MOLTING, FECUNDITY, AND LONGEVITY IN *WILLOWSIA JACOBSONI* (COLLEMBOLA: ENTOMOBRYIDAE)

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ABSTRACT

Molting, fecundity and longevity were investigated in two populations of *Willowsia jacobsoni* reared on plaster of paris-activated charcoal substrate at 30°C. Males reached maturity after an average of five molts and females after six. Number of immature instars varied between individuals. Average number of molts during a lifespan was 30.2 for males and 28.8 for females, highest number of molts was 41 by a male. The first stadium lasted three days and was longer than each of the next four stadia. Average molting frequency for both sexes was highest during the first two weeks of life (immature stage). From the third to the 13th week, molting frequency was about 2.5 molts per week. From the 14th week on, individuals molted twice a week until their death. Alternation of short and long instars occurred in 89% of males and 71% of females reared in isolation. Mean number of instars preceding cycling was 5.0 in males and 6.3 in females. All specimens stopped cycling several instars before their death. Parthenogenesis did not occur. Mean number of eggs laid by females that completed their reproductive lives was 361.3. Average number of ovipositions by these females was 11.6 and mean number of eggs per batch was 31. The latter number increased during the first six ovipositions, decreased gradually until the 10th batch and decreased rapidly thereafter. Mean number of days between successive egg batches was 3.05. Average number of days between hatching and the first oviposition was 14.1, mean length of reproductive life was 50.3 days and mean number of days from last oviposition to death was 11.9. Approximately 65% of the female's life was devoted to reproduction. Average lifespan for isolated males and females, and for reproducing males was 87 days but lifespan for reproducing females decreased to 64.5 days.

RESUMEN

Ecdisis, Fecundidad y Longevidad en *Willowsia jacobsoni* (Collembola: Entomobryidae). Se investigó el proceso de la muda, la fecundidad y la longevidad en dos poblaciones de *Willowsia jacobsoni* criadas en substratos de yeso y carbón activado a 30°C. Los machos alcanzaron la madurez sexual luego de unas cinco mudas y las hembras luego de unas seis. El número de estadios inmaduros varió entre los ejemplares. Los machos mudaron en promedio 30.2 veces durante su vida y las hembras en 28.8 ocasiones; el mayor número de mudas fue 41 por un macho. El primer estadio duró tres días y fue más largo que cada uno de los próximos cuatro. Para ambos sexos, el promedio de mudas fue más alto durante las primeras dos semanas de vida (etapa inmadura). De la tercera a la decimocuarta semana, la frecuencia de mudas fue aproximadamente 2.5 por semana. De la decimocuarta semana en adelante, los ejemplares mudaron dos veces por semana hasta su muerte. El 89% de los machos y el 71% de las hembras criadas en aislamiento alternaron mudas cortas con mudas largas. El número promedio de mudas antes de comenzar dicha alternancia fue 5.0 para los machos y 6.3 para las hembras. Todos los ejemplares suspendieron la alternancia varias mudas antes de su muerte. No sucedió partenogénesis. El número promedio de huevos producidos por las hembras que

Carib. J. Sci. 23(2): 298-304 (1987)

completaron su vida reproductiva fue 361.3. Número promedio de oviposiciones por estas hembras fue 11.6 y el número promedio de huevos por puesta fue 31. Esta última cifra aumentó desde la primera hasta la sexta oviposición, disminuyó lentamente entre la sexta y la décima puesta, y la disminución fue más rápida en oviposiciones subsiguientes. El número promedio de días transcurridos entre puestas consecutivas fue 3.05. Número promedio de días desde la eclosión hasta la primera oviposición fue 14.1, el largo promedio de la vida reproductiva fue 50.3 días, y el número promedio de días entre la última oviposición y la muerte fue 11.9. Aproximadamente, el 65% de la vida de la hembra fue dedicada a la reproducción. La vida promedio para machos y hembras criados en aislamiento, y para machos que se reprodujeron fue 87 días. La vida promedio de las hembras que se reprodujeron disminuyó a 64.5 días.

Introduction

Studies of the life history of tropical Collembola are scarce. Until recently, the only information available for Neotropical species was the paper by Rapoport and Aguirre (1973) on the population dynamics of the Venezuelan species *Onychiurus yolandae*. Mari Mutt et al., (1984) reported the effects of various temperatures on the duration of embryonic development in *Willowsia jacobsoni*. In the present contribution we investigate molting, fecundity and longevity in two laboratory populations of the latter species.

Materials and Methods

Materials needed for preparing cultures are listed by Mari Mutt et al., (1984). Differences in coloration that distinguish the sexes are described by Mari Mutt (1981). For the first experiment we transferred an egg into each of 50 4x4 cm plastic culture jars kept in an incubator at 30 ± 0.5°C and total darkness. Nine eggs failed to develop and four individuals were accidentally lost. The remaining 37 individuals were observed every 24 hours until they died. The days when molting occurred were recorded and exuvia were removed. Food (baker's yeast) was changed daily to avoid excessive fungal growth.

For the second experiment we placed in each of 20 culture jars a pair of third instar male and female. We proceeded as in the first experiment but this time also recording the number of eggs laid by each female.

Results and Discussion

MOLTING

Number of pre-reproductive molts

Mating experiments suggest that males reach maturity after an average of five molts and females probably after six molts. The data on number of instars preceding cycling of short and long stadia support this observation. Mean number of instars preceding the onset of cycling was 5.0 for males (4-7, n = 17) and 6.3 for females (5-9, n = 10). Variation in number of pre-reproductive molts has been reported for *Folsomia similis* (Sharma and Kevan, 1963a), *Pseudosinella alba* and *P. petterseni* (Sharma and Kevan, 1963b) and *Onychiurus armatus* (Snider, 1974).

The average number of days between hatching and the first oviposition by females (second experiment) was 14 days. Isolated males molted an average of 5.9 times during their first two weeks of life and females molted an average of 6.4 times.

Number of molts during lifespan

Average number of molts during lifespan was 30.2 for males (10-41, n = 16, S.D. = 8.96) and 28.8 for females (17-38, n = 13, S.D. = 7.93). The highest number of molts (41) was recorded for a male that lived 132 days. Two females molted 38 times during their lifespans of 112 and 121 days. The maximum number of molts during the lifespan of a springtail is 68, reported by Mertens et al., (1983) for *Hypogastrura viatica*.

Frequency of molting

In 33 of 34 specimens (19 males and 14 females), the first stadium lasted three days. Average duration of the next four stadia for both sexes was less than two days. Lindenmann (1950) working with *Orchesella*, and Waldorf (1971) working with *Sinella curviseta*, found that the first stadium lasted longer that the next few stadia. The opposite occurs in *Onychiurus* (Milne, 1960; Snider, 1974; Robles-Chillida, 1979) and *Hypogastrura* (Mertens et al., 1983).

Figure 1 shows the number of molts per week for 16 males and 13 females. For both sexes, molting frequency was highest during

the first two weeks, indicating rapid growth through the immature stage. During this time many specimens molted twice in less than 24 hours (zeros in Table 1). Average molting frequency from the third through the 13th week remained at 2.5 molts per week (a molt every 2.8 days). From then on, individuals continued to molt almost exactly twice per week until their death.

Snider and Butcher (1973) reported an increase in average stadium duration from the second through the 38th instar of *Folsomia candida*. Snider (1974) obtained similar results for the first 31 instars of *Onychiurus armatus*. Such a relation was not evident in *W. jacobsoni*.

Alternation of short and long instars

Table 1 presents the duration of successive molting intervals for 14 specimens reared in isolation. Specimens 10-14 showed no definite or sustained cycling but specimens 1-9 went through one or two well-defined periods of cycling. It should also be noted that a) the duration of cycling varied between individuals, b) cycling may be interrupted and later re-started, c) a number of instars precede the beginning of cycling and d) cycling ceases several instars before death of the specimens. Instars preceding cycling probably correspond to the immature stage. The period of cycling should correspond to the reproductive stage, and the final non-cycling period to the post-reproductive portion of the life cycle. Christiansen (1964) states: "In general, it appears that Collembola pass through three stages: (a) juvenile, (b) postmaturity growth, and (c) senile molts.

Joosse and Veltkamp (1970) found that 75% of the specimens of *Isotoma viridis* and 25% of *Tomocerus minor* showed definite alternation between short and long instars. They also noted that most individuals that did not cycle were females. In *W. jacobsoni*, 89% of the males and 71% of the females cycled. The data in table 1, and those for the other specimens not listed, indicate that cycling periods in males are more regular than in females.

FECUNDITY

Parthenogenesis and sperm storage

Isolated females did not lay eggs and those whose male partner died immediately stopped ovipositing. These observations indicate that parthenogenesis does not occur in *W. jacobsoni* and that females can not store sperm accross a molt.

Number of eggs laid by females

The mean number of eggs laid by the nine females that completed their reproductive life (egg laying stopped before their partner died) was 361.3 (279-502, S.D. = 92.6). The average number of egg batches laid by these females was 11.6 (10-14, S.D. = 1.42). Mean number of eggs per batch was 31 (8-62, S.D. = 11.9). These figures are among the highest reported for Collembola but comparisons between species are not reliable due to the variety of experimental methods used and to the effects of various environmental factors. Ashraf (1969) showed that an increase in substrate pH from 7.2 to 9.7 drastically reduced fecundity in *Onychiurus bhattii*. Hutson (1978) found that maximum fecundity in *Folsomia candida* occurred at pH of 5.2, with reduced oviposition at lower or higher pH. Food quality affected all parameters of fecundity in *Cryptopygus thermophilus* (Kurup and Prabhoo, 1982).

Number of eggs in successive batches

Number of eggs per batch increased during the first six ovipositions (Fig. 2) as a result of the continued growth of the females. Females started ovipositing when they measured about 1.4 mm but their maximum size was 2.2 mm. From the sixth to the tenth batch the number of eggs gradually decreased. From the tenth batch on, number of eggs decreased more rapidly. Two females laid a 13th batch (28 and 38 eggs) and only one laid a 14th batch (21 eggs).

Gradual increase in egg batch size during early reproductive life has been reported for *Lepidocyrtus lanuginosus* (Hale, 1965), *Sinella curviseta* (Nijima, 1973) and *Onychiurus armatus (Snider, 1974). Decrease in batch size during later ovipositions has been reported by Snider (1973) for Folsomia candida*, Nijima (1973) for *Sinella curviseta*, and Rapoport and Aguirre (1973) for *Onychiurus yolandae*.

Days between ovipositions

Average number of days between successive batches was 3.05 (2-5, S.D. = 0.76). There was little difference between any pair of batches, indicating that egg laying contin-

ued with about the same frequency during the female's life. In *Folsomia candida*, intervals between ovipositions increased with the age of the female (Snider, 1973).

Percent of female lifespan devoted to reproduction

Average number of days between hatching and the first oviposition was 14.1 (12-15, S.D. = 1.45). Mean length of reproductive life was 50.3 days (40-64, S.D. = 12.03). Average number of days from last oviposition to death was 11.9 (7-22, S.D. = 5.67). Mean duration of reproductive period divided by average lifespan (76.8 days) indicates that 65% of a female's life was devoted to reproduction. Rapoport and Aguirre (1973) reported that reproduction occupied 60.9% of the life cycle of *Onychiurus yolandae*. Bretfeld (1977) reported 66% for *Heterosminthurus insignis* and 74% can be obtained for *Cryptopygus thermophilus* from the data given by Kurup and Prabhoo (1982).

LONGEVITY

The average lifespan for males reared in isolation was 88.1 days (28-139, n = 16, S.D. = 32.2) and for reproducing males was 89.3 days (32-130, n = 20, S.D. = 28.5). Average lifespan for non-reproducing females was 86.1 days (45-121, n = 13, S.D. = 26.9) and for reproducing females was 64.5 days (63-69, n = 20, S.D. = 18.1). A STUDENT test for comparison of the means showed that the difference between the lifespan of reproducing females vs. non-reproducing females and males that did or did not reproduce is significant at the 0.025 confidence interval. Reproduction adversely affects lifespan duration in females but no such effect occurs in males.

The average longevity of *Willowsia jacobsoni* is considerably shorter than that reported for most Collembola. Most springtails can live four to five months and many can live more than a year (Christiansen, 1964). The short longevity of *W. jacobsoni* reflects its life cycle strategy as a tropical species adapted to fairly high temperatures. Nijima (1973), and Snider and Butcher (1973) reported an inverse relation between temperature and longevity.

ACKNOWLEDGMENTS

We wish to thank Drs. Renate Snider and Johann Mertens for their careful review of the manuscript and their many useful suggestions. We are solely responsible for not incorporating all of them.

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TABLE 1.-- Duration of successive molting intervals in days for 14 individuals of Willowsia *jacobsoni* reared in isolation. Numbers underlined indicate periods during which definite alternation between short and long molting intervals occurred. A zero means that two consecutive molts occurred in less than 24 hours.

Spec. No. and Sex	Duration of Successive Molting Intervals in Days
1. male	10112040406041314141606161413222232 2
2. male	0101304040313131313131221312
3. male	1011314121141322233214231313152334
4. female	0001122214131413122413133331333
5. female	2010242413132323142423121213122232
6. female	1101015161214131314131322222
7. male	1001313232414132432141313 1221
8. male	0102141414131414142214151515141222222
9. male	1010131413224213140423142323333333234 55
10. male	1111241213512222222222
11. male	1101011213221301213012222 32
12. female	0100222212131211131121310 31
13. female	1001151321142452423122222 22
14. female	0111022213155122222322221222231

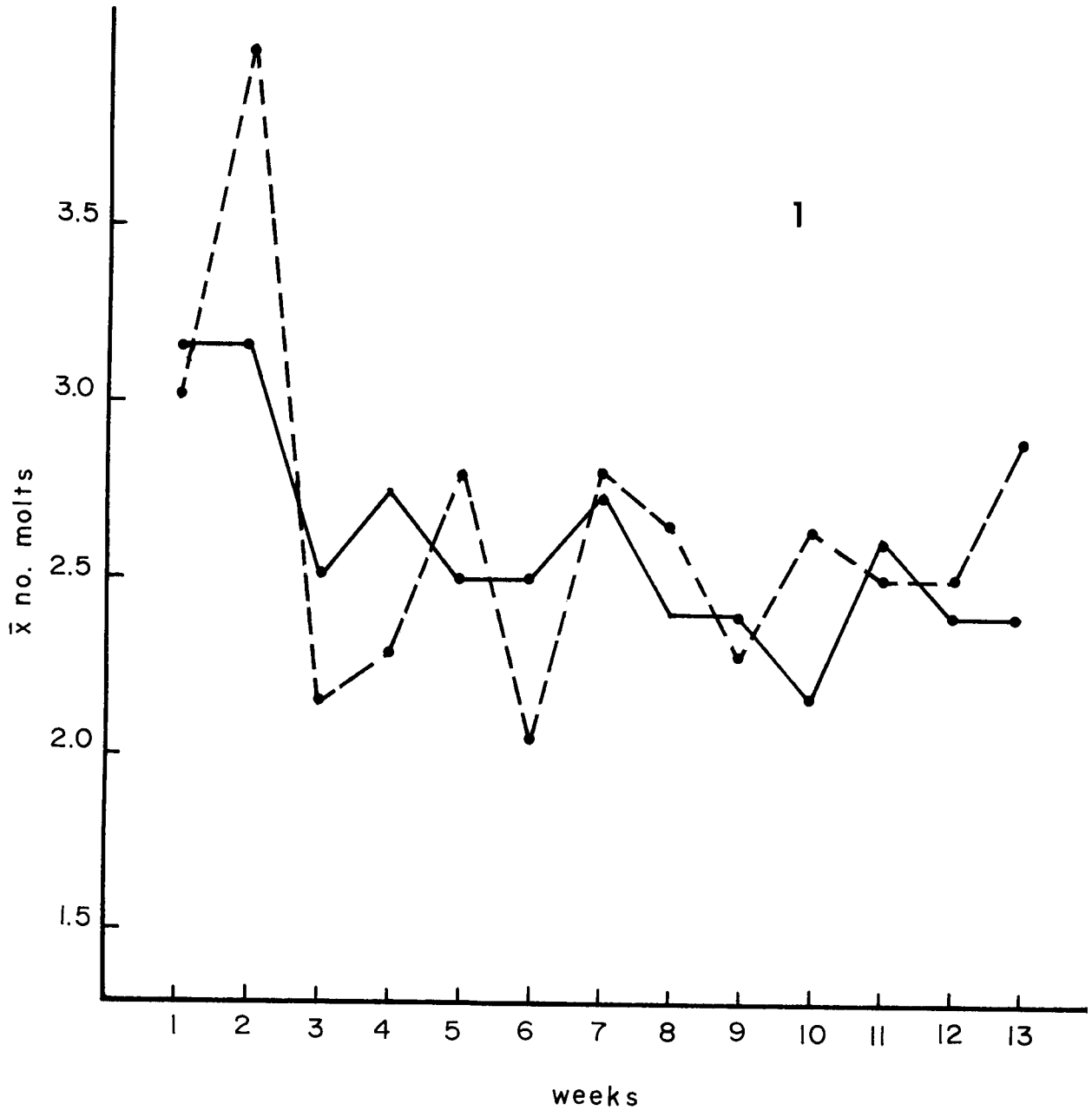

FIGURE 1. —Mean number of molts recorded during 13 weeks for 16 males and 13 females reared in isolation. Solid line represents males, broken line represents females.

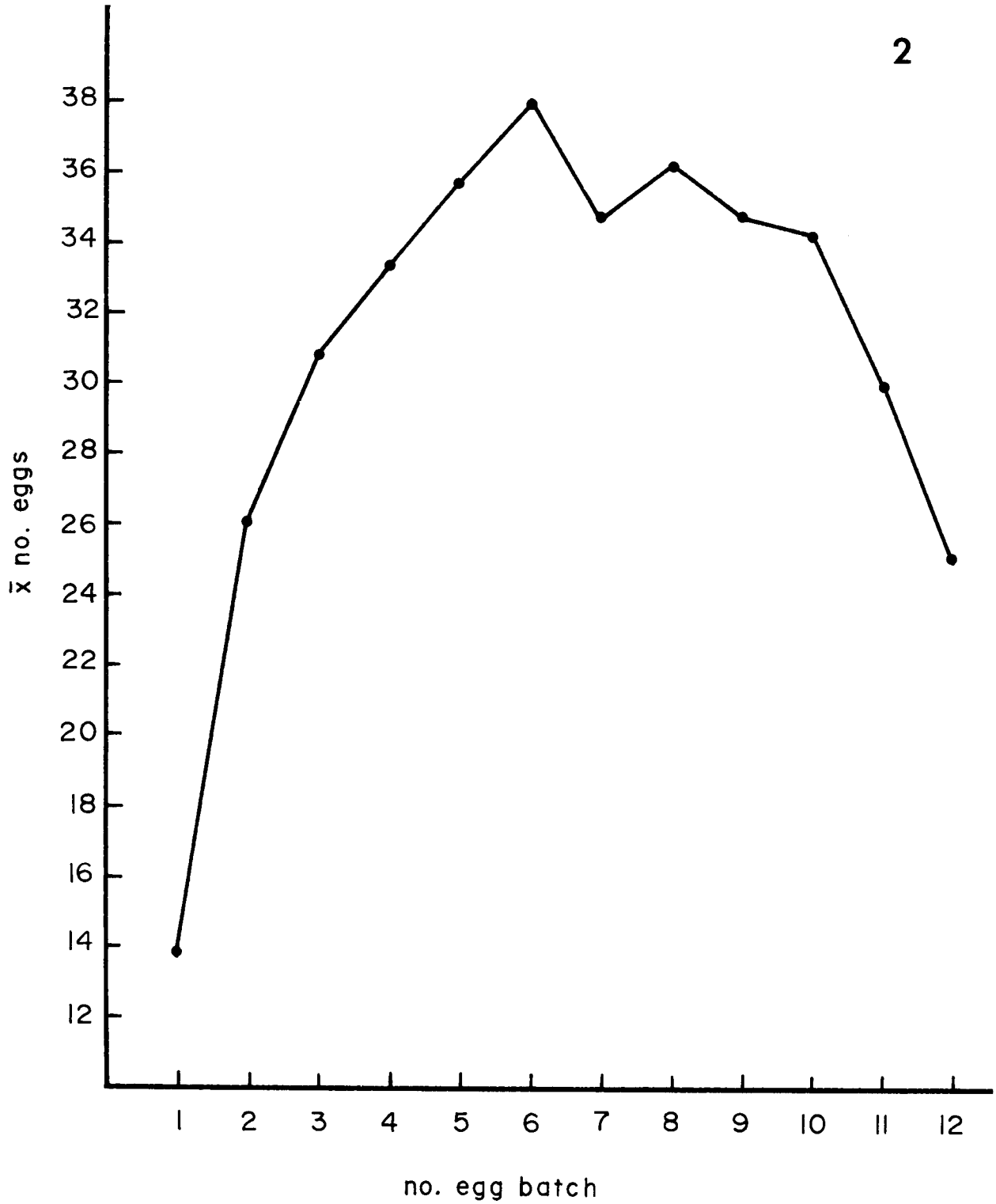

FIGURE 2. —Mean number of eggs in each of 12 consecutive batches produced by nine females that completed their reproductive life (stopped ovipositing before their partner died).