protonymphs	88	51	378	19	22	24	488	25
Deutonymphs	45	18	73	32	5	60	123	28
Tritonymphs	8	50	23	30	3	100	34	41
Adults (reared)	4	–	7	–	3	–	14	–
% (reared)	–	4.5	–	1.9	–	13.6	–	2.9

Table 1: *C. ischnocheles.* The number (A) of nymphs introduced into culture and the percentage (B) successfully reared to the next instar at 15, 20 and 25°C.

shown in Table 2. In this Table, time A represents the duration of the free-living protonymphal stage but time B includes time A as well as the time spent in the protonymphal moulting chamber and the deutonymphal free-living stage. Similarly time C includes time B and in addition the time spent in the deutonymphal moulting chamber and the free-living tritonymphal stage.

The time spent free-living as a protonymph (time A) was comparatively short at all temperatures (Table 2). By contrast, the time taken to reach the deutonymphal (time B) and the tritonymphal moulting chambers (time C) was proportionately very much longer at 15 than at either 20 or 25°C (Table 2). In terms of the two deleterious factors mentioned above, of cannibalism and the presence of free water, perhaps the greatest rearing success can be achieved where each stage is at risk to each of these for the shortest time. For deutonymphs and tritonymphs there is a tendency for an increase in the percentage of successfully reared nymphs to occur at the highest temperature (Table 1) which is correlated with the shortest developmental times (Table 2) and thus lowest risk. The situation in protonymphs is different. Since developmental times in protonymphs are short (Table 2) and hence risk is low in comparison with later stages, the best rearing success (51%) is correlated with, and is perhaps determined by, the lowest temperature of 15°C (Table 1).

Table 3 provides the consolidated data on the time spent in the breeding chambers as well as in each of the three moulting chambers, together with the calculated duration of each of the nymphal stages. The time spent in each stage varied inversely with the culture temperature. For instance, the time spent in culture by the free-living protonymphs was 19.4 days at 15°C, 15.0 days at 20°C and 12.2 days at 25°C (Table 3). At each temperature these effects were additive and thus the total developmental time from the female's construction of her breeding chamber to the appearance of a new adult generation from their tritonymphal moulting chambers was 238 days at 15°C, 90 days at 20°C and 76 days at 25°C (Table 3). To determine the total generation time from adult to adult we need to add the time interval between emergence as an adult to oviposition. One female constructed a breeding chamber 12 days after leaving her tritonymphal moulting chamber at 15°C and this period was about 8 days at 20°C (7.6 ± 1.9 days; N = 5, range 7-10 days). Thus generation time was about 250 and 98 days at 15° and 20°C respectively.

A smoothed estimate of the inverse relationship between developmental time and culture temperature was obtained by regression analysis of the data in Table 3. A regression line of the form Log $Y = a + bX$, where Y is the duration (days) of a particular stage and X is the culture temperature (°C) was fitted to the data. The resulting regression coefficients, the constants a and b and their 95% confidence limits are shown in Table 4. The probability values (P) for the correlation coefficients (r) are all less than 0.001.

The slope b in the regression equation is a measure of how much Y (days) increases for unit decrease of X (°C). The stages with the highest b values (Table 4)

	15°C		20°C		25°C	
Time	N	Mean	N	Mean	N	Mean
A	47	19.4 ± 2.7 (7 – 46)	72	15.0 ± 1.7 (5 – 35)	5	12.2 ± 4.7 (9 – 18)
B	17	92.2 ± 14.6 (60 – 143)	21	38.7 ± 6.2 (19 – 63)	2	38.0 ± 12.7 (37 – 39)
C	5	175.0 ± 11.6 (163 – 189)	9	62.1 ± 11.1 (42 – 84)	3	55.0 ± 12.9 (52 – 61)

Table 2: *C. ischnocheles.* The mean time (days) ± the 95% confidence limits between protonymphal emergence from the breeding chamber and the construction of the protonymphal (A), deutonymphal (B), and tritonymphal (C) moulting chamber; the observed ranges are shown in parentheses.

are the free-living deutonymphal stage and the deutonymphal and tritonymphal moulting stages. Perhaps surprisingly, the lowest *b* value (i.e. the least increase in stage duration with unit decrease in temperature) is recorded for the free-living tritonymphal stage (Table 4).

The calculated regression lines have been used to extrapolate developmental times at 2°C intervals over the range 2-30°C and these have been used to interpret the results obtained from samples of field populations (Wood, 1971). The times spent in the breeding chamber and in the free-living and moulting stages of protonymphs, deutonymphs and tritonymphs at 4°C intervals over the range 4-24°C are shown in Table 5. As temperature decreases by 20°C over this range the increase in the duration of the breeding, protonymphal and tritonymphal stages is by factors of 8.4, 10.4 and 9.6 respectively. By contrast the corresponding factor for the deutonymphal stage is 23.4 and this illustrates the sensitive response of deutonymphs to decreasing temperature by a proportionately larger increase in the duration of this stage.

Animals from the field

Nymphs were collected throughout the year from the field and placed in laboratory cultures. Few protonymphs were taken, however, and they subsequently died at all temperatures either in the free-living condition or within their first moulting chambers.

A similar lack of success was experienced when deutonymphs were introduced into culture. Six deutonymphs, however, survived at 5°C and constructed silken chambers. They were allowed to remain in these for between 91 and 138 days (but in one case for only 6 days) and then transferred to 20°C. At this temperature they all remained in the chambers and moulted to emerge as tritonymphs within 21 days (mean 12.8 days; N = 6, range 9-21

	15°C		20°C		25°C	
Time	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**
Breeding chamber	14	31.6 ± 3.6 (24 – 35)	25	17.9 ± 0.9 (15 – 23)	2	15.5 ± 19.1 (14 – 17)
Protonymph free-living (A)	47	19.4 ± 2.7 (7 – 46)	72	15.0 ± 1.7 (5 – 35)	5	12.2 ± 4.7 (9 – 18)
Protonymphal moulting chamber (D)	45	12.8 ± 1.0 (5 – 19)	73	7.5 ± 0.6 (2 – 14)	5	5.8 ± 1.4 (5 – 7)
Deutonymph free-living (B–(A + D))	17	60.0 ± 14.9	21	16.2 ± 6.5	2	20.0 ± 13.6
Deutonymphal moulting chamber (E)	8	40.2 ± 20.2 (16 – 84)	23	9.3 ± 1.5 (4 – 14)	3	7.5 ± 6.3 (7 – 8)
Tritonymph free-living (C–(B + E))	5	42.6 ± 27.5	9	14.1 ± 12.8	3	9.5 ± 19.2
Tritonymphal moulting chamber (F)	4	31.5 ± 26.5 (14 – 49)	7	10.1 ± 1.2 (9 – 12)	3	5.0 (5)
Total (Means)		238.1		90.1		75.5

Table 3: *C. ischnocheles.* The mean time (days) ± the 95% confidence limits spent in the breeding chambers and in the protonymphal (D), deutonymphal (E) and tritonymphal (F) moulting chambers, together with estimates of the free-living stages of protonymphs (A), deutonymphs (B–(A + D)) and tritonymphs (C–(B + E)); the observed ranges are shown in parentheses. Here and in Table 2 many apparent discrepancies in numbers (e.g. more tritonymphs than deutonymphs at 25°C) are the result of the inclusion of a few supplementary data from other broods.

days). This average of 12.8 days is consistent with the time spent in the deutonymphal moulting chamber at 20°C of 9.3 days (Table 3). Two of the resulting tritonymphs subsequently spent 28 and 35 days free-living at 20°C and then emerged from tritonymphal moulting chambers after 14 and 13 days respectively (cf. Table 3).

Thirteen tritonymphs collected during the period September-December 1969 behaved in a similar manner at 5°C. They all built silken chambers and one, after a period of 105 days, emerged as an adult. It is worthy of note that the expected time spent in the tritonymphal moulting chamber at 5°C, as calculated from the regression line (Table 4) is 149 days. The remaining twelve tritonymphs were kept at 5°C for 7-121 days and then transferred individually to cultures at 10, 15 and 20°C. The time spent in the chambers, after transference, before emergence as adults, was 14 days at 20°C (one individual), about 20 days at 15°C (mean 20.8 days; N = 8, range 16-26 days) and 53 days at 10°C (mean 53 days; N = 2, range 51-55 days). The comparable results from the laboratory reared animals were 10 days at 20°C and 32 days at 15°C (Table 3) and the expected duration of the time spent in the tritonymphal moulting chamber at 10°C, as calculated from the regression line (Table 4), is 63 days.

Other tritonymphs from the field were placed in 10, 15, 20 and 25°C cultures. All built tritonymphal moulting chambers and emerged as adults after 76 days (N = 8, range 40-140 days), 33 days (N = 17, range 16-110 days), 14 days (N = 17, range 9-26 days) and 10 days (one individual) respectively. Again these figures are consistent with those already quoted for laboratory-bred animals kept at these temperatures (Table 3).

In conclusion it is clear that deutonymphs transferred from 5 to 20°C, tritonymphs transferred from 5°C to higher temperatures and tritonymphs held in culture at 10, 15, 20 and 25°C spent about the same time in silken chambers as culture bred animals at these same temperatures.

N. muscorum

Laboratory bred animals

Only two females produced broods in culture after the construction of breeding chambers. They vacated these, with protonymphs after 49 and 31 days at 15 and 20°C respectively.

Time	*a* & 95% limits	*b* & 95% limits	(r)	(P)
Breeding chamber	2.187 ± 0.023	−0.046 ± 0.000	−0.902	<0.001
Protonymph free-living	2.265 ± 0.032	−0.057 ± 0.011	−0.665	<0.001
Protonymphal moulting chamber	1.557 ± 0.034	−0.034 ± 0.013	−0.428	<0.001
Deutonymph free-living	2.565 ± 0.040	−0.064 ± 0.014	−0.477	<0.001
Deutonymphal moulting chamber	2.530 ± 0.062	−0.076 ± 0.028	−0.847	<0.001
Tritonymph free-living	1.903 ± 0.062	−0.026 ± 0.022	−0.764	<0.001
Tritonymphal moulting chamber	2.552 ± 0.146	−0.075 ± 0.043	−0.721	<0.001

Table 4: *C. ischnocheles.* The calculated values and 95% confidence limits of the constants *a* and *b* in the regression equation Log Y = *a* + *b*X where Y is the duration (days) of a particular stage and X is the culture temperature (°C). The correlation coefficients (r) and the probability (P) values are listed for each regression.

Of the 15 protonymphs in the 15°C culture, only 4 survived to build protonymphal moulting chambers. The duration of the free-living stage was 80 days (N = 4, range 75-89 days). Only one successfully moulted to emerge as a deutonymph after 21 days.

Only one of the 17 protonymphs at 20°C survived to construct a moulting chamber after 21 days and emerged as a deutonymph after a further 11 days.

Animals from the field

Three protonymphs remained in their protonymphal moulting chambers at 20°C for 10 days (N = 3, range 5-16 days) before emergence. Only one deutonymph survived and this spent 30 days in the free-living condition and 15 days in the deutonymphal moulting chamber before emergence as a tritonymph.

A deutonymph remained in its moulting chamber for 54 days at 10°C, and a further two successfully emerged from moulting chambers as tritonymphs after 22 days (N = 2, range 21-23 days) at 20°C.

Tritonymphs survived in their moulting chambers to emerge as adults at 10, 15, and 20°C after 47 days (one individual), 33 days (N = 4, range 26-47 days) and 20 days (N = 3, range 14-26 days) respectively. At 5°C a tritonymph constructed a silken chamber and remained in it for 100 days until it was transferred to 15°C. It then moulted in this chamber and emerged as an adult 13 days later.

R. lubricus

Laboratory bred animals

All attempts to maintain protonymphs at various temperatures failed; all died within a week of emerging from the female's breeding chamber.

Animals from the field

Two deutonymphs survived at 20°C. They spent 31 and 51 days in the deutonymphal moulting chamber and 23 and 58 days in the free-living tritonymphal stage before entering the tritonymphal moulting chamber where they died.

Three tritonymphs survived at 15°C and four at 20°C. They remained in their tritonymphal moulting chambers for 96 days (N = 3, range 68-146 days) and 59 days (N = 4, range 35-101 days) respectively. Five further tritonymphs remained alive in their silken chambers for 546 days (18 months) at 5°C until the cultures were discontinued.

Discussion

The present data for rearings of *C. ischnocheles* to maturity in laboratory culture at various temperatures, confirm Kew's (1929) observations that as nymphal pseudoscorpions grow, there is an alternation between a free-living stage and a period of encasement in a silken chamber for the purpose of moulting. Protonymphs leave the maternal breeding chamber, feed, and then construct a silken chamber in which they moult to deutonymphs. This sequence is repeated by deutonymphs and tritonymphs and finally adults leave the tritonymphal moulting chamber. This procedure can also be inferred from the less complete data for *N. muscorum* and *R. lubricus*.

There is an increase in the duration of each of the life-history stages, both free-living and moulting, with decrease in temperature (Table 3). Regressions have been fitted to the data for reared nymphs over the

	Temperature (°C)					
	4	8	12	16	20	24
Breeding chamber	101	66	43	28	18	12
Protonymph: free living & moulting chamber	135	84	52	33	21	13
Deutonymph: free living & moulting chamber	374	198	106	56	30	16
Tritonymph: free living & moulting chamber	241	139	84	53	35	25
Total	851	487	285	170	104	66

Table 5: *C. ischnocheles*. The calculated duration (days), by extrapolation from the regression data of Table 4, of the breeding chamber and the free-living and moulting stages of protonymphs, deutonymphs and tritonymphs over the range 4-24°C.

temperature range 15-25°C (Table 4) and extrapolations made for other temperatures (Table 5). Additional observations on the duration of stages based on a limited number of individuals collected from the field are either consistent with the observations on the laboratory reared animals (Table 3) or with the extrapolated data (Table 5).

The regressions show a logarithmic increase in the duration of each stage as temperature decreases. These become so extended at the lower temperatures that for practical purposes growth probably ceases at about 5°C. Evidence in support of this contention comes from data (Table 5) which show a doubling in the time taken to reach maturity by *C. ischnocheles* as the temperature falls from 8 to 4°C and the observation on the tritonymphs of *R. lubricus* which remained encased in silken chambers for nearly 550 days at 5°C.

Adults respond to low temperature (5°C) by building hibernation chambers and remain in them for considerable periods, in excess of 250 days by *C. ischnocheles* (♀) and about 200 days by *R. lubricus* (♂) (Wood & Gabbutt, 1979). Nymphs also respond by building a silken chamber which may ultimately be used for moulting. For instance, a tritonymph of *C. ischnocheles* completed its maturation moult after 105 days in a chamber at 5°C. In addition, the experimental transfer of deutonymphs and tritonymphs of *C. ischnocheles* and tritonymphs of *N. muscorum*, all encased in chambers at 5°C for upwards of 140 days, to cultures at higher temperatures all resulted in the chambers being used for moulting. In *C. ischnocheles* the time taken to complete the moult after transfer was similar to that recorded for laboratory reared individuals at the appropriate higher temperature.

The pseudoscorpion population in the beech litter on this site has been studied by Gabbutt (1967) and Wood (1971). The nymphs, like the adults show a return migration cycle with annual periodicity (Wood & Gabbutt, 1978). Nymphs move downwards into the lower layers from June-July onwards and the survivors return to the upper layers in March-May. The majority of nymphs overwinter as deutonymphs and there is little change in the relative proportions of each of the three nymphal stages during the period October-March, implying that growth is at a standstill. A reduction in the density of each of the nymphs during the winter period, and especially during February, suggests that the seasonal vertical migration is accompanied by the construction of silken chambers. Since pseudoscorpions in chambers are less likely to be extracted by Tullgren funnels (Gabbutt, 1970) there is the clear possibility that nymphal density will be underestimated during the winter. In the field it is possible that, as the temperature falls during the autumn, the nymphs respond by building a silken chamber for hibernation or, alternatively, they may have already constructed a moulting chamber in which they remain indefinitely. Thus one silken chamber may be used for hibernation in late autumn and winter as growth ceases and for moulting in the following spring as growth recommences. It is not possible to estimate accurately what proportion of the nymphs occupy chambers but probably half the deutonymphs of *C. ischnocheles* in February do so (cf. Wood & Gabbutt, 1978, fig. 7). As the temperature rises in the spring the time spent in silken chambers will be reduced and thus it will be less likely that nymphal densities are underestimated at this time.

The time spent in culture at 5°C by nymphs in silken chambers, before their transfer to high temperatures, can be as long as 138 days for deutonymphs and 121 days for tritonymphs of *C. ischnocheles*. The minimum estimates are of the same order as those recorded for the adults of *C. ischnocheles* (Wood & Gabbutt, 1979) and clearly indicate the ability of nymphs to survive within chambers for periods of time equal to the period of lowest temperatures in the field (December-February, 90 days) and possibly for the whole of the winter period (October-March, 182 days).

Finally the observations that deutonymphs form 50% (Gabbutt, 1967) and 60-70% (Wood & Gabbutt, 1978) of the overwintering nymphal population can be seen now in the context of the developmental process. The present data show that the deutonymphs are more sensitive to decreasing temperature than either the protonymphs or tritonymphs (cf. values for *b* in Table 4). The extrapolated data (Table 5) suggest that the time spent in the deutonymphal stage (both free-living and within the moulting chamber) is proportionately much longer, representing 44% of the time to maturity at 4°C (i.e. 374 days out of 851) as compared with 29% at 20°C. There is thus a physiological explanation, based on differential growth

rates, which inevitably leads to the accumulation of deutonymphs during the winter.

Acknowledgements

Our thanks are due to Gordon Blower for his helpful criticism of this manuscript. One of us (P.A.W.) wishes to thank the Science Research Council for their support during the period 1967-1970.

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