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THE LIFE CYCLE RELATIVE TO TEMPERATURE OF *PROTAPHORURA ARMATUS* (TULLBERG) (COLLEMBOLA: ONYCHIURIDAE), A PARTHENOGENETIC SPECIES[1]

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Apparent parthenogenetic reproduction in Collembola has sometimes been attributed to accidental transfer of spermatophores with the food material from one culture to another (Schaller, 1953; Mayer, 1957). Conclusive evidence of parthenogenesis has only in recent years been accumulated for a number of species of Collembola, of which some were found in field populations consisting entirely of females (Choudhuri, 1958; Hüther, 1961; Marshall and Kevan, 1962; Petersen, 1965; 1971; Snider, 1973). In Onychiuridae, parthenogenesis is apparently quite common. *Onychiurus parthenogeneticus* Choudhuri and *Tullbergia krausbaueri* (Börner) undoubtedly reproduce in the absence of males (Choudhuri, 1958; Hale, 1966; Petersen, 1971); so does *Tullbergia granulata* Mills, where individuals reared in isolation from the time of hatching invariably lay viable eggs (unpublished observations). Large females of *Onychiurus procampatus* Gisin 1956 breed through a form of thelytokous parthenogenesis (Hale, 1964). The size groupings found in *O. procampatus* (two sizes of females and only small males) were also observed in *O. fimatus* Gisin 1952 and *O. quadriocellatus* Gisin 1947 and may indicate the existence of both parthenogenetic and sexually reproducing forms in these species (Hale, 1964).

Recent laboratory observations on *Protaphorura armatus* (Tullberg) revealed that this species too reproduces parthenogenetically. The present study was undertaken to investigate the effect of temperature on the biology of the species.

MATERIALS AND METHODS

Clear plastic jars (3.5 × 2.5 cm) were used as culture containers. They were filled to a depth of 1 cm with a plaster-charcoal substrate. Brewer's yeast was provided as food. Distilled water was added when required in order to maintain a humidity of close to 100 percent. Whenever regular scraping of the substrate surface did not suffice to keep the jars free of mold, the animals were transferred to a new container.

From *Protaphorura armatus* stock cultures, single eggs were transferred to each of a number of containers and incubated at 15°; 21°; and 26°C. Upon emergence of the juveniles, observations were made at 24 hour intervals throughout the life of the animals. Exuvia were recorded and removed from the containers. Deaths were recorded and the specimens preserved in alcohol. All eggs laid were left in the jars and allowed to hatch. At each temperature, the progeny of 15 parent individuals were reared to maturity and preserved for later sex determination.

MORTALITY, LONGEVITY, INSTAR DURATION

Figure 1 illustrates the survival pattern of *P. armatus* at 15°, 21° and 26°C. While juvenile mortality was highest at 26°C, the over-all survival patterns at 26° and 21°C were closely similar. At 15°C, 50% survival was reached in 345 days. Average longevity was 320 days at 15°C, but only 139 and 129 days at 21° and 26°C respectively.

Table 1 summarizes the data on duration of the stadia at the three test temperatures. At all temperatures the first instar stadium was of shorter duration than any of the subsequent stadia. At 15°C the duration of the stadia was considerably longer than at 21°C or 26°C, while differences between the length of the stadia at 21°and 26°C were only slight. At all temperatures the number of days between moults gradually increased with progressing age. The mean number of instars in a life time was 23 at 15°C and 20 at both 21° and 26°C.

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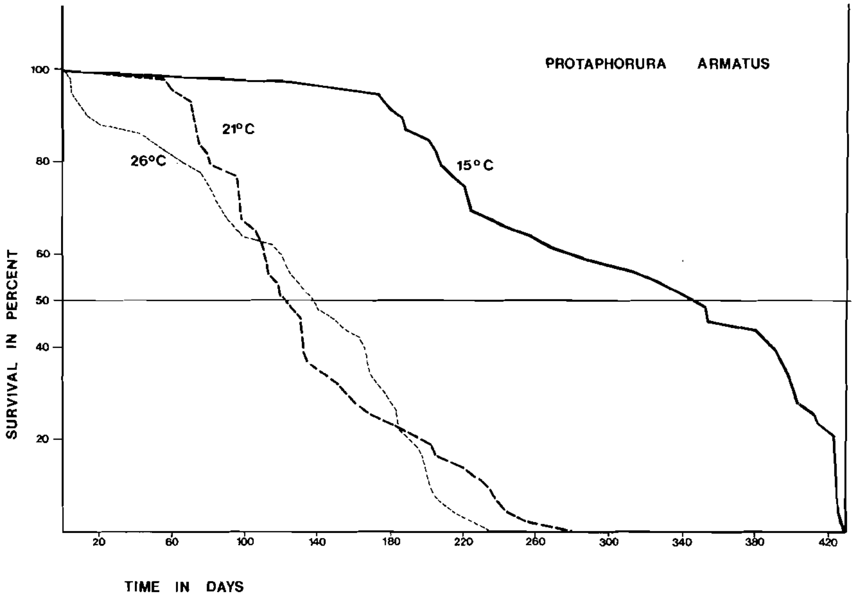

Fig. 1. Survival of *Protaphorura armatus* (Tullberg) at three temperatures.

The moulting process in juveniles and young adults was normally completed within a period of 24 hours. However, from the 10th or 12th instar on, ecdysis often lasted from 2 to 5 days, during which the animals remained in one place and took no food. A drop of water placed on or beside them usually released the exuvia without injury to the animal. In several very old individuals ecdysis lasted from 5 to 10 days and sometimes resulted in death of the animal.

Table 1. Average duration of selected stadia of *Protaphorura armatus* at three temperatures.

	15°C			21°C			26°C		
Instar	Mean	Range	No. repl.	Mean	Range	No. repl.	Mean	Range	No. repl.
1	11.0	10-12	40	6.2	5-7	48	5.7	5-8	44
2	11.7	10-14	40	6.5	5-9	48	5.8	4-8	44
3	11.2	9-13	40	6.5	5-9	47	6.0	4-8	44
4	12.5	7-18	40	6.5	5-9	47	6.1	3-11	44
5	13.7	10-12	40	7.0	5-10	47	6.2	4-8	44
6	14.3	10-18	40	7.7	6-10	46	6.7	5-10	44
7	14.3	11-19	40	7.3	5-9	46	7.0	4-12	44
8	16.0	10-21	39	7.2	5-10	46	7.1	5-11	43
9	15.6	11-22	39	7.4	6-9	44	7.0	4-11	42
10	16.1	12-22	39	7.8	6-10	44	7.0	5-9	41
15	14.0	8-21	30	7.6	6-10	32	7.3	5-11	36
20	13.6	9-20	25	8.1	6-11	18	7.3	5-11	30
25	14.5	9-20	22	8.3	6-15	12	8.0	5-14	21
28	15.3	12-19	17	8.1	4-11	9	7.6	6-12	16
31	17.3	11-24	9	9.7	8-11	5	8.0	5-10	7
35				8.7	7-11	3			

This extended duration of the moulting process was observed at all temperatures. At 26°C it occurred first in a 55 day old individual (10th instar), at 21°C in a 63 day old animal (12th instar), and at 15°C in a 136 day old individual (12th instar).

EGG PRODUCTION

All observed individuals of *P. armatus* originated from isolated eggs and, with few exceptions, laid viable eggs at least once during their adult life. Microscopical examination of the specimens after death revealed that even the non-laying individuals were all females. At least in the laboratory, evidence of parthenogenesis in *P. armatus* was conclusive. Specimens collected from Michigan agricultural and forest soils have so far also been all female. However, sampling has not been extensive; the existence of entirely female populations of *P. armatus* in the field has yet to be established.

As in several other species of Collembola (Hale, 1965; Waldorf, 1971a; Snider, 1973) a close relationship between moulting and oviposition was found in *P. armatus*. The time interval elapsing between ecdysis and oviposition however varied with the temperature. At 26°C oviposition generally occurred within 1-2 days of ecdysis, while at 15°C the interval was commonly 2-4 days. In cases where the moulting process lasted for several days, oviposition was delayed accordingly, although a few females laid eggs while the exuvia was still attached to the dorsal end of the abdomen.

P. armatus lays clumps of smooth white eggs, often in holes or against the container wall. The earliest that eggs were laid was at the beginning of the 5th instar, but initiation of egg production varied with the individual. There appeared to be no pattern in the sequence of ovipositions. Many individuals laid eggs in each of 8 to 12 successive instars; others produced eggs at variable intervals, with 1 to 5 and rarely more than 6 nonproductive instars intervening.

The total number of ovipositions by one female ranged from 1 to 22, with a maximum of 20 ovipositions at 15°C and 22 at 21°C and 26°C. On the average, a female oviposited 9 times at 15°C; 9.5 times at 21°C; and 11.5 times at 26°C.

Eggs produced during one oviposition were invariably laid in one single clump. At all temperatures the number of eggs per laying period (and clump) increased gradually up to the 6th oviposition and remained fairly constant over the next 7 or 8 ovipositions.

Although the mean number of laying periods was lowest at 15°C, the average number of eggs per oviposition per laying female was highest at that temperature (Fig. 2). The total number of eggs laid by one female in a life time varied from 1 to 298. Average egg production per female as well as clump size were highest at 15°C and lowest at 26°C (Table 2).

Taking into consideration the total number of females alive at a given time, the effect of temperature on the reproductive rate was revealed in an unexpected way. In a given instar, a smaller proportion of females was reproducing at 15° than at 21° or 26°C (Table 3). Accordingly, fecundity averages were sometimes lowest at 15°C. Cumulation of

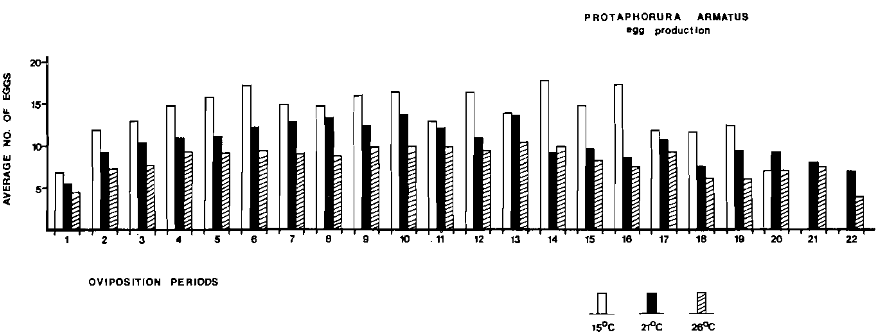

Fig. 2. Average egg production per oviposition and female of *Protaphorura armatus* (Tullberg) at three temperatures.

Table 2. Total egg production and clump size per female of *Protaphorura armatus* at three temperatures.

	15°C	21°C	26°C
Total no. of eggs (average/female)	123.8	102.6	98.1
Range	7-289	1-298	13-262
Max. no. of eggs per clump	30	24	22
Average clump size	13.7	10.8	8.6

fecundity means per instar demonstrates the interaction between clump size and percentage of laying females (Fig. 3). A temperature of 26°C, although inducing egg production in a high number of females, also reduces the number of eggs laid (136.4 total). At 21°C the number of eggs laid is higher, combined with a high percentage of productive females (150.7 eggs total). At 15°C the low number of egg laying females at first reduces fecundity below the 21° level; but the large size of the clumps finally balances average fecundity to a point where it reaches the 21° values (147.8 total).

Of the original 150 individuals of *P. armatus* used in this study, 131 reached maturity. Over 1200 of their progeny, taken from cultures at all experimental temperatures, were reared to maturity and preserved. Microscopical examination revealed that all individuals of this second generation were again females.

EGG CANNIBALISM

Egg cannibalism has been observed in several species of Collembola. Green (1964) showed that in *Folsomia candida* (Willem) cannibalism was independent of population density. Vail (1965) observed that faulty eggs were more prone to consumption than normal eggs in cultures of *Hypogastrura manubrialis* Tullberg. Recently, Waldorf (1971b) demonstrated for *Sinella curviseta* Brook a pronounced selectivity in egg cannibalism:

Table 3. Average fecundity per instar and female of *Protaphorura armatus* at three temperatures, up to the 20th instar.

	15°C			21°C			26°C		
Instar	Ave. eggs	No. fem. alive	% fem. laying	Ave. eggs	No. fem. alive	% fem. laying	Ave. eggs	No. fem. alive	% fem. laying
5	2.4	40	35.0	4.4	47	70.2	2.9	44	70.5
6	3.2	40	40.0	7.3	47	80.9	5.7	44	86.4
7	3.2	40	32.5	7.7	46	80.4	5.2	44	75.0
8	8.1	39	66.6	8.0	46	73.9	6.2	43	67.4
9	7.3	39	56.4	8.0	45	68.9	7.4	43	74.4
10	8.5	39	58.9	7.8	44	65.9	4.3	41	46.3
11	8.4	38	50.0	8.7	42	66.7	5.3	41	58.5
12	5.9	38	42.1	8.4	38	68.4	4.8	40	47.5
13	8.2	36	52.8	8.5	37	67.6	4.1	39	48.7
14	5.0	33	39.4	7.7	35	60.0	4.7	39	51.3
15	7.0	30	40.0	8.2	32	68.7	3.6	38	47.4
16	4.3	29	31.0	6.9	30	50.0	5.1	34	52.9
17	1.7	27	14.8	5.7	29	44.8	5.8	32	56.3
18	4.7	26	23.1	5.4	27	51.9	5.2	32	50.0
19	4.9	26	38.5	6.4	21	52.4	4.2	31	41.9
20	5.4	25	36.0	3.2	18	38.9	6.9	30	66.6

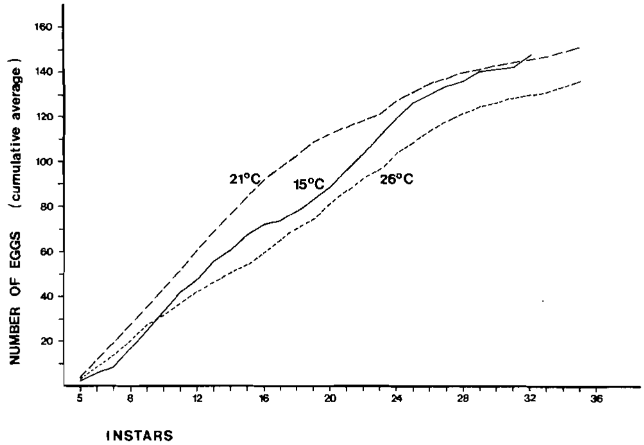

Fig. 3. Cumulative average fecundity of *Protaphorura armatus* (Tullberg) at three temperatures.

young, smooth eggs were preferred to rough eggs in advanced stages of development. In *P. armatus* cannibalism occurred frequently. As in *S. curviseta*, only young eggs with intact chorion were ingested. Once the chorion had ruptured the eggs were no longer subject to cannibalistic attack.

Owing to 24 hour intervals between observations, consumption of eggs immediately after oviposition could not be accurately determined. Where eggs were only partially ingested, the visible remains of egg shells were included in the egg counts. Possible consumption of whole eggs or entire clumps in those first 24 hours and resulting errors in fecundity and cannibalism data had to be disregarded.

Egg cannibalism proved to be considerable at all temperatures. At 15° and 26°C, 11 percent of all observed eggs were eaten. At 21°C cannibalism was slightly less with only 7 percent of all eggs consumed. The age of the parent did not influence the rate of ingestion. Eggs were subject to predation at any time from the first to the last oviposition in the life of a female.

In most egg clumps there were one to a few eggs that never developed, although at first they could not be distinguished from the rest of the clump. *P. armatus* also laid eggs that were distinctly faulty at first glance: they assumed neither the spherical shape nor the opaque white appearance of freshly laid eggs and were often deposited in amorphous masses. The females seemed unable to discriminate between such faulty eggs and healthy young eggs, since both were ingested. On the other hand, both types of eggs often remained untouched until they either hatched or deteriorated.

Thus egg cannibalism affected only young eggs, but was otherwise erratic and indiscriminate. Lack of a required nutritional component in the diet may have been the cause for both the cannibalistic behaviour and the production of faulty eggs in *P. armatus*. However, no food substances other than yeast were used in the investigation.

EGG VIABILITY

Aside from cannibalistic attack by the females, eggs of *P. armatus* were also found to be susceptible to excessive fungal and bacterial contamination. Fungal growth was particularly heavy at 26°C, in spite of constant efforts to keep the jars clean. Many egg clumps were therefore not suited for precise counts of egg viability, including those which had been only partially ingested or were partly overgrown by fungi.

At each temperature over-all data on hatching success were finally derived from egg clumps which showed no fungal infection and had not been attacked by the parent. Eggs laid at 15°C had a higher percentage of viability than those laid at 21° and 26°C (Table

Table 4. Viability of eggs of *Protaphorura armatus* at three temperatures.

	15°C	21°C	26°C
No. of eggs	1216	1062	884
No. hatched	949	719	567
Percent	78.0	67.7	64.1

4). At least under laboratory conditions, large clump size and high egg viability may possibly compensate for the low percentage of females reproducing at 15°C.

The over-all viability figures given in Table 4 are probably an overestimate, since data on faulty eggs were treated separately. At 26°C, 4.5% of all eggs laid were faulty and clearly non-viable, as compared to 3.1% at 21°C and 3.5% at 15°C.

SUMMARY

Laboratory observations on *Protaphorura armatus* (Tullberg) disclosed parthenogenetic reproduction in the species. Males have as yet not been found in either the stock cultures or among specimens collected from Michigan soil samples.

Isolated individuals of *P. armatus* were reared at 15°, 21° and 26°C. Longevity and survival were greatly extended at 15°C, at which temperature the duration of the stadia was longest. Eggs were laid in clumps within a few days of ecdysis. The largest clumps were recorded at 15°, but at that temperature a lower percentage of females laid eggs than at 21° or 26°C. Egg cannibalism occurred frequently and affected both healthy and faulty young eggs.

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