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THE LIFE HISTORY OF *FOLSOMIA CANDIDA* (WILLEM) (COLLEMBOLA: ISOTOMIDAE) RELATIVE TO TEMPERATURE[1]

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INTRODUCTION

The parthenogenetic mode of reproduction in Collembola, although frequently questioned in the past (Schaller, 1953; Mayer, 1957; Falkenhan, 1932), has only recently been recorded and confirmed for several species; *Onychiurus parthenogeneticus* Choudhuri (Choudhuri, 1958), *Folsomia candida* (Willem) (Goto, 1960; Marshall and Kevan, 1962; Green, 1964; Husson and Palévody, 1967), *Folsomia cavicola* Cassagnau and Delamare (Goto, 1960), *Tullbergia krausbaueri* (Börner) (Hale, 1966; Petersen, 1971), and *Isotoma notabilis* Schäffer (Petersen, 1971).

Sex-ratios in populations of the above cited species are often unknown. Existing data indicate that the composition of a population may vary with the geographical distribution of the species. Populations of *Folsomia candida* (Willem), known to be bisexual in England (Goto, 1960), have been found so far to consist entirely of females in Canada (Sharma and Kevan, 1963a) and in Michigan (Snider, 1973). Similar to *I. notabilis* and *T. krausbaueri* (Petersen, 1971), investigations throughout the year and over larger geographic areas are necessary before northern USA and Canada *F. candida* may be labeled as obligatory parthenogenetic.

Snider (1973) recorded in detail the life cycle of *F. candida* at 21°C. The present study provides information on the influence of temperature on the bionomics of the species.

MATERIALS AND METHODS

As in previous studies (Snider, 1973) plastic containers (3.5 × 2.5 cm) with clear snap-on lids, filled to a depth of 1 cm with a 1:1 plaster-charcoal substrate, were used as culture containers. Addition of distilled water ensured a constant humidity of close to 100 percent. Powdered brewer's yeast was provided as food.

First instar juveniles were isolated and observed at 24 hour intervals throughout the duration of their life. Ecdysis, oviposition, hatching success of the eggs and mortality were recorded at each of two temperatures, 15° and 26°C. Data previously obtained (Snider, 1973) on the bionomics of the species at 21°C were incorporated into the study for comparison.

The animals originated from the same stock cultures that had been used in previous observations. These cultures had been maintained in the laboratory continuously for eight years. Recently, additional stock cultures were started with specimens collected from loose soil near Lansing, Michigan; preliminary investigation indicated that this population consisted entirely of females. For corroboration of the data obtained on "old stock" individuals, isolated "new stock" specimens were reared at 21°C, using the methods described above. Observation of this check series was discontinued after 180 days.

LONGEVITY AND MORTALITY

Longevity of Collembola is temperature dependent and most probably species specific (Thibaud, 1970). Under laboratory conditions, which usually imply rearing at constant temperature, several species have been cultured for more than a year at temperatures between 5° and 20°C (Milne, 1960; Strebel, 1932; Joosse and Veltkamp, 1971). In general, a rise in temperature shortens the life span of Collembola.

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Table 1. Life span, in days, of *Folsomia candida* (Willem) at three temperatures.

	15°C	21°C	26°C
Mean	240.6	136.2	72.4
Range	19-352	6-198	35-115

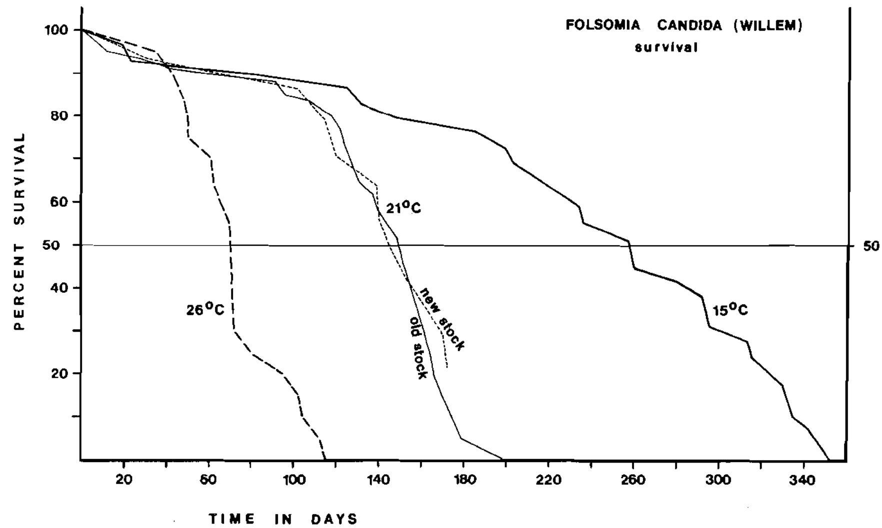

Fig. 1. Survival of *Folsomia candida* (Willem) at three temperatures. Data for 21°C "old stock" taken from Snider (1973).

The mean life span of *F. candida* at 15°C was 240 days as compared to 136 days at 21°C (Snider, 1973). At 26°C longevity was reduced to an average of 72 days (Table 1).

Survival was drastically reduced at 26°C, with 50% of the individuals dead after 70 days. At 21°C 50% of the animals had died after 150 days, whereas at 15°C mean survival was prolonged to 258 days. Longevity and survival pattern of "old stock" and "new stock" individuals reared at 21°C showed no significant differences with mean survival in both series reaching approximately 150 days (Fig. 1).

The number of instars in a life time also was temperature dependent. At both 15° and 21°C an average of 30 instars was completed. At 26°C no female underwent more than 22 instars, with a mean of 16 instars per individual.

INSTAR DURATION

In *Tullbergia krausbaueri,* several species of *Onychiurus,* and a number of *Hypogastruridae* instar duration tends to increase with progressing age (Hale, 1965a; Choudhuri, 1961; Thibaud, 1970). These data confirmed previous findings by MacLagan (1932) and Davis and Harris (1936) for other species. Hale (1965a) showed a relationship between instar duration and temperature. This was further exemplified by Thibaud (1970) who demonstrated that in a given species temperatures close to the upper lethal limit induce a considerable increase in instar duration.

At all experimental temperatures the first instar stadium of *F. candida* was of longer average duration than the subsequent three or four stadia. This agrees with Green's observations at 25°C (Green, 1964). Mean duration of the stadia in aging individuals was found to be almost twice as long at 15°C than at 21°C (Table 2). At 26°C the duration of the stadia was occasionally longer than at lower temperatures. Occurrence of uncommonly wide ranges (3 to 26 days for the 5th stadium, 4 to 30 days for the 11th stadium) and frequent intervals of 9 to 17 days between moults indicate that 26°C possibly approaches the upper limit of tolerance for *F. candida*.

At 21°C intervals between moults in "old stock" and "new stock" individuals were not significantly different (Table 2). A relevant cause for occasional discrepancies may be found in the relatively low number of "new stock" replicates observed.

Although the reproductive rhythm in *F. candida* is well defined (Snider, 1973) it is not reflected in the duration of the stadia. In other species, periodic deposition of eggs and spermatophores relates to marked differences in the length of the stadia; sometimes in males only (Poggendorf, 1956; Mayer, 1957; Waldorf, 1971); sometimes in both males and females (Joosse and Veltkamp, 1970; Thibaud, 1970). So far as has been observed, none of the known parthenogenetic species have alternating long and short stadia which can be related to egg production.

EGG PRODUCTION

Hale (1965b) gives a synopsis of fecundity estimates for a number of Collembola species. The estimated number of ovipositions usually varies between two and four, but occasionally rises to ten probable ovipositions, as in *Tullbergia krausbaueri.* This species was later proven to reproduce parthenogenetically (Hale, 1966; Petersen, 1971). Sharma and Kevan (1963b), dealing with a bisexual population of *Isotoma notabilis,* recorded a maximum of four ovipositions at intervals of six days. Petersen (1971) gives no account of the number and timing of egg depositions in *I. notabilis,* though he established that the species reproduces successfully in the absence of males.

A direct relation between ecdysis and oviposition was found in *T. krausbaueri* as well as in two species of *Dicyrtoma* (Hale, 1965b). In these egg laying always occurs directly after moulting, often in successive instars. The same is true for *Protaphorura armatus* where older females often lay eggs while the exuvia is still attached to the dorsal end of the abdomen (unpublished data). Waldorf (1971) found that females of *Sinella curviseta* begin to oviposit eight hours after ecdysis, with a tendency toward alternating productive and non-productive instars. A similar sexual rhythm was described for both males and females of *Isotoma viridis* and *Tomocerus minor* by Joosse and Veltkamp (1970) who in turn linked spermatophore and egg production to alternate stadia of longer duration.

In *F. candida* a somewhat irregular egg laying rhythm was noted by Green (1964), with intervals of up to three instars between ovipositions. However, both in past observations (Snider, 1973) and in the present study, *F. candida* was found to oviposit with great regularity, there being alternating productive and non-productive instars at all experimental temperatures. The majority of the intervals between ovipositions encompassed two instars; variation was greatest at 26°C and least at 15°C (Table 3).

As the experiment progressed, it became clear that at 15° and 21°C eggs were laid predominantly in the 6th, 8th, 10th . . . instars. At 21°C 100 percent of all females followed this pattern; however, at both 15° and 21°C slight variations in the percentage of laying females were brought on by pauses in oviposition and by occasional deposition of eggs in consecutive instars, especially in older females. At 26°C only 52.6% started laying in the 6th instar and the remaining females laid their first batch of eggs in the 7th or 8th instar. This difference in the time of initiation of egg production at 26°C, coupled with greater variability of the intervals between ovipositions, altered the 6-8-10th instar rhythm predominant at lower temperatures (Table 4). Examples of egg production by single females, as given in Fig. 2, demonstrate that both the 6-8-10th instar and the 7-9-11th instar rhythm were common at 26°C.

Compared to "old stock" reared at 21°C (Snider, 1973) females kept at 15°C showed greatly increased egg production, with the increase being significant at the 1% level.

Table 2. Average duration, in days, of selected stadia of *Folsomia candida* (Willem) at three temperatures (number of replicates in parentheses). Data for 21°C "old stock" taken from Snider (1973).

Instar	1	2	3	4	5	6	7	8	9	10	15	20	25	30	34	38
15°C	7.0	5.2	5.5	5.5	6.5	6.3	6.9	7.2	7.0	8.0	11.3	10.0	9.8	11.3	11.1	12.7
	(32)		(31)	(30)							(29)	(26)	(25)	(18)	(14)	(7)
21°C	4.0	3.7	3.7	3.6	4.5	4.2	4.1	4.7	4.9	5.6	5.5	5.5	5.7	6.7	7.0	8.0
old stock	(60)	(59)	(57)				(56)				(54)		(49)	(38)	(28)	(8)
21°C	4.8	3.7	3.7	4.1	4.8	4.2	5.4	5.7	5.4	5.6	5.9	6.6	6.5	6.3	7.0	
new stock	(13)												(11)	(7)	(3)	
26°C	5.4	3.2	4.1	4.0	5.3	4.4	4.6	4.8	5.2	4.9	6.4	5.3				
	(19)							(18)		(17)	(14)	(3)				

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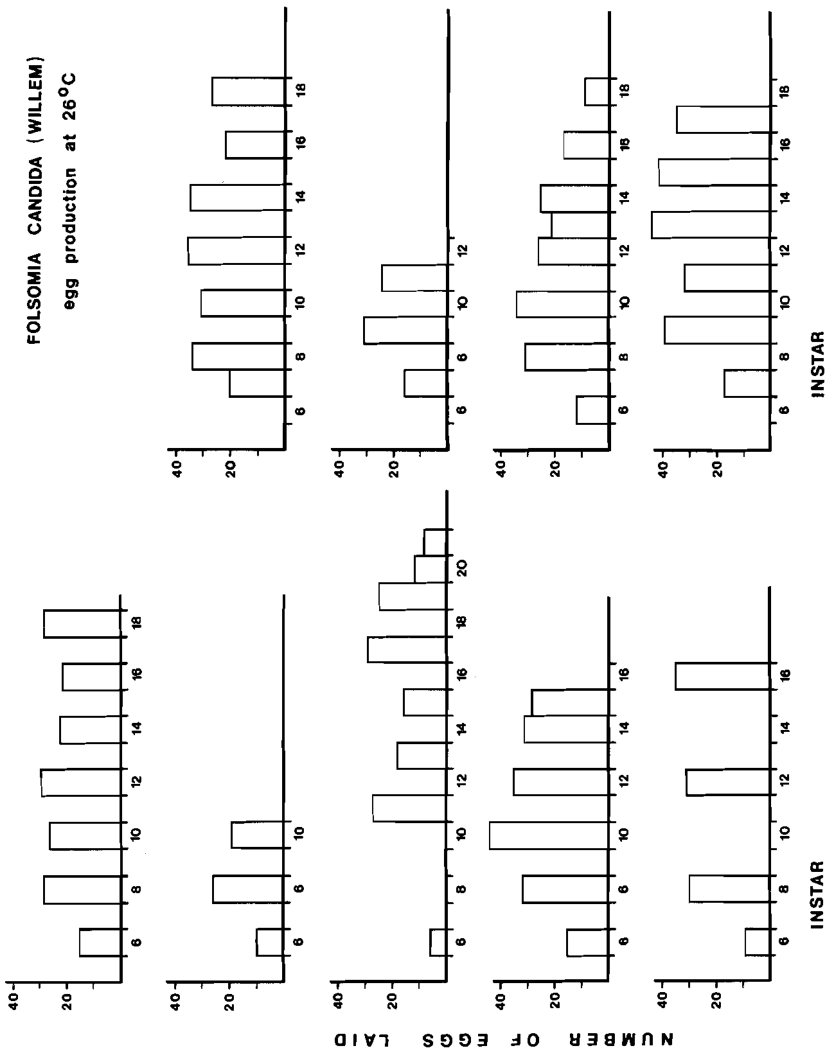

Fig. 2. Egg production by nine single females of *Folsomia candida* (Willem) at 26°C.

Table 3. Intervals, in instars, between ovipositions of *Folsomia candida* (Willem) at three temperatures.

	Percent of all observed intervals		
Intervals in instars	15°C	21°C	26°C
1	0.3	3.3	9.6
2	97.3	94.7	84.3
3	0.5	0.6	1.2
4	1.6	1.3	3.6
5			1.2

Table 4. Percentage of egg laying females of *Folsomia candida* (Willem) in instars 6 through 18.

	Productive females, in % of all females alive		
Instar	15°C	21°C	26°C
6	86.6	100.0	52.6
7	10.0	00.0	42.1
8	90.0	100.0	57.8
9	10.0	00.0	38.8
10	90.0	100.0	50.0
11	10.0	00.0	50.0
12	90.0	100.0	53.3
13	10.3	00.0	53.3
14	82.7	100.0	57.1
15	6.8	00.0	50.0
16	89.6	92.3	50.0
17	3.7	00.0	44.4
18	96.3	100.0	71.4

Females at 15°C commonly laid from 160 to over 200 eggs during one oviposition, while the highest number of eggs recorded at 21°C was 157. No more than 44 eggs were laid in any given instar at 26°C and none of the females produced more than 209 eggs in a life time (Table 5). The mean number of ovipositions per female was 13 at both 15° and 21°C and only five at 26°C.

Table 5. Average and maximum egg production per female of *Folsomia candida* (Willem) in a life time. Data for 21°C taken from Snider (1973).

	15°C	21°C	26°C
Mean total/ fem./ life	1344	1011	130
Max. eggs by one female	2355	1654	209

Animals of "new stock" origin reared at 21°C showed an egg laying pattern as well as a fecundity rate similar to "old stock" individuals. Discrepancies in the timing of fecundity peaks are thought to be due to the great difference in the number of replicates observed (Fig. 3).

In order to include all eggs laid per female, the data on egg production per instar were summarized in groups of two instars (Fig. 4). Females reared at 15°C were clearly the most productive. A temperature of 26°C drastically reduced the number of eggs laid; the relatively low number of ovipositions was due to increased mortality, since all females laid eggs until a short time prior to death. In *Isotoma notabilis* the process is somewhat reversed; at temperatures lower than the recorded optimum (17°C) the number of laying periods is reduced, although the animals apparently live long past the attainment of maturity (Sharma and Kevan, 1963b).

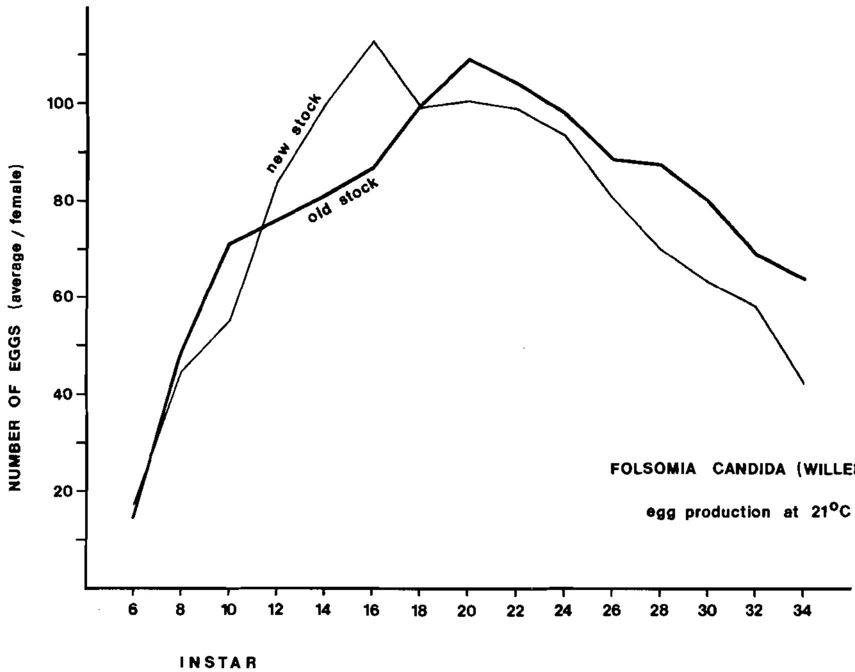

Fig. 3. Average egg production per instar in "old stock" and "new stock" females of *Folsomia candida* (Willem) at 21°C. Data for "old stock" taken from Snider (1973).

At 15°C a mean of 27.5 (24-43) days elapsed from the day of hatching to the first oviposition, as compared to 17.7 (16-25) days at 21°C. At 26°C longer instar durations slightly delayed the onset of egg production. A mean of 20.6 days of development with a range of 15-42 days was needed until the first oviposition.

EGG VIABILITY

The presence of non-viable eggs in a batch of otherwise viable eggs has been recorded in the past (Waldorf, 1971; Marshall and Kevan, 1962) and may be a common occurrence in Collembola. At the first oviposition of *Isotoma notabilis*, Sharma and Kevan (1963b) noted small eggs which failed to develop and related the phenomenon to possible

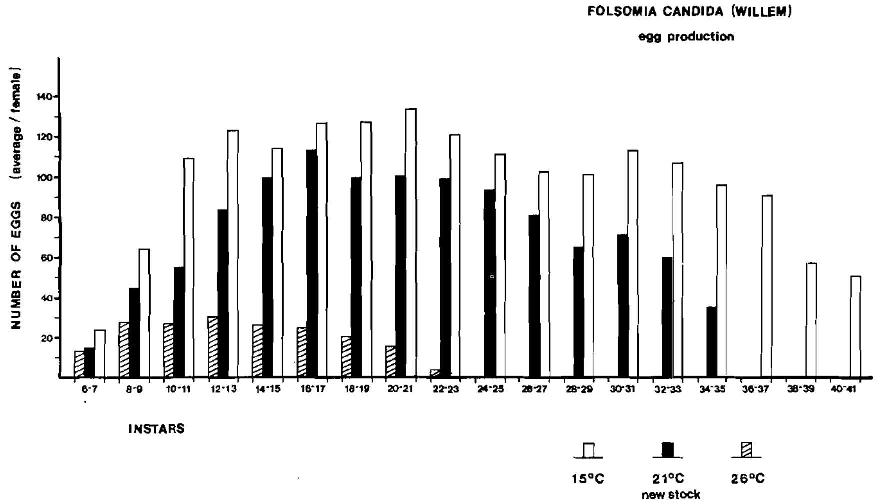

Fig. 4. Average egg production per female of *Folsomia candida* (Willem) at three temperatures.

immaturity of the females. In *F. candida* a somewhat similar observation was made (Snider, 1973). Moreover, a pattern in egg viability throughout the life of the females was established: hatching success increases concurrently with the increase in egg production and decreases with progressing age and decreasing fecundity.

Data obtained previously (Snider, 1973) on viability of eggs at 21°C are not included in the presentation of results. "Old stock" individuals at 15° and 26°C and "new stock" at 21°C, all of which were reared concurrently, allowed a more valid comparison of data in view of the time when observations were made. Imperceptible changes in the technique of handling and counting eggs may have contributed to discrepancies between present and past data.

The first batch of eggs showed a relatively low viability at all temperatures. Generally, 15°C proved to favor egg viability more than either of the higher temperatures. At 26°C viability rose to 87.7% in the 10th instar, then declined rapidly and somewhat irregularly. At any time from the second to the 10th oviposition, females at 15°C laid highly viable eggs (96 to 98%) and at 21°C viability reached a level of about 95%. Decrease in viability with age was found to be gradual, with a low of 90% in the 18th oviposition at 15°C (Table 6).

SUMMARY

Parthenogenetic females of *Folsomia candida* (Willem) were reared in isolation at 15° and 26°C and observed throughout their life time. Results were compared to previously obtained data on the bionomics of the species at 21°C (Snider, 1973).

1. Duration of the stadia in older females was about twice as long at 15°C as it was at 21°C. A 26°C temperature slightly lengthened instar duration, indicating that 26°C may approach the species specific upper temperature limits. At all temperatures intervals between moults lengthened with progressing age.

2. A temperature of 26°C shortened the life span to a mean of 72 days as compared to 136 days at 21°C. At 15°C average longevity was extended to 240 days. Mortality reached 100 percent after 115 days at 26°C, 198 days at 21°C and 352 days at 15°C.

3. Egg production was highest at 15°C. The maximum number of eggs laid in a life time was 209 eggs at 26°C, 1654 eggs at 21°C and 2355 eggs at 15°C. Productive and

Table 6. Viability, in percent, of eggs of *Folsomia candida* (Willem) at three temperatures.

Ovipos.	Instar	old stock 15°C	new stock 21°C	old stock 26°C
1	6	86.6	74.7	73.5
2	8	96.6	87.9	86.1
3	10	97.5	93.3	87.7
4	12	97.7	95.6	74.6
5	14	98.1	95.8	58.9
6	16	96.7	96.2	72.7
7	18	96.3	94.4	64.6
8	20	96.2	96.6	53.9
9	22	95.7	91.1	
10	24	96.8	91.2	
11	26	94.5	90.8	
12	28	94.7	87.9	
13	30	93.8	84.9	
14	32	92.2	87.6	
15	34	91.3	92.8	
16	36	91.5	79.3	
17	38	91.8		
18	40	90.1		

non-productive instars alternated in a distinct rhythm, although irregularities were common at 26°C. At both 15° and 21°C temperatures, a mean of 13 ovipositions was recorded per female, whereas at 26°C the number of layings averaged five.

4. Egg viability was highest at 15°C. In general, hatching success was low at the first oviposition; it increased with increasing fecundity and decreased with progressing age.

5. Females of "new stock", collected in the field prior to the investigation and reared at 21°C, showed mortality and fecundity patterns similar to those of "old stock" females originating from cultures maintained continuously in the laboratory for the past eight years.

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