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Trade-off between reproduction and length of adult life in males and mating females of aphids

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Aphids, *Cavariella aegopodii*, cost of reproduction, length of adult life, sexuals

Abstract. Males of the willow-carrot aphid, *Cavariella aegopodii* (Scopoli) (Sternorrhyncha: Aphididae), that were caged with five or more females had shorter adult lives than those caged with one or no females. Similarly mated females had a shorter adult life than unmated females. The difference in lifespan appears to result from a change in the time of onset of senescence rather than a change in the rate of senescence. Contrary to what is observed in most other animals unmated males of the willow-carrot aphid had much longer lives than unmated females. The asymmetry of the sexes in terms of the factors that affect their fitnesses and the deadline to further egg maturation imposed by leaf fall possibly accounts for why the males of this aphid are potentially the longer lived sex.

INTRODUCTION

Life history theory predicts that reproductive activity should shorten adult life (Roff, 1992). However, there is little unequivocal support for this idea because of the confounding effect of an organism's size and condition on survival, and mating success (Partridge & Harvey, 1985). Manipulative experiments with *Callosobruchus* (Coleoptera), *Drosophila* (Diptera) and *Rhagoletis*, however, have clearly indicated that reproduction carries a cost in terms of future survival (Partridge & Farquhar, 1981; Roitberg, 1989; Tatar et al., 1993). However, the generality of this phenomenon needs to be established by similar studies on other groups of insects. In addition it is of interest to know whether reproduction results in a change in the timing of the onset of senescence or in the rate of senescence and whether one sex lives longer than the other, as has been recorded for other animals (Hazzard, 1990; Tatar & Carey, 1994).

This paper presents results of manipulative experiments, using the willow-carrot aphid, *Cavariella aegopodii* (Scopoli) (Aphididae), on the length of adult life of males allowed access to different numbers of sexually receptive mating females, and of mating females that were mated and laid eggs compared with those that were unmated and did not lay any eggs.

MATERIAL AND METHODS

The willow-carrot aphid is a host-alternating aphid that moves between willow (*Salix* spp.) and carrot (*Daucus carota* L.) in early summer and autumn. The remigrants that return to willow in autumn were obtained by rearing the aphid on carrot at 12°C and a short day length of 12 h (Kundu & Dixon, 1993). The remigrants are made up of two distinct morphs; winged males and winged parthenogenetic females. The latter after returning to willow give birth to the mating females. That is, the males and mating females mature at the same time but on different host plants. On reaching maturity individual males were confined on

willow leaves in 5 cm diameter clip cages with different numbers of recently matured mating females and the males observed daily until they died. The third instar unwinged parthogenetic females used in this experiment were reared on willow and were replaced every two days. The experiment was carried out at 12°C and a 12 h day length. Within a day of becoming adult mating females are attractive to males. Mated and unmated mating females were kept without males on small willow saplings kept at 12°C and 12 h of daylight and observed daily until they died. The aphid terminology used above is that recommended by Blackman (1994), but below for simplicity mating female will be abbreviated to female.

RESULTS

Longevity of males

Males kept in isolation or with one female survived significantly longer than those kept with 5 or more females. When kept with one female the removal of the female once mated did not have a significant affect on the length of life of the males (Table 1).

TABLE 1. The longevity of males kept with different numbers of females.

No. of females	No. of replicates	Mean longevity (days ± S.E.)	
0	6	32.3 ± 2.6^a	
1*	6	27.8 ± 1.8^a	28.9 ± 1.5^a
1	6	26.5 ± 2.8^a	
5	6	17.8 ± 2.4^b	
10	6	19.0 ± 1.9^b	18.0 ± 1.2^b
15	6	17.2 ± 2.3^b	

* The female was removed after it had been mated.
Statistical test: One-way ANOVA followed by range test, values in the same column with different letter suffixes are significantly different at $P = 0.05$.

To determine whether the reduction in longevity was due to the presence of other aphids, i.e., a crowding effect, males were kept with either 5 females or 5 third instar parthenogenetic females. A reduction in longevity was only observed in the presence of females ($t = 3.2$, $df = 10$, $P = 0.01$; Table 2).

TABLE 2. The longevity of males kept with sexual and parthenogenetic females.

No. of females	No. of replicates	Mean longevity (days ± S.E.)
5 mating	6	17.3 ± 2.0
5 parthenogenetic (3rd instar)	6	30.3 ± 3.0

The results for the survival of males fall into two groups: those (n = 18) that were kept on their own or with one female (group 1), and those (n = 24) that were kept with 5 or more females (group 2) ($t = 5.75$, $df = 34$, $P < 0.01$; Tables 1 and 2). The survival curves of these two groups of males also indicate that keeping the males with 5 or more females reduced their longevity (Fig 1). On day 16 all of the males in the first group were alive whereas significantly fewer (61%) of the second group were alive ($\chi^2 = 8.6$; $P < 0.01$). This indicates that the onset of senescence occurred earlier in the second group of males.

Although the small size of our data set precludes statistical analysis of the shapes of the survival curves for the two groups of males (cf. Tatar et al., 1993) nevertheless these

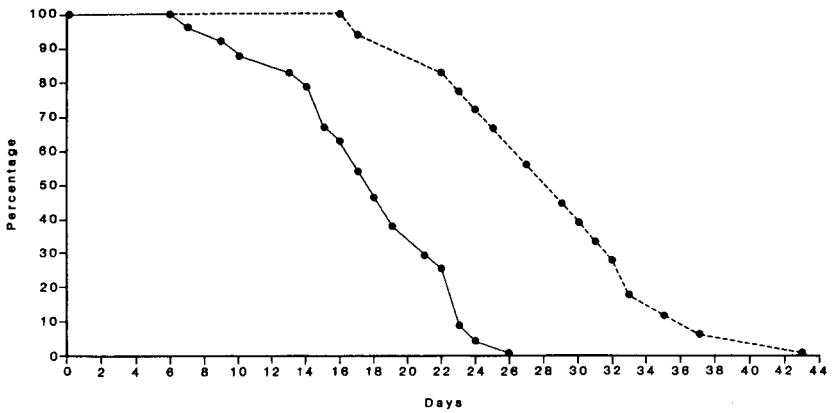

Fig. 1. Percentage survivorship in time of males of *C. aegopodii* that were kept on their own or with one mating female (- - - -) and of those kept with five or more mating females (——).

results and the above analysis support the view that reproduction advanced the onset of senescence rather than increased the rate of senescence.

Longevity of females

Unmated females survived for significantly longer (20.7 ± 1.9 days) than mated females (14.8 ± 1.5 days; $t = 2.5$, $df = 15$, $P < 0.05$). Although relatively few females (9 and 8, respectively) were used in this experiment nevertheless the change in the percentage survival in time shown by these two groups of females (Fig. 2) again indicates that reproduction tended to advance the onset rather than increase the rate of senescence.

Does one sex live longer than the other?

The unmated males lived on average 12 days longer than unmated females ($t = 3.7$, $df = 13$, $P < 0.01$). That is, when not mated males live on average 1.6 times longer than unmated females. However, males that are kept with five or more females did not survive longer than mated females.

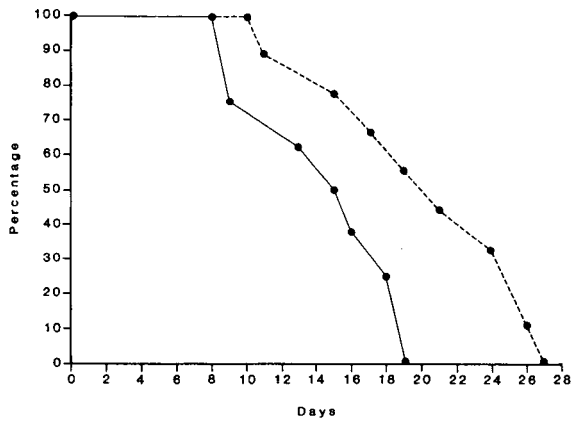

Fig. 2. Percentage survivorship in time of mating females of *C. aegopodii* that were mated (——) and unmated (- - - -).

DISCUSSION

In conformity with life history theory reproductive activity in both the males and the females of *C. aegopodii* reduced their longevity. A trade-off between reproduction and longevity has now been recorded in three orders of insects: Coleoptera, Diptera and Hemiptera.

Although the small size of the data set precluded rigorous statistical analysis, nevertheless the survival curves for both males and mating females tend to support the conclusions of Arking (1987), Arking & Wells (1990), Rose (1984) and Tartar et al. (1993), working with other insects, that changes in longevity associated with reproduction are a consequence of a change in the time of onset of senescence rather than a change in the rate of senescence. The availability of mates in the case of males, and mating, egg development and oviposition in the case of females could result in a cessation or suspension of feeding and a rapid depletion of their nutrient reserves, which could account for the advancement in the onset of senescence.

Contrary to the general rule of zoology that females are the longer lived sex (Hazzard, 1990), unmated males of the willow-carrot aphid live longer than unmated females. That unmated females of the bean beetle, *Callosobruchus maculatus*, live longer than unmated males has been attributed to the faster depletion of the energy reserves in the smaller males (Tatar & Carey, 1994). The males of the willow-carrot aphid are the smaller of the two sexes but have the larger lipid reserves; 37.2 and 32.8% of their dry weight for males and females, respectively. As the reserves of the male are not destined for egg production it is possible that more of the total is available for sustaining life. In addition, male aphids are not known to fight for access to females and mating appears to be a very simple affair.

The main reason why in aphids males live longer than females, however, may be because the fitness of a male depends on the number of females he fertilises, while the fitness of a female depends on her probability of mating and laying eggs. Both sexes can and do feed as adults. Females attract males while feeding, which they do by releasing sex pheromone from glands on the tibiae of their hind legs (Pettersson, 1970, 1971). Males, however, have to cease feeding in order to find females (Kozlowski, 1991). That is, selection is likely to favour males that spend more time searching. In the case of the wingless and less mobile females the deadline for the acquisition of resources for developing eggs is leaf fall. Therefore, selection is likely to favour females that mature and lay their eggs early in adult life. In addition, unlike many other insects aphids develop and lay their eggs on the same plant, therefore, little time is needed for locating oviposition sites. Thus in aphids the asymmetry of the sexes in terms of the factors that affect their fitnesses and the more definite deadline for females imposed by leaf fall possibly accounts for males being potentially the longer lived sex.

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