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Silken chambers built by adult pseudoscorpions in laboratory culture

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Summary

Three species, *Chthonius ischnocheles, Roncus lubricus* and *Neobisium muscorum* were maintained in cultures at 5, 10, 15, 20 and 25°C. Some adults built hibernation chambers at 5 and 10°C and, in addition, some females constructed breeding or abortive breeding chambers at 10, 15, 20 and 25°C. The percentage of each type built is given for each temperature. Estimates are provided for (a) the total time spent in culture by those building and not building chambers, (b) the time spent in culture before the construction of hibernation or breeding chambers, (c) the time spent encased in hibernation or breeding chambers and (d) the number of protonymphs produced by females in breeding chambers. The implications of these laboratory observations are considered in relation to the difficulties encountered in interpreting phenological data based on Tullgren funnel extraction techniques.

Introduction

A number of observations by Godfrey (1908, 1909, 1910), Kew (1914, 1929), Vachon (1951), Gabbutt (1962, 1966) and Weygoldt (1969) confirm that pseudoscorpions construct silken chambers for the purposes of moulting, breeding and, in some cases, hibernation.

This habit complicates the interpretation of quantitative data based on the extraction of pseudoscorpions from leaf litter by means of Tullgren funnels (Gabbutt, 1967). The apparent reduction in the densities of all instars in litter during the winter months and the paucity of females prior to the appearance of the new generation of protonymphs, in *Chthonius ischnocheles* (Hermann) for instance (Gabbutt & Vachon, 1963), are explicable only in terms of either migration and/or the building of silken chambers for the purposes of hibernation and breeding respectively. Although seasonal vertical migration has been demonstrated in this species (Wood & Gabbutt, 1978) it does not provide a satisfactory answer for the observed reduction in densities. Gabbutt (1970) suggested that individuals encased in chambers are not extracted by means of Tullgren funnels and thus conclusions concerning pseudoscorpion phenology are based only on numerical changes occurring in the free-living population. Since there are no accurate estimates of that part of the population encased in chambers, or whether the encased animals are unresponsive to the dryness and heat of Tullgren extraction, any observations, which contribute to our understanding of the factors responsible for their construction, may prove to be crucial in our understanding of the phenological data.

The observations reported in the present paper arose as by-products of other work on pseudoscorpions (Wood, 1971) and refer mainly to *Chthonius ischnocheles* (Hermann) and *Roncus lubricus* L. Koch and more casually to *Neobisium muscorum* (Leach).

Site and methods

The pseudoscorpions used for the laboratory work were collected monthly, during the period May 1969 – December 1969, from a beechwood site in Lambridge Wood, near Henley-on-Thames, Oxon. (Grid Ref. SU 746839). They were extracted from beech litter by Tullgren funnels (Gabbutt, 1967) and collected alive by using receptacles modified to prevent escapes and containing damp filter paper to maintain a high humidity.

Adults were kept separately, or in pairs, in 25 mm x 75 mm tubes containing 10 mm of acid-washed fine sand (40-100 mesh). This sand was thoroughly wetted and a 50 mm strip of filter paper was placed down the inside of the tube and embedded in the sand. Subsequently the paper was kept moist and this maintained a relative humidity of 90-95% with adequate gaseous exchange across a tightly fitting cork. Small

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depressions were made in the sand near the wall of the tube to encourage the construction of silken chambers in a position where the behaviour of the pseudoscorpions could be observed through the glass. The tubes were kept in darkness in constant temperature cabinets maintained at 5, 10, 15, 20 and 25°C, each to within ± 2°C. It proved impossible to keep pseudoscorpions in culture at 0 and 30°C as all animals died within a week of introduction.

Most of the adults in culture were killed for cytological examination in a study of the gonadial cycle (Wood, 1975). This, or death in culture, accounts for the apparent discrepancies between the numbers (N) in Tables 1-11. Individuals were killed at intervals either before or after building chambers, and there was generally no bias against either free-living individuals or those in chambers. Those maintained in culture until death occurred were examined each day and fed two or three times a week on either a collembolan (*Folsomia* sp.) or vestigial-winged fruit flies (*Drosophila* sp.).

The designation of the use to which silken chambers are put is somewhat arbitrary. However, since post-adult ecdyses have not been recorded in the literature or during the present observations, it must be concluded that silken chambers built by adults are not used for moulting purposes. Further, males do not use chambers for breeding and thus the chambers they construct must be used to withstand adverse conditions. Males only build these chambers at the lower temperatures of 5 and 10°C and they have been designated as hibernation chambers. Females, on the other hand, use chambers for breeding and, in addition, to withstand adverse conditions. The production of eggs, and subsequently of protonymphs, clearly distinguishes the first category. When no eggs were carried the chambers were presumed to be hibernation chambers in 5 and 10°C cultures, by analogy with males. Other chambers built at higher temperatures could have been abortive breeding chambers or constructed to withstand temperature stress. Since males do not respond to high temperatures by building chambers it is presumed that those constructed by females were abortive breeding chambers. Clearly if this type of chamber is produced at the lower temperatures then the number of genuine hibernation chambers may have been over-estimated.

Only a minimum value for the average time spent in culture by males building hibernation chambers and females building hibernation, breeding and abortive breeding chambers was calculated since most were removed and fixed whilst in these chambers or shortly after leaving them. The time to death quoted for the above categories (see Tables 3, 7 and 11, lines a) combines death by killing and by natural causes. The time to death given for males and females not building silken chambers refers only to death by natural causes (see Tables 3, 7 and 11, lines b, and Table 4). Thus any differences between the time spent in culture by animals building and not building chambers will be greater than the figures may suggest.

Results

Males

Hibernation chambers

None of the 101 males of *N. muscorum* placed in cultures over the range 5-25°C constructed silken chambers. Subsequent microscopical examination of the sectioned chelicerae and prosoma revealed the absence of silk glands and their ducts. Males of this species are thus incapable of building silken chambers and in consequence, and in contrast to the females (see below), may be less able to withstand the adverse conditions of low temperatures.

Silken chambers were constructed by males of *C. ischnocheles* and *R. lubricus* at 5 and 10°C but not at 15, 20 or 25°C. The percentage number of chambers produced was relatively low overall but each species built at least twice as many hibernation chambers at 5° as at 10°C (Table 1). At each of these temperatures *C. ischnocheles* made about twice as many chambers as *R. lubricus* (Table 1). Although the

	N	Silken chambers	%
5°C			
C. ischnocheles	41	12	29.3
R. lubricus	47	8	17.0
10°C			
C. ischnocheles	48	6	12.5
R. lubricus	53	3	5.7

Table 1: The percentage number of males building hibernation chambers at 5 and 10°C.

number of *C. ischnocheles* placed in culture each month from May to December was low, a closer examination of the data suggests an increasing tendency to build chambers by those males collected later in the year; 10 out of the 12 hibernation chambers built at 5°C belonged to males collected during August-December. The greater reluctance of *R. lubricus* to build hibernation chambers is also illustrated by the 7 additional animals transferred from cultures at higher temperatures to 5°C culture of which only one constructed a chamber.

The average time spent by *C. ischnocheles* free-living in culture before hibernation chamber construction was less at 5°C (58 days; N = 12, range 15-161 days) than at 10°C (104 days; N = 6, range 44-141 days). The small number of observations on *R. lubricus* necessitated combining the data for both the 5 and 10°C cultures to give an average of 148 days (N = 11, range 83-288 days). This increase in both the average and the range again suggests that *R. lubricus* is more reluctant to prepare hibernation chambers than *C. ischnocheles.*

The time spent within the hibernation chamber, by both species, before their re-appearance free-living in culture, was longer at 5° than at 10°C but *C. ischnocheles* spent longer encased than *R. lubricus* at both temperatures (Table 2). The relative ease with which *C. ischnocheles* builds hibernation chambers can be gauged from 14 additional free-living males which were transferred to the 5°C cultures from cultures at higher temperature. Seven of them (50%) constructed hibernation chambers and remained in them for an average of 115 days (range 89-142 days) which is very similar to the figure quoted (124 days) for individuals kept in the 5°C cultures since collection (Table 2).

The minimum average time spent in culture before death by *C. ischnocheles* which built hibernation chambers was about the same, approximately 160 days, at both 5 and 10°C (Table 3). This was more than double the time spent by individuals which did not build chambers at 5°C (65 days) but less than double the time at 10°C (92 days) (Table 3). Similarly *R. lubricus* which built chambers survived 50% longer in culture (about 210 days) than those which did not build hibernation chambers (about 135 days) at both temperatures (Table 3). *R. lubricus* survived longer in culture, both building and not building chambers, than *C. ischnocheles* at each temperature.

The average time spent in culture before death from natural causes by individuals not building hibernation chambers, over the range 5-25°C, can be gauged by considering the appropriate data in Tables 3 and 4. All species survived longest in cultures at lower temperatures and all showed the general trend to an increasingly earlier death as temperature increased. Duration of life in culture was some 60-80% shorter at 25°C than at 5°C for all species. In addition *R. lubricus* clearly survives longer in culture

	N	Mean	Range
5°C			
C. ischnocheles	5	124	98-140
R. lubricus	4	92	42-199
10°C			
C. ischnocheles	2	74	70-77
R. lubricus	2	26	10-42

Table 2: The time (days) spent by males in hibernation chambers at 5 and 10°C before emergence. The figures for N are smaller than those shown in Table 3 because some individuals were killed or died in the chambers.

		5°C			10°C		
		N	Mean	Range	N	Mean	Range
C. ischnocheles	(a)	12	166	90-264	5	159	92-228
	(b)	15	65	6-274	15	92	8-227
R. lubricus	(a)	6	204	119-335	2	213	95-330
	(b)	27	133	9-392	29	135	7-393
N. muscorum	(b)	15	103	16-281	16	73	5-133

Table 3: The time (days) spent by males at 5 and 10°C before death by killing or natural causes by those (a) building, and before death by natural causes by those (b) not building hibernation chambers.

	15°C			20°C			25°C	
	N	Mean	Range	N	Mean	Range	N	Mean	Range
C. ischnocheles	13	39	6-117	24	40	4-93	22	23	2-43
R. lubricus	28	117	4-358	33	68	5-194	27	44	6-131
N. muscorum	8	59	41-77	18	51	4-138	19	21	3-53

Table 4: The time (days) spent by males not building chambers, at 15, 20 and 25°C, before death ensued from natural causes.

at each of the five temperatures than either *C. ischnocheles* or *N. muscorum.*

Females

Hibernation chambers

These chambers were built by females of all three species at 5 and 10°C. The percentage number made by both *C. ischnocheles* and *R. lubricus* was remarkably uniform (about 40%) at both temperatures (Table 5); *N. muscorum* built fewer hibernation chambers. Further analysis of the data for *C. ischnocheles* suggests that females collected later in the season are more likely to build hibernation chambers; 16 of the hibernation chambers at 5°C were produced by 19 females collected during the period August-December.

The average time spent by *C. ischnocheles* free-living in culture before hibernation chamber construction was about the same at 5°C (48 days; N = 22, range 13-105 days) and 10°C (49 days; N = 18, range 15-113 days). A similar time was spent by *R. lubricus* free in culture before building at 5°C (54 days; N = 15, range 14-167 days) but this species spent twice as long before building when at 10°C (113 days; N = 20, range 32-325 days). The figures for N quoted above are smaller than those shown in Table 5 because a few individuals were held in culture for periods which were not precisely recorded.

The time spent within hibernation chambers b both species was longer at 5°C than at 10°C but *C. ischnocheles* spent about three times longer encased than *R. lubricus* at both temperatures (Table 6). Of the 22 additional females of *C. ischnocheles* transferred to 5°C cultures from cultures maintained at higher temperatures, 14 constructed hibernation chambers (64%). These remained in them for an average of 120 days which is similar to the figure quoted (126 days) for females kept wholly in 5°C cultures (Table 6).

The minimum average time spent in culture before death by *C. ischnocheles* which built hibernation chambers was about the same (159 days) at both 5 and 10°C and about twice, or more, the time spent in culture by individuals which did not build chambers (Table 7). *R. lubricus* spent slightly less time in culture (146 days) at both temperatures but again this was 50-100% longer than those animals not building chambers.

Breeding chambers

The construction of breeding chambers was observed in all species in culture at 10, 15 and 20 °C (Table 8). They were also built by *C. ischnocheles* in

	N	Silken chambers	%
5°C			
C. ischnocheles	65	27	41.5
R. lubricus	40	17	42.5
N. muscorum	7	2	28.5
10°C			
C. ischnocheles	49	21	42.9
R. lubricus	52	21	40.4
N. muscorum	7	1	14.3

Table 5: The percentage number of females building hibernation chambers at 5 and 10°C.

	N	Mean	Range
5°C			
C. ischnocheles	6	126	35-264
R. lubricus	14	38	7-112
10°C			
C. ischnocheles	6	69	28-133
R. lubricus	9	25	7-58

Table 6: The time (days) spent by females in hibernation chambers at 5 and 10°C before emergence.

		5 °C			10°C		
		N	Mean	Range	N	Mean	Range
C. ischnocheles	(a)	18	165	40-306	13	152	34-320
	(b)	17	97	7-318	8	41	8-76
R. lubricus	(a)	15	152	52-353	20	140	46-337
	(b)	18	75	7-260	12	90	9-248
N. muscorum	(a)+(b)	7	69	29-102	5	149	5-279

Table 7: The time (days) spent by females at 5 and 10°C before death by killing or natural causes by those (a) building, and before death by natural causes by those (b) not building hibernation chambers.

25°C cultures but not by either *R. lubricus* or *N. muscorum*; only abortive chambers were built by the latter two species at this higher temperature. A higher percentage of *C. ischnocheles* produced breeding chambers over the range 10-20°C than *R. lubricus*, the data for *N. muscorum* are meagre and inconclusive (Table 8). It should be noted that abortive chambers are not recorded at 10°C, such chambers being designated hibernation chambers, by analogy with males.

Abortive chambers were less abundant than breeding chambers at 15°C and only in 25°C cultures was there a general preponderance of abortive chambers. This suggests that the preferred range for breeding is at the lower end of the scale 10-20°C in *C. ischnocheles* and perhaps *N. muscorum*; witness the increasing percentage of breeding chambers with decreasing temperature (Table 8). On the same basis 15°C is about the optimal temperature for breeding by *R. lubricus* (Table 8); note the large number of abortive chambers at 20°C.

The average time spent within breeding chambers is shown in Table 9. The most complete set of data, for *C. ischnocheles*, show that the period of encasement decreases as temperature increases, from 66 days at 10°C to 16 days at 25°C. Crude extrapolation suggests that the minimum temperature at which breeding can be accomplished is just below 10°C (since no individual building a breeding chamber survived for longer than 78 days in culture at 10°C – Table 11) and that the minimum time spent in a chamber at 25°C is about 14 days. Observations were only available for *R. lubricus* at 15 and 20°C where the average time spent in breeding chambers was 79 and 57 days respectively (Table 9). This was about three times longer than the corresponding values of 32 and 18 days respectively for *C. ischnocheles* at these two temperatures.

The average number of protonymphs which were present with, or emerged with, females from these breeding chambers is shown in Table 10. Most data are available for *C. ischnocheles* and the average numbers of about 22 per female are similar at both 15 and 20°C. The corresponding figures for *R. lubricus* are somewhat lower at 18 protonymphs in 15°C cultures.

The minimum average time spent in culture before death by individuals which built either breeding or abortive breeding chambers is very similar (about 60 days) for *C. ischnocheles* at all temperatures (Table 11). By contrast *R. lubricus* shows a reduction in the length of life in culture as temperature increases. This species survived longer than *C. ischnocheles* at the lower temperatures.

The average time spent in culture before death by individuals which did not build chambers can be

	10°C				15°C				20°C				25°C			
	N	A	B	%A	N	A	B	%A	N	A	B	%A	N	A	B	%A
C. ischnocheles	28	12	–	42.9	44	17	7	38.6	66	22	5	33.3	47	2	7	4.3
R. lubricus	35	3	–	8.5	51	15	12	29.4	49	6	15	12.2	34	–	10	0
N. muscorum	6	2	–	33.3	12	3	1	25.0	11	1	4	9.1	7	–	3	0

Table 8: The number of females building (A) breeding or (B) abortive breeding chambers, and the percentage of breeding chambers, at 10, 15, 20 and 25°C.

	10°C			15°C			20°C			25°C		
	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range
C. ischnocheles	2	66	63-68	14	32	24-35	25	18	15-23	2	16	14-17
R. lubricus	–	–	–	6	79	62-107	4	57	41-77	–	–	–

Table 9: The time (days) spent by females in breeding and abortive breeding chambers at 10, 15, 20 and 25°C before emergence.

assessed by considering the data in Tables 7 and 11. Both species survived better at lower temperatures and, apart from a number of discrepancies, the general trend was for shorter length of culture life as temperature increases.

Some females can build more than one breeding chamber. In *C. ischnocheles* four females built 2 chambers each and two females were allowed to build three each before their removal from culture for cytological fixation and examination. The average time between exit from one chamber and entry to another was 15 days at 15°C (N = 2, range 11-18 days) and 16 days at 20°C (N = 6, range 6-24 days). In *R. lubricus* a female in 20°C culture built a second breeding chamber 7 days after leaving the first.

Discussion

Temperature and longevity

Despite a number of anomalies, both males (Tables 3 and 4) and females (Tables 7 and 11) of *C. ischnocheles, R. lubricus* and *N. muscorum* which did not build chambers of any kind, show an inverse relationship between temperature and average time spent in culture before death. Individuals of each species lived at least two or even three times longer in cultures at 5°C than at 25°C. *R. lubricus* survived longest in culture at all temperatures and this could be due to this species having the greatest natural longevity and/or to culture conditions having a greater adverse effect on *C. ischnocheles* and *N. muscorum.*

In males, for instance, it has been calculated that length of life in culture at 25°C is 60-80% shorter than at 5°C (see earlier). This is compatible with a temperature coefficient (Q_{10}) of about 2, for over the range 5-25°C metabolic rate would quadruple. If longevity is proportional to the reciprocal of the metabolic rate then, taking length of life in culture at 5°C as a base line (100%) it could be anticipated that this parameter would have a value of ¼ (25%) at 25°C. This crude estimate of a length of life 75% shorter at 25°C is close to the figure of 60-80% quoted above.

Hibernation chambers

It is clear that the construction of hibernation chambers by both males (Table 3) and females (Table 7) of *C. ischnocheles* and *R. lubricus* significantly increased average time in culture by a factor of about two and it is conceivable that this may have survival value under field conditions. If the construction of a hibernation chamber is a positive means of combating low temperatures, then the threshold at which this might occur could show specific differences. The general impression that *R. lubricus* has a greater tolerance of low temperatures than *C. ischnocheles* is reflected in the present series of observations. *R. lubricus* spends longer free-living in culture before hibernation chambers are built, tends to build fewer chambers (Table 1) and both males (Table 2) and females (Table 6) spend less time encased. By contrast *C. ischnocheles* is much less reluctant to build chambers, builds more chambers (Table 1) and spends longer in such chambers once they have been built (Tables 2 and 6).

The effect of low temperatures as a factor influencing the construction and maintenance of hibernation chambers can be noted from the higher per-

	10°C			15°C			20°C			25°C		
	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range
C. ischnocheles	1	26	–	13	23	17-30	24	21	12-29	1	17	–
R. lubricus	1	18	–	7	18	14-23	1	15	–	–	–	–

Table 10: The number of protonymphs emerging from breeding chambers at 10, 15, 20 and 25°C.

		10°C			15°C			20°C			25°C		
		N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range
C. ischnocheles	(a)	5	58	43-78	14	62	31-275	18	60	12-210	4	60	24-92
	(b)	8	41	8-76	11	51	7-174	24	47	5-131	6	31	3-94
R. lubricus	(a)	3	128	88-201	27	112	55-321	19	68	24-115	3	44	37-56
	(b)	12	90	9-248	9	51	9-232	18	68	5-237	21	47	8-132

Table 11: The time (days) spent by females at 10, 15, 20 and 25°C before death by killing or natural causes by those (a) building breeding or abortive breeding chambers, and before death by natural causes by those (b) not building chambers.

centage built at 5°C by males of *C. ischnocheles* and *R. lubricus* (Table 1), from the shorter time spent in culture at 5°C before construction commences by males of *C. ischnocheles* and females of *R. lubricus* and from the longer time spent in hibernation chambers by males (Table 2) and females (Table 6) in the 5°C cultures. Although it is not possible to provide substantial evidence from the present data, there is certainly the suspicion that the time of collection in the field may have an important bearing on whether hibernation chambers are, or are not, built. Animals caught late in the season appear more likely to build chambers than those caught before August. This seasonal effect may be due to the previous field experience of animals caught late in the season, either directly to the lower autumnal temperatures or to some other factor such as day-length, which itself has been thought to be implicated in initiating the seasonal vertical migrations of pseudoscorpions (Wood & Gabbutt, 1978).

Breeding chambers

The percentage number of breeding chambers eventually produced (Table 8) by females, kept separately after capture, partly reflects the previous pattern of insemination in the field population by means of spermatophore transfer. The maximum time from capture to the construction of a breeding chamber is a crude measure of sperm viability, these figures are 31 and 70 days for *C. ischnocheles* and *R. lubricus* respectively. These figures are perhaps surprising since it is known that neither *C. ischnocheles* (Legg, 1975a) nor *R. lubricus* (Legg, 1975b) possess spermathecae although both species produce encysted sperm at spermatophore formation (Legg, 1973). Two additional females of *R. lubricus* kept with males produced chambers and eggs in 15°C cultures, 125 and 134 days respectively after the death of the males, thus doubling the estimate of sperm viability in this species.

The number of protonymphs produced by females of *C. ischnocheles* averaged about 22 over the range 10-25°C (Table 10) and this is close to a field observation (Gabbutt, 1967) of 18 eggs or larvae per female (N = 7, range 12-27). These are both higher than Vachon's (1936) figure of 4-8 eggs (based on three specimens) and Godfrey's (1910) observations on *C. rayi* (= *ischnocheles*) when two females were accompanied by 8 and 14 young nymphs respectively.

Hibernation chambers and population estimates

The seasonal changes in density of the pseudoscorpions on the site, from which the experimental animals were collected, have been monitored by Wood & Gabbutt (1978). Both species, *C. ischnocheles* and *R. lubricus* show a return migration cycle with annual periodicity. From June-July onwards a large part of each population moves downward to the lower layers, in general *C. ischnocheles* moves from litter to humus and *R. lubricus* from humus to soil, and surviving individuals return to the upper layers in March-May. To account for the lower densities during October-March, and particularly in February, it is supposed that migration is accompanied by the construction of hibernation chambers. This would substantially reduce the chance of extraction by means of Tullgren funnels and thus underestimate the density of each species.

As the temperature falls in the soil to reach its lowest value of between 0-5°C during the three month period December-February (Wood & Gabbutt, 1978) there will be an increasing possibility of hibernation chamber construction on the evidence of Tables 1 and 5. At these times it is likely that the density of males and females is underestimated by a

minimum of 30% (Table 1) and 40% (Table 5) respectively in the case of *C. ischnocheles* and by 20% and 30% respectively for *R. lubricus*. Due to its reluctance to build hibernation chambers, and the shorter time it remains encased if they are built, *R. lubricus* is less likely to be underestimated than *C. ischnocheles*. It is possible, however, that the errors of density estimation are higher than these minimum values since both species are likely to build a higher percentage of chambers as a function of a seasonal factor.

The estimate of the average time spent in hibernation chambers by males is about 4 months for *C. ischnocheles* (124 days – see Table 2) and 3 months for *R. lubricus* (92 days – see Table 2) at 5°C. This at least demonstrates that both species can survive in hibernation chambers for time intervals equal to the period of lowest temperatures in the field. The maximum time spent in hibernation chambers of 264 days by a female *C. ischnocheles* (Table 6) and 199 days by a male *R. lubricus* (Table 2) clearly indicates the capacity of some individuals to survive in such chambers for a period equal to the entire winter period October-March (182 days).

Breeding chambers and population estimates

If the incidence of breeding chambers built by females in the laboratory were to be paralleled in the field then female density would be underestimated during the breeding season July-September. If females present in breeding chambers are not extracted in Tullgren funnels then female density could be underestimated by about 40% in *C. ischnocheles* and 30% in *R. lubricus* (see Table 8). At 15°C the average time spent in breeding chambers by *C. ischnocheles* and *R. lubricus* is 32 days and 79 days respectively (Table 9). Both these values exceed the time interval between successive field collections and lead to further underestimation of female density. In addition the possibility that females can produce a number of broods during the breeding season (see earlier) has important implications in terms of the level of recruitment to any new generation.

Finally the fact that males and females collected in October, which in all probability have bred at least once, can be kept alive in culture for a further year (Table 7) suggests that they can breed at least twice and may live for two years or more. This supports the view of Gabbutt (1967), based on calculations derived from sampling, that more than half of the adults of *C. ischnocheles* present in July have experienced at least one winter in the adult condition.

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