Variable longevity in the rusty grain beetle, *Cryptolestes ferrugineus*

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Abstract

Cryptolestes ferrugineus adults at 30 insects/15 g of food and 30°C had a shorter mean lifespan (24 weeks for 30 females and 13 weeks for 30 males) than adults mated with a single partner (25 weeks) or isolated virgins (32 weeks). Males in populations had the shortest lifespans, and the lifespans of females were inversely proportional to the number of males in the population.

The production of live adult offspring per female in populations of 30 adults was approximately half that of females mated once. Longevity was also negatively related to feeding effort when virgin adults of an inbred strain and outbred strain were individually fed either ground whole wheat (mean 32 weeks) or whole kernels of wheat with the seed coat over the germ removed (mean 23 wk) at 30°C, 75% r.h.

To simulate over-wintering of adult beetles, virgin adults or the inbred and the outbred strain were held at temperatures which decreased from 30°C or 22°C to 5°C, then increased to 25°C. Maximum lifespans were over 1 year and a few of the outbred beetles raised at 30°C lived for 1.5 years. Adults of both the inbred and outbred strains raised at 22°C had shorter lifespans than adults raised at 30°C. These results indicate that the probability of survival at low temperatures is significantly increased when the immature stages and a few weeks of adult life are passed at relatively high temperatures.

Introduction

The lifespans of insects are strongly influenced by population density, sexual activity, temperature and other environmental variables (Lints 1985; Sohal 1985). It has generally been found that density has a more adverse effect on males than on females and that isolated individual insects live longer than insects in groups (Ragland and Sohal 1973).

With *Tribolium* spp. the proportion of males in the population appears to be a strong determinant of lifespan. Spratt (1980) found that for the red flour beetle *Tribolium castaneum* (Herbst), individually isolated males, and females in all-female groups lived an average of 50 weeks. Males and females in mixed-sex groups lived an average of 40 weeks and males in all-male groups had mean lifespan of less than 20 weeks. The confused flour beetle, *T. confusum* J. du Val was not as long-lived as *T. castaneum*, but the lifespans of corresponding groups were in the same relative order (Spratt 1980). For isolated individuals of the American black flour beetle, *T. audax* Halstead and single-sex groups of 2, 4, 10, and 40, male lifespan decreased with each increase in density, but female lifespan did not show a consistent relationship to density (Soliman 1977).

Temperature is an important factor affecting longevity in poikilotherms and Kawamoto et al. (1989) found that 77 to 97% of *Cryptolestes ferrugineus* adults, kept individually isolated in cells at different constant temperatures in the range 10 to 30°C, were still alive when the experiment was terminated at 32 weeks, but at 35°C only 38% of the adults were still alive. It is not known how long *C. ferrugineus* (Stephens), the principal insect pest of stored grain in western Canada (Sinha and Watters 1985), can survive at different temperatures and still be capable of initiating new infestations in grain storage facilities. This information would be useful in devising control strategies and preparing computer models of population growth in grain bulks.

In the present study we determine how the lifespan and reproductive rate of the rusty grain beetle, *C. ferrugineus* are affected by density and sex ratios, and evaluate possible causes for variations in survivability and reproductive rate between these groups. The survival times of beetles living exclusively on a diet of whole kernel wheat or ground wheat were measured. We also determined the lifespans of individually isolated virgin adults of a laboratory strain and an outbred strain of *C. ferrugineus* at different constant temperatures and at temperatures that simulate field conditions.

Materials and Methods

C. ferrugineus strains

The rusty grain beetle is a small reddish-brown dorsoventrally flattened beetle, 1.5 to 2.5 mm in length. Thirty males and 48 females in a random sample taken from a culture (GV strain) had mean live weights of 0.283 mg and 0.274 mg, respectively. Two strains were used in this study: the SS strain (malathion susceptible), a relatively inbred strain, cultured in our laboratory since 1975; and the GV strain, an outbred genetically variable strain, prepared by making crosses between the SS strain and field strains collected in Manitoba, Canada, Kansas, USA., and northern England.

General methods

All experiments were conducted in the dark at 30 ± 1°C. Relative humidity was controlled at 75 ± 5% by saturated NaCl solutions (Winston and Bates 1960). Food used in the studies, except the experiment to determine the effect of living on whole kernel wheat, was ground whole wheat plus wheat germ that was ground fine enough to pass through a sieve with 420 µm apertures. Individually isolated virgin adults were kept in small vials, 1.5 cm by 4.5 cm; mated adults were kept in large vials, 2.8 cm by 7 cm.

The immature stages were reared in gelatin capsules. Eggs were placed individually in separate gelatin capsules, size 00 (2.5 cm long, 0.8 cm diam.), which were half full of ground wheat plus wheat germ. When adults emerged their sex was

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determined and they were placed in different mating situations or kept as virgins isolated from the other sex.

Lifespan of individually isolated adults

The lifespan of individually isolated virgin adults was determined with 45 males and 61 females of the GV strain in separate small vials containing 1 g of ground wheat plus wheat germ. The vials were taken out of the incubator once every 2 weeks for approximately 30 minutes and deaths were recorded.

Lifespan and reproductive rate of male/female pairs

The lifespan and reproductive rate of isolated male/female pairs were determined using large vials each containing one male and one female and 10 g of ground wheat plus wheat germ. There were 30 male/female pairs of the GV strain. Adults were 1–7 days old when mated. Ten male/female pairs adults were transferred to new food every week and the number of deaths that had occurred during the week was recorded. The old food from each vial, along with eggs and larvae, was emptied into a 224-mL jar containing 50 g of whole kernel wheat and 10 g of ground wheat plus wheat germ. The jars were kept in an incubator at 30 ± 1°C, 60 ± 5% r.h. and 5 weeks later the F_1 adults were counted. A similar procedure was followed for the other male/female pairs, except that parental adults were transferred to new food and deaths were recorded every 2 weeks.

The production of offspring by females mated with males for only 24 hours was investigated using 10 males and 10 females of the SS strain. One male and one female, 1–5 days old, were placed together in a large vial containing 10 g of ground wheat plus wheat germ. After 24 hours the males were separated from the females. The females were transferred to new food every week for 20 weeks and the F_1 offspring were raised by the same procedure that was used for mated pairs. None of the females produced offspring in the 6 weeks between the 13th and the 19th weeks so they were re-united with their original male partners for the 20th week.

Lifespan and reproductive rate of adults in groups

The lifespan and reproductive rate of adults of the GV strain kept together in groups of 30 were determined using 11 large vials with 30 adults and 10 g of ground wheat plus wheat germ in each vial. Three vials had 10 males and 20 females, three vials had 15 males and 15 females, three vials had 20 males and 10 females, one vial had 30 virgin males, and one vial had 30 virgin females. F_1 adults were raised and counted using the same procedure that was used in the experiment with male/female pairs.

Lifespan of adults living on whole kernel wheat

Newly emerged adults of the GV and SS strains, raised from eggs at 30°C on ground wheat in separate gelatin capsules, were placed separately in small vials, each containing 50 wheat kernels that had the seed coat over the germ removed. There were 104 adults of the GV strain and 115 adults of the SS strain. They were kept for the duration of adult life at 30°C. The lifespans of these adults were compared with the lifespans of adults at 30°C where the insects were fed ground wheat.

Adult lifespan at different constant temperatures and at temperatures that were varied during adult life

The lifespans of adults of the SS and GV strains were determined at constant temperatures of 22, 25, 30 and 35°C. The adults kept at each temperature were raised from eggs at the same temperature.

To simulate overwintering of adult beetles at temperatures likely to occur inside grain bulks, in grain elevators or large grain bins in Manitoba, Canada, adults of the SS and GV strains, raised from eggs at either 22°C or 30°C, were kept for various periods at a series of temperatures which decreased from 22°C or from 30°C to 5°C then increased to 25°C. The time that each group of adults was kept at each temperature interval is given in Figure 7.

Statistical procedures

Mean adult lifespans and mean developmental periods were compared with a one-way analysis of variance test. A two-sample Kolmogorov-Smirnov test (K-S test) was used to determine the significance of differences between the survival functions graphed in the figures. This is a non-parametric test recommended for survival data by Mode et al. (1984).

Maximum lifespan is the mean of the last surviving 10% of the population. Maximum lifespan was measured from the deposition of the egg to the death of the adult.

Results

Lifespan

Individually isolated virgin adults lived much longer than mated pairs or adults in groups of 30. Virgin adults in separate vials lived an average of 32 weeks, mated pairs of the GV strain in separate vials lived an average of 22 weeks, and the average lifespan of adults in mixed sex groups of 30 per vial at different sex ratios was 13 weeks (Fig. 1).

When isolated there was no difference between male and female longevity. When kept in separate vials with one female, males of both strains lived longer than females ($P < 0.01$), but in groups of 10 males and 20 females, 15 males and 15 females, and in groups of 30 virgin males or 30 virgin females, the females lived longer than males ($P < 0.01$). Adults in the group with 20 males and 10 females per vial had the shortest mean lifespan and the difference between males and females in this group was not significant ($P > 0.05$) (Figs. 2 and 3).

Differences in sex ratio in the groups with 30 adults together in one vial, including the all-male group, did not produce significant differences in male lifespan ($P > 0.05$). However, the lifespan of females in the groups with 30 adults per vial decreased as the proportion of males increased.

Reproductive rate

The maximum reproductive period for females was 20 weeks. During most of this time, females of the GV strain that were isolated in separate vials with one male produced offspring at a higher rate than females in the groups with 30 adults per vial, and their mean lifetime production of offspring was 1.8 to 2.3 times greater than the mean lifetime production of females in the 30-adult group that had the highest number of offspring (Fig. 4).

Within the groups with 30 adults per vial the production of offspring per female was inversely proportional to the number of females in the group; each decrease of five females per group increased lifetime production of offspring per female by approximately 50%.

Fig. 1. Survival curves for *C. ferrugineus* GV strain virgin female adults kept individually in separate vials (●), or in the following groups: 1 male and 1 female (○), 15 males and 15 females (△), 10 males and 20 females (▲), 20 males and 10 females (×) at 30°C, 75% relative humidity.

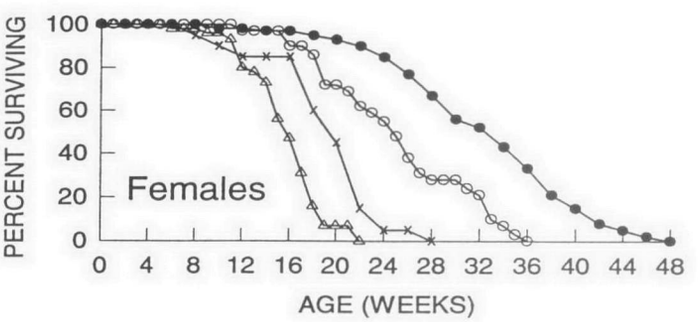

Fig. 2. Survival curves for *C. ferrugineus* GV strain virgin female adults kept individually in separate vials (●) or in a group of 30 in one vial (○), mated females kept in groups of 15 males and 15 females in one vial (△), or 1 male and 1 female in one vial (×) at 30°C, 75 % relative humidity.

Fig. 3. Survival curves for *C. ferrugineus* GV strain virgin male adults kept individually in separate vials (●) or in a group of 30 in one vial (○), mated males kept in groups of 15 males and 15 females in one vial (△), or 1 male and 1 female in one vial (×) at 30°C, 75% relative humidity.

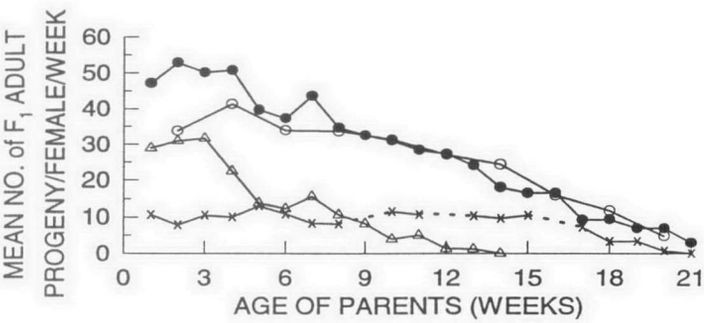

Fig.4. Rate of production of F_1 progeny per female per week by *C. ferrugineus* SS strain females after a single 24 hour period with a male (△), by mated pairs of the GV strain kept 1 male and 1 female per vial with new food every week (●) or every two weeks (○) and by groups of 15 males and 15 females in one vial (×) at 30°C, 75% relative humidity.

Among the groups with mated pairs in separate vials the GV strain group that was provided with fresh food every week produced the largest number of offspring per female, both during the first 8 weeks and during the entire lifetime of the females.

Females of the SS strain kept in separate vials after being mated with a male for only 24 hours, produced a mean of 180 offspring during a period of 13 weeks. No viable eggs were laid in the period from 13 to 19 weeks but when the nine females still alive were reunited with their male partners at 20 weeks, 14.5 offspring per female were produced by four females (Fig. 4). This suggests that to reach their maximum potential production of offspring, females need to mate a number of times over a relatively long period.

Lifespan of adults living on whole kernel wheat

Adults of both the SS and GV strains lived longer on ground wheat than on whole kernel wheat with exposed germs (ANOVA and K-S test, $P < 0.01$) (Fig. 5). There was no difference in lifespan between strains ($P > 0.05$) or between the sexes ($P > 0.05$) on either type of food. It was evident that beetles living on whole kernel wheat had sufficient food because at the time of death even the longest-lived beetles left 15–25 wheat kernels with the germ still intact. The rest of the kernels had the germ partially or completely eaten out.

Lifespan of adults at different temperatures

Individually isolated virgin adult males of the GV strain had longer mean lifespans than individually isolated virgin females of the GV strain at all of the eight temperature treatments used for this strain, and at seven of the temperature treatments males had longer maximum lifespans than females.

The mean lifespans of virgin adults of the inbred strain (SS) (Fig. 6) and the outbred strain (GV) at constant temperatures of 25 and 30°C were similar ($P > 0.05$), but at constant temperatures of 22 and 35°C, mean adult lifespans of the outbred strain were significantly longer ($P < 0.05$). In general, beetles of the inbred strain survived as long as beetles of the outbred strain only at those constant temperatures that were close to the temperatures at which they had been cultured in the laboratory for the last 15 years.

On the varied temperature schedules, mean adult lifespans of the GV strain were longer than those of the SS strain ($P < 0.05$) (Fig. 7). Beetles of the SS strain that were kept on the overwintering temperature schedule starting from 30°C, decreasing to 5°C, then rising to 25°C (Fig. 7), had a mean adult lifespan that was 40% longer than beetles of the SS strain on the overwintering temperature schedule starting from 22°C, decreasing to 5°C, then rising to 25°C ($P < 0.01$). The mean adult lifespan of beetles of the GV strain on the overwintering temperature schedule starting from 30°C was 52% longer than that of beetles of the GV strain that were on the overwintering temperature schedule starting from 22°C ($P <$

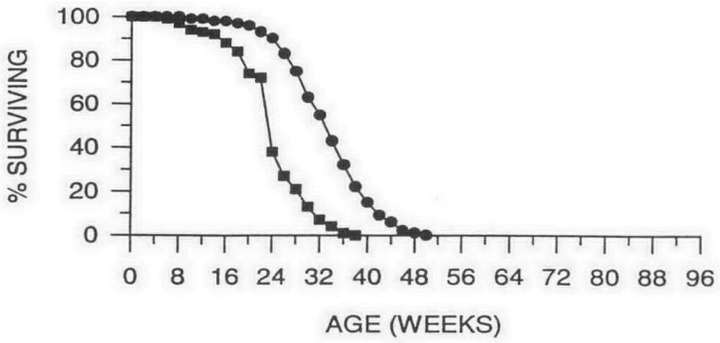

Fig. 5. Survival curves for *C. ferrugineus*, GV strain virgin adults, living on ground wheat (●), or on whole kernels of wheat with exposed germs (■) at 30°C, 75% relative humidity.

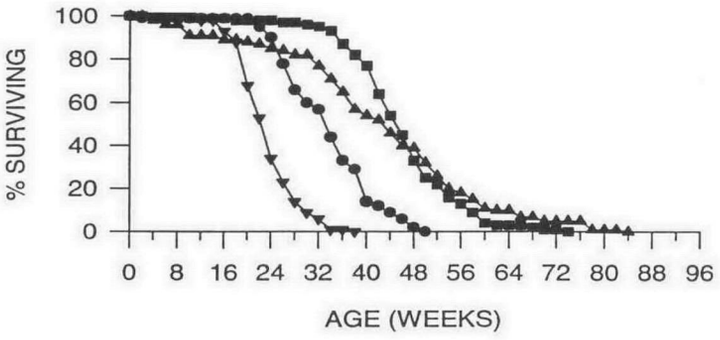

Fig.6. Survival curves for *C. ferrugineus*, virgin adults of the SS strain, kept individually in separate vials for the duration of life at 75% relative humidity and constant temperatures of 25°C (▲), 25°C (■), 30°C (●) and 35°C (▼).

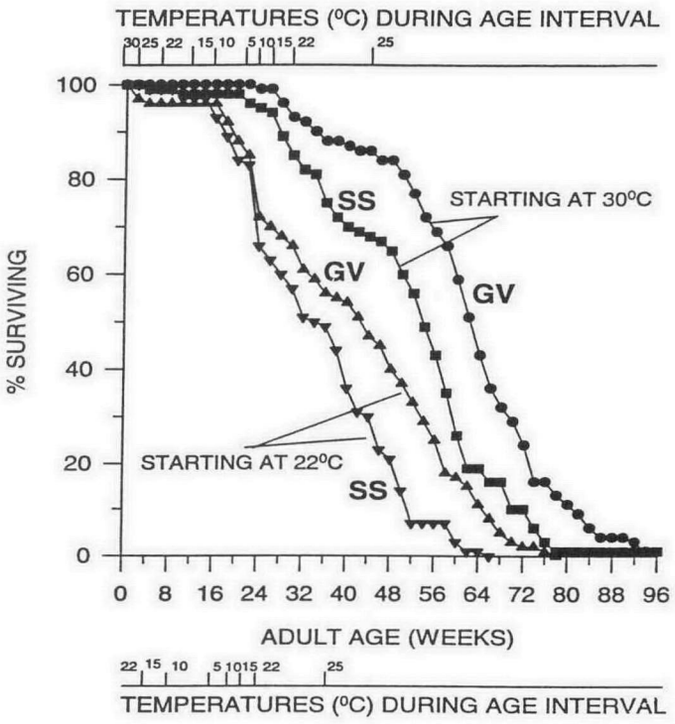

Fig. 7. Survival curves for *C. ferrigineus*, virgin adults, raised from egg to adult at 30°C then transferred to 25, 22, 15, 10, 5, 10, 15, 22 and 25°C at the ages indicated at the top of the graph (upper curves, SS strain, ■; GV strain, ●), or raised from egg to adult at 22°C then transferred to 15, 10, 5, 10, 15, 22 and 25°C at the ages indicated at the bottom of the graph (lower curves, SS strain, ▼, GV strain, ▲).

0.01). At 48 weeks of age, percent survival of beetles of each strain on the overwintering temperature schedule starting from 30°C was double the percent survival of beetles of the same strain on the temperature schedule starting from 22°C (K-S test, $P < 0.01$) (Fig. 7). These large differences in lifespan were not correlated with average temperature. The weighted mean temperature up to the age of 42 weeks for the two groups initially at 30°C was 17.7°C; for the two groups initially at 22°C the weighted mean temperature was 17.4°C and after 42 weeks of age all four groups were kept at a constant temperature of 25°C.

Discussion

Factors causing differences in lifespan

The males of *C. ferrugineus* had the highest mortality rates in mixed-sex groups and in the all-male group; female mortality was also high in mixed-sex groups but relatively low in the all-female group. This suggests that in the presence of a number of females and other males, males are strongly stimulated to compete for sexual partners and may cause injury to themselves or to other adult beetles during copulation attempts. Aggressive male sexual behaviour has been identified by Spratt (1980) as an important factor in reducing the lifespan of *T. castaneum* and *T. confusum* adults kept in groups. *Tribolium* beetles have no courtship routine to aid males in identifying receptive females; males have been observed attempting to mate with other males, dead beetles, or small objects that resemble other beetles (Taylor and Sokoloff 1971).

Factors causing differences in oviposition rate

The results of the oviposition experiments suggest that *C. ferrugineus* females reduce their oviposition rate as the number of larvae and the number of other females in the immediate environment increases. Higher larval density may have been the cause of the lower oviposition rate during the first 8 weeks in the groups with food renewed every 2 weeks. Larvae of *Oryzaephilus surinamensis* (L.), another beetle of the family Cucujidae, emit volatile compounds which reduce oviposition rate (Pierce et al. 1990).

It appears that when *C. ferrugineus* adults are at low density (1 male and 1 female per vial), with time for larvae to accumulate, oviposition rate decreases with increasing larval density, but at high adult density (30 beetles per vial), with larvae or eggs removed oviposition rate decreases with increasing density of adult females.

Lifespan of adults living on whole kernel wheat

Since both ground and whole kernel wheat had the same nutrients the most likely cause of the reduced lifespan of beetles living on whole kernel wheat was a difference in rate of energy expenditure. Beetles that were forced to chew their food out of the hard germ tissue had to expend energy at a higher rate than beetles that were able to ingest particles of ground wheat with very little effort. Sohal and Buchan (1981) and Sohal (1982) have shown that raising the activity level of *Musca domestica* L. without changing ambient temperature can shorten their lifespan.

Developmental periods and lifespan of adults at different temperatures

At constant temperatures in the range 25 to 35°C the lifespan of *C. ferrugineus* was inversely correlated with temperature. This result is consistent with the rate of living theory (Pearl 1928).

However, when *C. ferrugineus* adults were kept on the overwintering temperature schedule starting from 30°C they lived much longer than adults that were kept on the overwintering temperature schedule starting from 22°C, although the weighted mean temperatures of the two treatments were almost the same, and adults that were kept for the first 16 weeks at 22°C, then transferred to 30°C, had shorter lifespans than adults kept continuously at 30°C, while adults kept for the first 12 weeks at 30°C, before transfer to 22°C, lived longer than adults kept continuously at 22°C.

Sohal (1986) has discussed some of the reasons why departures from the inverse relationship between lifespan and temperature occur, and why he believes that the rate of living theory, as a statement of the relationship between lifespan and metabolic rate, is still valid.

In our experiments all groups of *C. ferrugineus* that had shorter mean adult lifespan than groups of the same strain at higher average temperatures were raised from egg to adult at 22°C, and at least the first 5 weeks of adult life were spent at 22°C. There are a number of indications that this temperature is slightly below the lower limit at which this insect can achieve an optimum state of physiological maturity. A short period at 30°C early in life seemed to prepare the beetles to tolerate the shift to lower temperatures, while early life at 22°C produced a weakened population with poor tolerance for low temperatures.

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