AN ABSTRACT OF THE THESIS OF

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Title: Fecundity and Longevity in Tribolium castaneum: a Selection Experiment

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Abstract approved: _____
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Recent experimental and theoretical work has examined the possible genetic causes of senescence. These are reviewed, and four types of factors are found to be responsible for the evolution of senescence and age specific fecundity curves: 1. Age specific mortality schedules, 2.Density dependent factors, 3. Density independent factors, 4. Random fluctuations in environmental conditions. A discussion of alleles with different age specific effects explores their behavior under a variety of mortality schedules.

An experiment involving natural and artificial selection for high fecundity at 10 and 100 days of age in a laboratory population of Tribolium castaneum resulted in significant increases in 100 day fecundity in all lines. No change in 10 day fecundity was seen in any line. Percent mortality was not changed by selection. The heritability of fecundity at 10 and 100 days was

measured: heritability was estimated to be .53 + .35 for 10 day fecundity and zero at 100 days. These results are shown to support the hypothesis that this *T. castaneum* population is polymorphic with respect to age specific fecundity distributions and that the life history strategy of this organism has been molded by fluctuating juvenile mortality.

Fecundity and Longevity in *Tribolium castaneum*: a Selection Experiment.

by

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Typed by Nancy C. Treneman for Nancy C. Treneman

This work is dedicated in memory of my father,

Dr. James Dyke Treneman

The work presented here has been accomplished with the help of many people. I would like to express my thanks to Dr. Peter Dawson, who gave me good advice and my mother who has supported me all that I have accomplished. My thanks to Liz Walsh, who listened to many drafts of this work, and last but not least, the staff of the Zoology Department.

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Introduction

The reproductive schedule of an organism is closely related to the ageing process. Senescence is defined by Rose (1984c) as: "a decline in age specific fitness components". In iteroparous organisms (except in the case of indeterminant growth) peak reproduction is followed by a decline in reproductive ability which continues until death. The assumption that this decline is due to senescence is made by many authors who address this subject (Williams, 1957; Rose, 1984c, 1983; Emlen, 1983) and one that will be made here. Senescence due to extrinsic causes such as accident, low food resources, predation, or "wear and tear" on the body must be separated from deterioration due to the genetic makeup of an organism; it is the latter which will be discussed here.

Medawar (1952) proposed a hypothesis to explain the ageing process which did not involve direct selection for longer or shorter life span. He suggested that senescence resulted from an accumulation of alleles with negative effects on reproductive ability later in life. Reproductive value as defined by Fisher (1930) is a measure of the expected remaining contribution to future

generations by an individuals of a given age. As age increases reproductive value decreases because of the increasing probability of death due to external hazards. The intensity of selection on alleles that affect fitness decreases with age because of the decreasing worth of offspring with age (Cole, 1954, Mertz, 1975). This decrease in the intensity of selection with age allows accumulation of alleles that are deleterious to fitness at that age. The degree of senescence seen at a certain age would reflect the reproductive value at that age.

The environment an organism lives in determines what type of life history leads to the highest overall fitness. Three main kinds of age specific mortality schedules are discussed in the literature (Stearns, 1976):

1. High adult mortality and low juvenile mortality.
2. Low adult mortality and high juvenile mortality.
3. Constant mortality at all ages.

Note that the factors responsible for mortality can be density independent factors or density dependent factors such as competition.

High adult mortality, caused by factors such as predation, unpredictable resources, or extreme effort in reproduction (as in salmon) makes it unlikely that an adult will live to the next breeding season. Therefore organisms that have higher reproductive rates early in

life will have the highest fitness except in cases of indeterminant growth (Cole, 1954; Horn, 1978). Although organisms that reproduce over a longer time span may have more children, the more they have early in life the higher their fitness becomes in terms of their overall genetic contribution in grand- and greatgrandchildren. The life history strategy associated with this type of environment is semelparity, where there is little reproductive value at later ages. In theory, organisms that have evolved in this type of environment should age rapidly after reproduction, due to the accumulation of many late acting deleterious alleles (Medawar, 1957) and the pleiotropic effects of alleles which have positive effects on fitness early in life and negative effects later in life (Williams, 1957: Rose, 1983, 1984a,b,c).

The second mortality schedule favors multiple breeding seasons since they increase the possibility that some offspring will succeed in surviving to reproductive maturity (Charnov and Schaffer, 1973; Stearns, 1976; Warner and Chesson, 1985). Alleles that delay ageing would be favored by selection in this type of environment, and organisms would evolve a life history strategy balanced between two selective forces: high early reproduction produces more grandchildren, and high juvenile mortality favors longer lifespans and multiple breeding seasons (Guthrie, 1969). Selection would be

against alleles with late negative effects; senescence would occur at a slower rate and appear at later point in the life cycle than closely related species in environments favoring semelparity.

The third schedule leads to either semel- or iteroparous life histories depending on the causes of mortality, following the classic "r" and "K" scenario. Two situations can occur: one where mortality is high and carrying capacity is never reached, therefore early reproduction is always selected for (Solbrig, 1970). If there is little mortality and K is reached then density dependent factors will become the major selective forces and a strategy of fewer offspring and a longer life would be most successful.

The discussion above does not include environments which have temporal fluctuations in age specific mortality curves. In environments of this type populations that contain individuals with different age specific fecundity curves (genetic polymorphism) are more successful than monomorphic populations. This is hypothesized to be due to the ability of such populations to "track" environmental changes and ensure some successful reproduction (Geisel, 1974, 1976).

The ability within an organism to delay reproduction during times of environmental stress is well documented in vertebrates (Brown, 1973; Delong, 1966; Hartmann and

Osborn, 1972) and invertebrates (Murdoch, 1966, King, 1982). It is hypothesized that energy normally used for reproduction is used for maintenance until resources become more plentiful. The act of reproduction itself may make the organism vulnerable to predation or disease, as well as deplete energy reserves. This type of plasticity keeps unsuccessful reproduction from occurring.

To summarize, there are several major types of environmental parameters thought to be responsible for shaping the life history of an organism:

1. Age specific mortality schedules.
2. Density dependent factors.
3. Density independent factors.
4. Degree of random fluctuation in environmental conditions.

Alleles or gene combinations of several types can exist for any one gene (or gene complex); these are listed in table 1.

Table 1. A summary of the different combinations of possible age specific effects of an allele. (+ = positive effects on fitness, - = negative effects, 0 = no effect)

early in life	late in life
+	+
+	0
+	-
0	+
0	0
0	-
-	+
-	0
-	-

Alleles with -- and -0 effects should be at very low frequency, unless they contribute to fitness in the heterozygous state or through epistatic relationships, in accordance with the tenet that traits directly involved with fitness have undergone extensive selection already and alleles with negative effects have been removed from the population. Alleles of the -+ type should also be rare in that a negative or lower fitness early in life may decrease the probability of survival to sexual maturity. Neutral alleles (00) would be governed by stochastic processes such as drift.

Environments that favor a semelparous life style would select for ++, +0, and +- alleles. The negative benefits of an +- allele must come after reproduction. 0- alleles would be governed by drift as long as their negative effects did not come before reproduction. The accumulation of negative influences on fitness by +- alleles are what Williams (1957), and Rose (1984) suggest is the cause of senescence (see also Guthrie, 1969; Edney and Gill, 1968).

The existence of 0- alleles was tested by Rose and Charlesworth (1980). They predicted that if there was an accumulation of 0- alleles then additive genetic variation (Va) in fitness components would increase with age. They measured egg lay in <u>D. melanogaster</u> throughout life, and found no increase or decrease with age in Va

for this trait. This would indicate that few 0- or 0+ alleles were present in their population.

The evolution of a longer and longer life span is linked to environments which favor iteroparity. The frequency of ++ and 0+ would increase in environments where reproductive success is low: +- and 0- would be increasingly selected against as the environment becomes more unfavorable for juveniles. Adults must live and reproduce for longer periods of time, therefore senescence would be postponed. It should be mentioned that regulatory genes which would delay the negative effects of +- alleles could be selected for in this case.

Several experiments testing this theory have been carried out (Rose and Charlesworth 1981; Rose 1984; Luckinbill et.al. 1984; Sokal, 1969) and the mathematical theory has been worked out by Hamilton (1966) and Charlesworth (1980). Rose (1984) and Luckinbill et.al. (1984) carried out similar experiments on D. melanogaster selecting for high reproductive ability late in life and comparing these "old" lines to populations that experienced selection for high fecundity early in life (young lines). Both researchers succeeded in increasing the life span of D. melanogaster significantly by selecting for late fecundity, and these same populations showed depressed fecundity early in life. Rose and

Charlesworth (1981) subjected D. melanogaster to artificial and natural selection at early and late ages. Late lines showed significant increases in life span and higher fecundity late in life, and early lines shorter life spans and higher fecundity early in life.

The physiological results of selection for postponed senescence in the lines produced by Rose (1984) were investigated in two other studies (Service, et.al, 1985; Rose 1984). Body parts of flies from both old and young lines were weighed and it was found that the ovaries of the flies from lines with delayed senescence were significantly lighter than those from young lines at ages less than one week after eclosion. There was no difference in ovary weight after one week of age between the two treatments. Service, et.al. (1985) tested the resistance of these same fly populations to starvation, heat desiccation, ethanol vapor, and compared body water content of the two treatments. The long lived lines were more resistant to starvation, heat desiccation, and 15% ethanol vapor than young lines. These studies support energy trade off theories which propose that the amount of energy an organism receives is partitioned between maintenance and reproduction (Guthrie, 1969, Emlen, 1970) and show a positive correlation between the ability to survive in stressful conditions and longevity. Alleles of the ++,0+, and -+ types are very likely to produce

changes in the way energy is used early in life; energy used for reproduction could be redirected to maintenance. Reproduction would decrease early in life, but there would be better overall physiology and "hardiness", as well as improved reproductive capacity at older ages.

Sokal (1970) measured the longevity of Tribolium castaneum from populations that were allowed to lay eggs from days 4 to 7 of adult life, and compared these measurements to those of beetles from stock cultures. There was a significant decrease in longevity in the selected lines.

Mertz (1975) selected for fecundity at 10 days and 20 days of age in T. castaneum, and compared values obtained from these lines to values from lines where beetles were allowed to live out their lives in self limiting populations. There was a significant increase in fecundity in the 10 day lines, and but no difference between the 20 day lines and the controls. There were no changes in life span for any of the treatments.

Tribolium beetles have a life expectancy well past 20 days, and certainly lay eggs for much of that time. (see fig.5, pg.27). T. castaneum is an iteroparous organism which has a mean life span of 119 days for females and 191 days for males (Young, 1970), and females start laying eggs after the fourth day of adult life (Dawson, 1964). Because of its longevity and high

fecundity it is an excellent model with which to study the relationship between these two life history traits. The following selection experiment was performed on T.castaneum and involved selection for high fecundity at 10 days and 100 days of adult life. Its goal was to look at the effect these selection regimes have on fecundity at these two ages and on age specific mortatility.

Materials and Methods

Two types of selection regimes were undertaken, each one having control and selected lines (A= selection on fecundity at 10 days of age, B = 100 days) The lines which experienced selection for high fecundity at 100 days were labeled B1,B2,B3 and B4, and their counterpart control lines CB1,CB2,CB3,and CB4. The A lines were labeled in the same manner. The word age will mean days after eclosion unless otherwise indicated.

The base population from which all lines were started was a population of beetles, called ORCS, that was created by the combination of several different strains and maintained by husbandry conditions specified by Dawson (1979) for 16 years in the laboratory. These husbandry conditions involved discarding all life stages except the adults and combining 40 beetles from one bottle started 8 weeks (56 days) earlier with 40 from another bottle started 7 weeks (49 days) earlier. This procedure is followed to maintain a high level of variation. Since *T. castaneum* larvae and adults cannibalize eggs and pupae, early born offspring have an advantage over offspring produced later. *T. castaneum* beetles start laying eggs within 4 days after eclosion, and the eggs take around 4 days to hatch. The mean time between egg laying and pupation was 24 days (earliest

pupation was 18 days) in the base population and from pupa to adult the mean time was 6 days. Therefore the generation time for ORCS is a minimum of 24 and has a mean of 30 days. Beetles lay eggs within 4 days of eclosion, therefore only quick developing first offspring (F1) of the original 80 could have their offspring (F2) included in the next colonizing group. The chance of this however is fairly small considering the amount of cannibalism on in Tribolium cultures. Longevity after thirty days of age would be important if there was a high probability that a beetle from the original 80 at a time t would be included in the 40 taken at time t + 1. After 49 or 56 days the population in a bottle is numbered in the hundreds, therefore this probability is fairly low. The F1 cohort would then have the highest frequency in the group taken to start the next bottle, and so selection would be the most intense on fecundity from 19 to around 30 days of age.

To start all blocks of lines 200 adult beetles were removed randomly from ORCS, and maintained for 7 days in coarse ground wheat flour supplemented with 5% yeast (CWY). They were then transferred into new flour for a 24 hour egg collection. Starting at day 18, which was the first day pupae appeared, pupae were separated by sex and placed in jars. The number of pupae counted each day was used to estimate the mean day of pupation, which as

mentioned above was 24 days. Eight days after eclosion the virgin beetles were mated in single pairs which were placed in vials containing 3 grams CWY. This procedure was done 4 different times, each time producing one of the following blocks of lines:

block 1: B1,CB1,B2,CB2
block 2: B3,CB3,B4,CB4
block 3: A1,CA1,A2,CA2
block 4: A3,CA3,A4,CA4

The A lines were created about 1 year after the B lines so that the final assays of fecundity in the F3 generations occurred at approximately the same time (within 2 months of each other). All lines and populations were kept in incubators at a constant temperature of 29 degrees and about 60% humidity. The blocks of lines were kept in boxes with 144 vials to each box and 2 boxes per block. Boxes within a block were placed next to each other in the incubator. Despite these precautions it cannot be assumed that environmental influences on mortality and fecundity were the same throughout the time of the experiment (around 1 year and 9 months). The fact that there are two blocks, and 2 control and 2 selection lines within a block was designed to allow comparisons between treatments, between generations, and within generations.

For all B and CB lines 80 pairs of beetles were mated for each generation. This was to allow for

mortality before 100 days so that 50 pairs could used to measure fecundity at 100 days. The 80 pairs were mated at the age of 8 days and kept in CWY which was changed every 21 days. At each flour change it was noted how many beetles had died. When a beetle died its mate was discarded as well. Therefore the measure of mortality was the number of vials discarded. The simultaneous death of beetles in the same pair was never seen. It was not possible to replace the dead mate with a live one kept in a replacement stock of pairs because the sexing of an adult beetle can do an unmeasurable amount of damage to it. Solitary beetles have different mortality rates then beetles with mates (King and Dawson, 1972), and therefore solitary beetles were removed from the population.

At day 100, 52 pairs chosen randomly from the survivors of the original 80 were placed in vials containing 3 grams of Gold Medal (GM) flour. The vials were placed in the incubator for 48 hours after which the beetles were removed from the vials. The pairs were numbered and placed in vials. The eggs of the first 50 pairs were counted, and for all selected lines (B1-B4) the 15 pairs with the highest egg count were then placed together in a jar containing CWY. The control lines received identical treatment except that the 15 pairs were chosen randomly. One day after this mating the 30

beetles were transferred to a new jar and a 72 hour egg collection was made. The progeny from this collection were separated on the basis of sex as pupae and mated at 8 days of age to form the next generation. All subsequent generations were treated in the same manner; selection proceeded for 3 generations.

The A and CA lines were mated at 8 days of age, 55 pairs to a line, using the same method described above for the B and CB lines. On the 10th day a 48 hour egg collection was taken. Selection was carried out as in the B lines, the best 15/50 for the A lines and 15/50 randomly chosen for the CA lines were used to start the next generation.

The second block of A lines; A3, A4, CA3, and CA4 experienced technical and temporal differences which resulted in a much weaker selection regime then the one above. Selection occurred in the parental generation on fecundity at 20 days, and for the F2 fecundity was measured on day 10 at room temperature. The selection intensity in F1 and F2 was the best 15 out of 30 pairs. The fecundity of the F3 generation of the A3 line was not measured because the virgin females that eclosed early cannibalized most of their companions which were still pupae, and not enough females were present for a valid measurement. Because of these difficulties, unless stated otherwise statistical procedures were performed only with

the A and CA lines from block 3.

For the final assay of fecundity in the F3 generation of all lines (B,CB,A,CA), 135 pair matings were made on day 8. Eighty of these were kept for 100 days with flour changes and mortality measured every 21 days. The fecundity of 50 of the survivors was measured at 100 days using the same method as mentioned above. Fifty-five of the pairs mated at 8 days of age had a 48 hour egg collection taken at 10 days of age in the same manner as described above.

Heritability measurements on 10 day and 100 day fecundity were made using a half-sib design. The heritability of 10 day fecundity was measured using two blocks of 5 sires, three dams to a sire, 5 progeny/dam. One hundred day estimations used three blocks, two of which had three sires each, 3 dams/sire and 5 progeny/dam; the third had 5 sires, 3 dams/sires and 5 progeny/dam.

To start the half-sib families sires and dams were taken randomly from ORCS as pupae, and families were put into vials, using one male and 4 females per family. After 7 days the individuals of each family were isolated in separate vials and allowed to lay eggs for 72 hours. At the end of that time the adult beetles were removed and the vials were checked periodically for pupae. From three dams nine daughters were taken for 100 day

heritability measurments, and 6 daughters/dam were kept for 10 day estimates. Different families were used for 10 day and 100 day assays. Measurements were made on 5 daughters per dam; the excess daughters in the 100 day groups were insurance against mortality. Daughter pupae were kept isolated until 8 days of adult age and were then mated to virgin males of the same age taken from ORCS. This procedure was used to start both the 10 day families and the 100 day families.

Pairs used to estimate heritability at 100 days of age were maintained in vials with flour changes every 21 days until day 100 when a 48 hour egg count was made using the methods described above. Pairs used to estimate the heritability of 10 day fecundity were transferred at 10 days to GM and 48 hour egg counts were made.

Results

100 Day Fecundity

Figure 1 shows the distribution of 48 hour egg lay for the block 1 B and CB lines for the four generations of this experiment. Very similar results were obtained for the block 2 lines. The number of pairs producing from zero to three eggs increased in the F1 and then decreased in subsequent generations. The mean egg count/pair of beetles (which is this experiment's measure of fecundity) for a 48 hour egg collection at 100 days, and its standard error, for generations P through F3 for all B and CB lines are listed in table 2, and graphed in figure 2A.

A three-way analysis of variance (ANOVA) (Sokal and Rohlf,1981) on the mean egg count/pair for each population in each generation showed that blocks and generations had significant effects ($P < .01$); the ANOVA is shown in table A, appendix I. There was no significant difference between control and selected lines, and no significant interaction between generation and treatment.

A two-way ANOVA was done comparing the means of the F3 B's and CB's to the base population (parental) means (table B, Appendix I). There was a significant effect of generations ($P < .01$), with no significant effects of

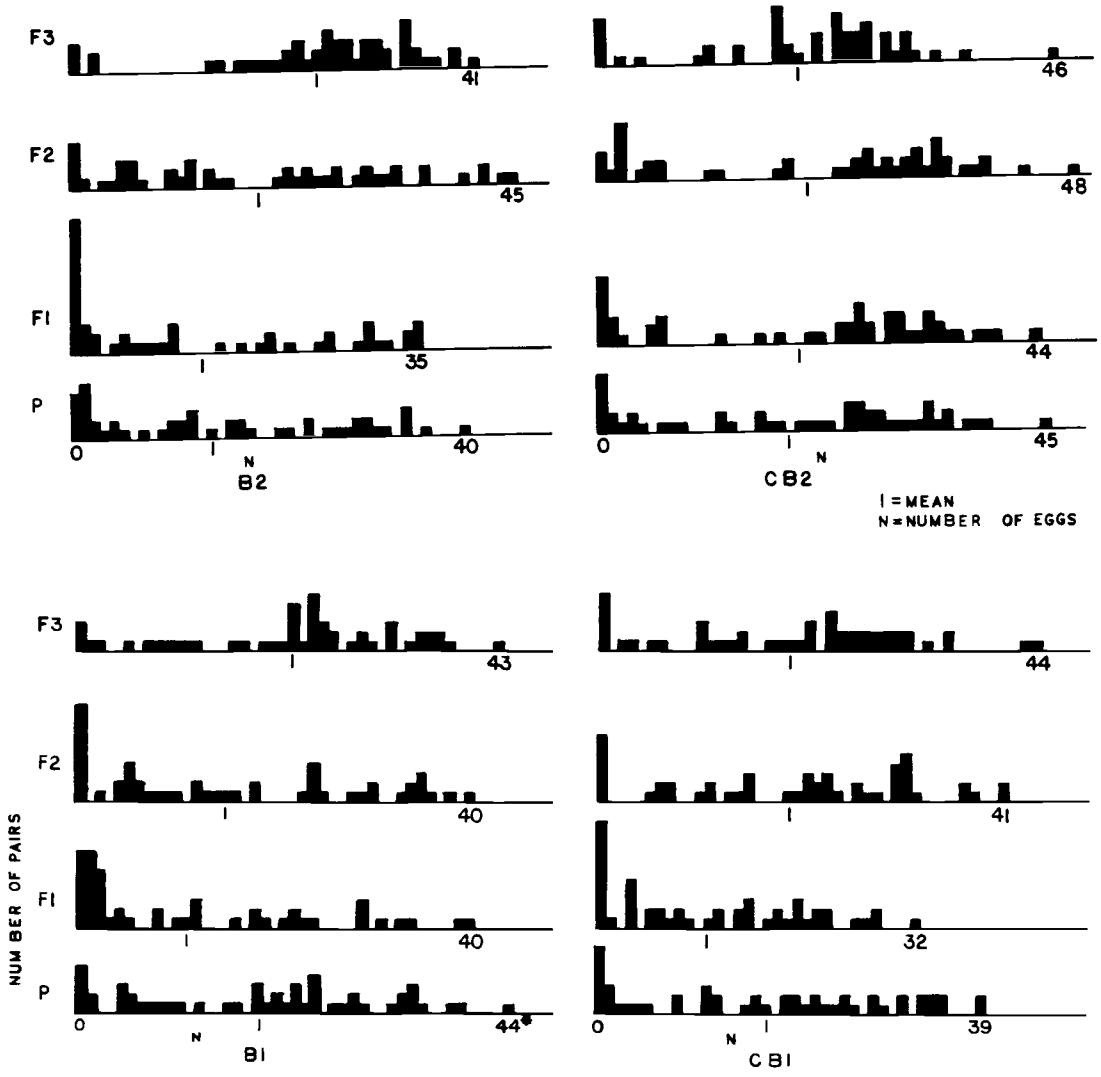

Fig. 1. The distribution of eggs produced in 48 hours at 100 days of age for block 1 100 day lines and their controls over four generations. (*maximum value for that population in that generation) P=parental generation.

Table 2. Mean number of eggs produced/pair in lines at 100 days of age with the standard error (s). 50 pairs per line were counted unless indicated otherwise.

	P	F1	F2	F3	A&CA	F3
B1	18.72	11.36	15.50	22.10	A1	27.50*
	s (1.75)	(1.69)	(1.87)	(1.59)		(2.11)
CB1	16.98	11.24	19.68	19.38	CA1	29.93*
	(1.77)	(1.36)	(1.73)	(1.66)		(2.32)
B2	14.98	13.56	19.13	25.33	A2	24.13*
	(1.78)	(1.87)	(1.96)	(1.45)		(2.98)
CB2	19.44	20.34	21.57	20.67	CA2	30.23*
	(1.88)	(1.97)	(2.06)	(1.51)		(1.83)
B3	18.10	17.38	27.00	24.00**		
	(1.70)	(1.76)	(2.19)	(7.94)		
CB3	14.16	12.48	22.67	26.17*		
	(1.68)	(1.59)	(2.11)	(1.76)		
B4	14.92	18.32	27.70	29.08*		
	(1.68)	(2.01)	(2.55)	(1.96)		
CB4	23.84	19.58	26.75	26.17*		
	(1.96)	(1.85)	(2.54)	(2.34)		

* number of pairs = 32
** number of pairs = 5

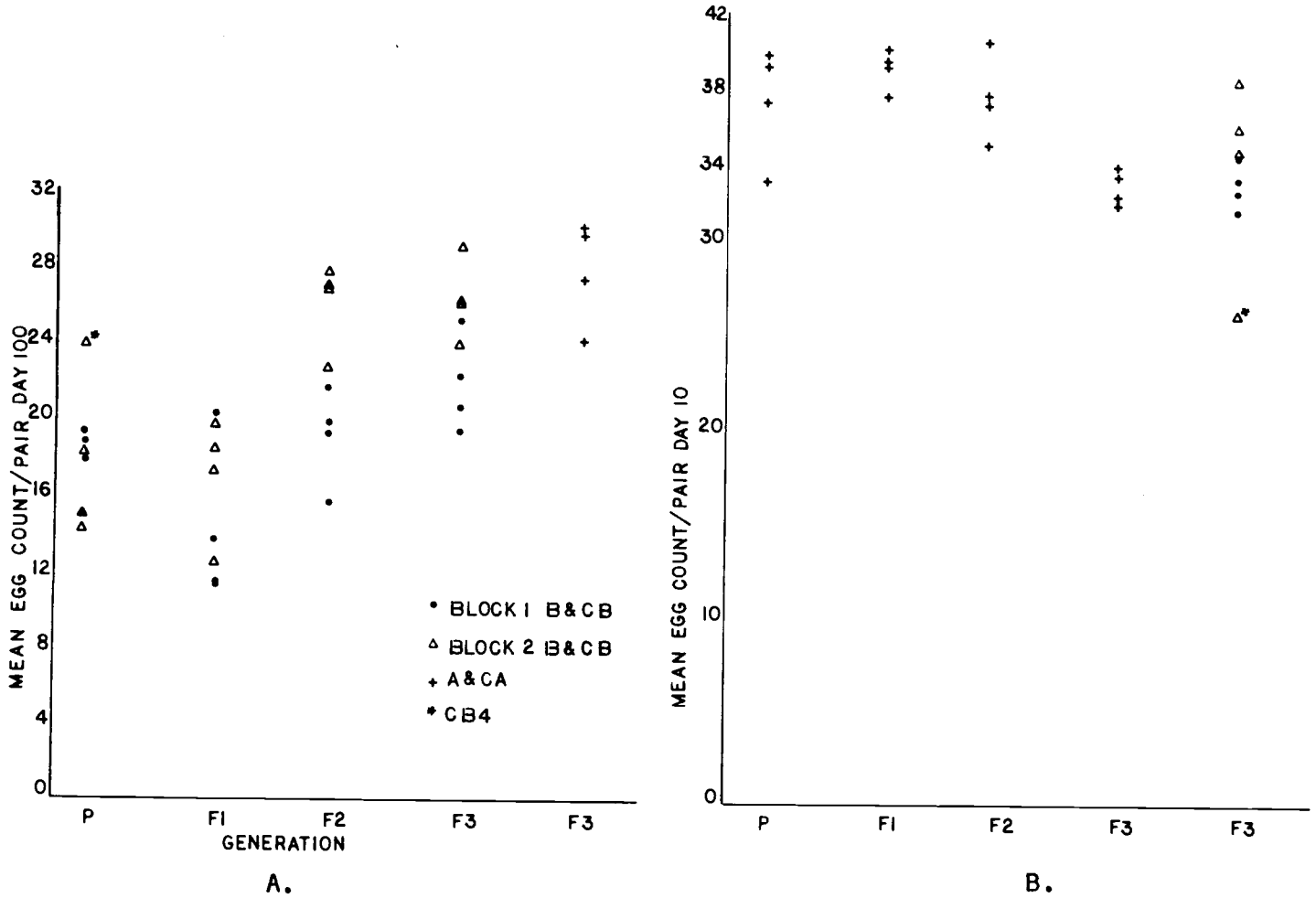

Fig. 2. A. Mean values of lines for 48 hour egg lay at 100 days of age (note A and CA F3 are included).
B. Mean values of lines for 48 egg lay at 10 days of age. (B and CB F3 included).
Filled triangles indicate lines with overlapping values.

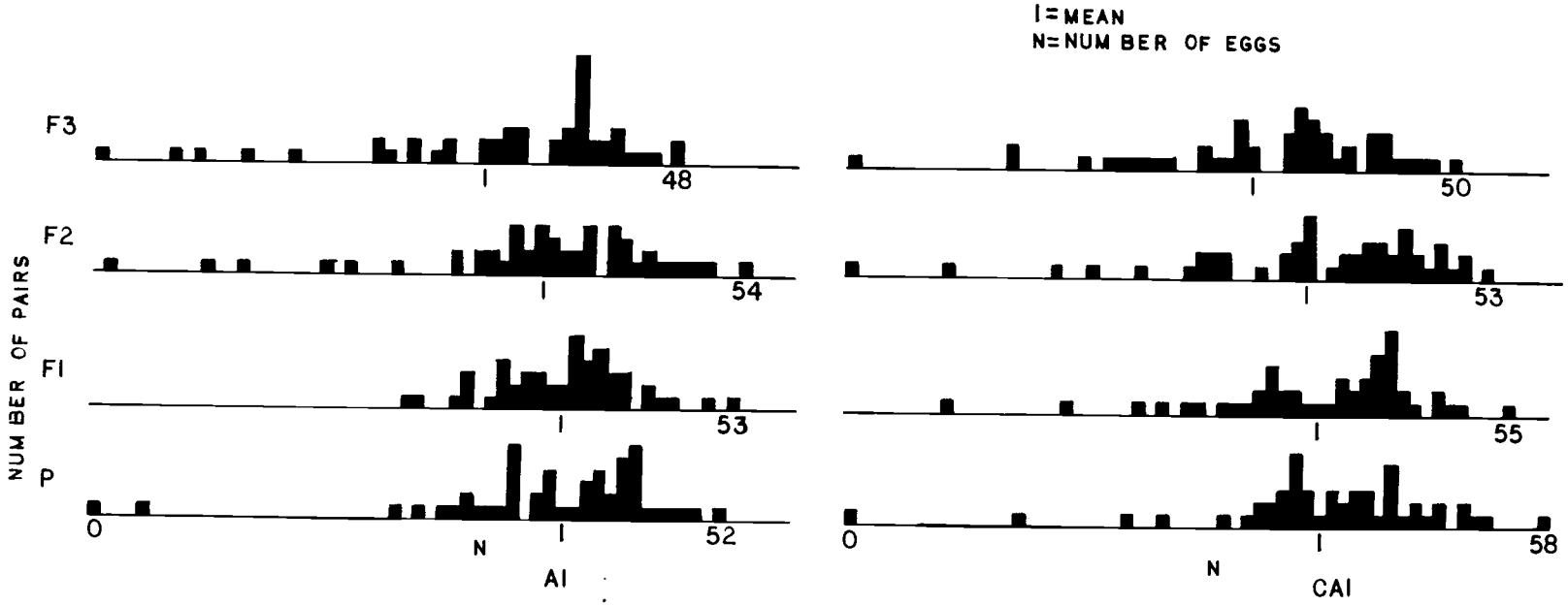

Fig. 3. The distribution of eggs produced in 48 hours at 10 days of age for A1 aand CA1 over four generations. Notation is as in fig. 1.

Table 3. Mean number of eggs produced/pair in lines at 10 days of age with standard error (s). 50 pairs per line were counted unless indicated otherwise.

	P	F1	F2	F3	B&CB	F3
A1	39.06 (1.17)	39.12 (0.80)	37.52 (0.18)	32.51 (1.74)	B1	34.60 (0.94)
CA1	39.70 (1.35)	39.50 (1.22)	38.38 (1.54)	33.53 (1.53)	CB1	31.78 (1.65)
A2	33.00 (1.25)	38.04 (1.37)	35.20 (1.87)	32.04 (1.12)	B2	33.05 (1.16)
CA2	37.20 (1.45)	40.22 (0.93)	40.72 (1.67)	34.26 (0.96)	CB2	32.85 (1.18)
					B3	34.96 (0.63)
					CB3	38.72 (0.57)
					B4	36.36 (1.17)
					CB4	26.03* (2.65)

*number of pairs counted = 31

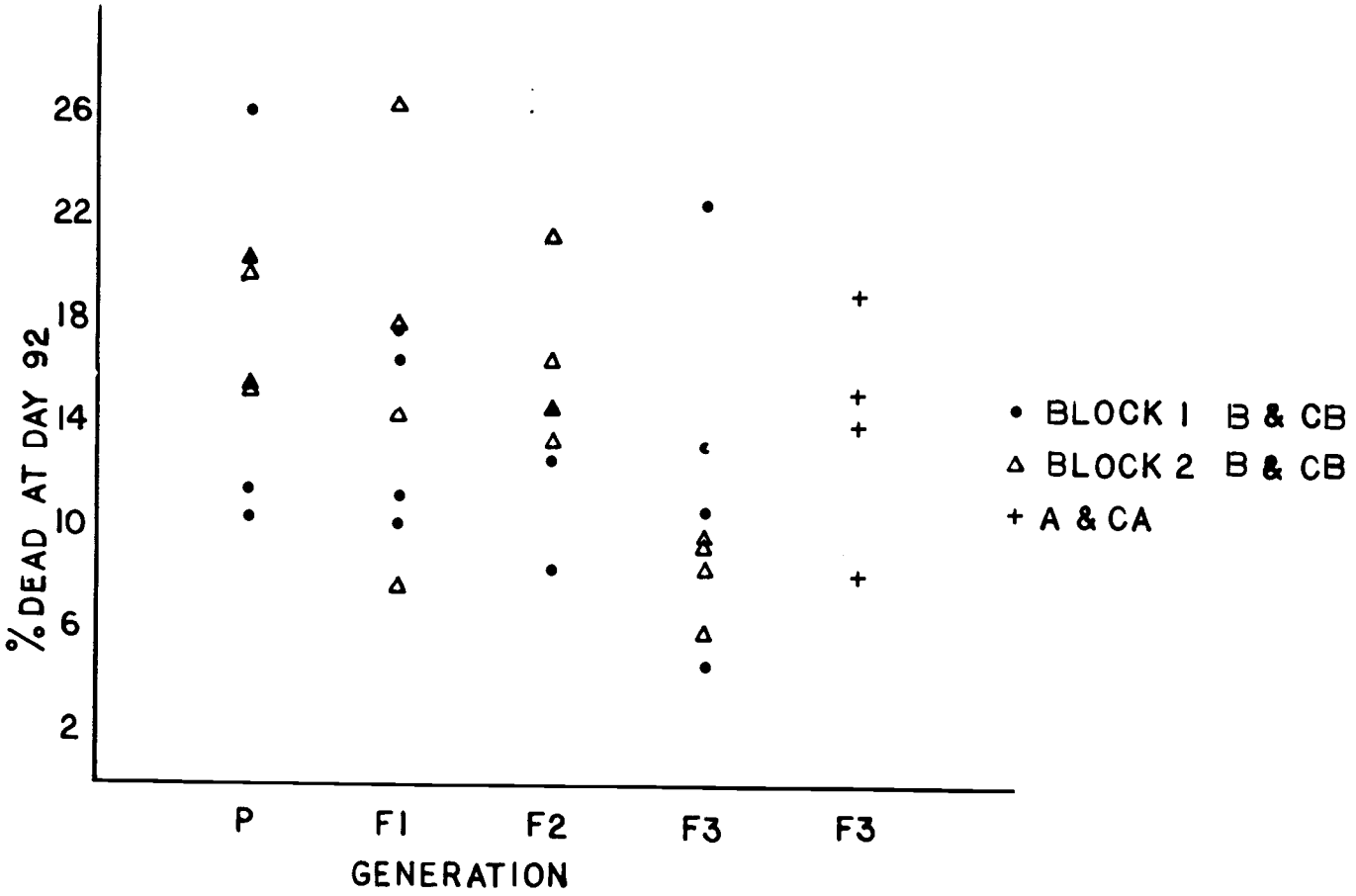

Fig. 4. Percent mortality at day 92 of adulthood in B and CB lines for 4 generations, and for A and CA F3. Filled triangles indicate where lines overlapp in values.

blocks or block X generation interactions.

One-way ANOVAs were performed comparing each F3 generation to its parental generation. Significant increases in the F3 means were found in lines B2, CB3, and B4 ($P < .01$). Valid measurements could not be performed on 100 day fecundity for F3 of B3 because of technical problems; the sieve used to collect eggs had a hole in it which went unnoticed until most of the vials had been counted. When the F2 generation was compared to the parental population a significant difference was found ($P < .01$). These tests show that significant increases in fecundity occurred in 3 out of the four selection lines and one of the control lines.

These analyses indicated that there were significant differences between blocks. An ANOVA comparing all the parental lines B1, B2, B3, B4, CB1, CB2, CB3, CB4 showed that all were from the same population except CB4 which was significantly different from the rest ($P < .01$) The parental mean of CB4 was 23.84 which is higher then some of the F3 means for the other B and CB lines. The block effect may be due to this sampling error.

The mean egg counts at 100 days for F3 A and CA lines (table 2) were compared to those of F3 B and CB lines as well as base population means (tables C and D, appendix I.) No significant difference was found between the F3's of 100 day and 10 day lines. F3 A and CA

lines had significantly higher means than the base populations ($P<.01$). This is indicated in Fig. 2A: the points for F3 A and CA are at the same level as the F3 B and CB lines.

10 Day Fecundity

Figure 3 shows representative distributions of eggs laid/pair at 10 days for the A1 and CA1 lines. Fig. 2B. graphs the mean eggs laid/pair at 10 days for all 10 day lines and F3 B and CB. A two-way ANOVA on the A1, A2, CA1, CA2 lines (table E in appendix I) showed a significant difference between generations ($P<.05$). There was no significant difference between control and selected lines. The means of the F3's were tested against the base population means for 10 day fecundity and there were no significant differences. Table 3 shows the means of the A and CA lines through the four generations. The F3 means are consistently lower than the parental means; therefore the significant difference between generations can not be due to an increase in mean 10 day fecundity. A one-way ANOVA comparing the A and CA F3 with B and CB F3 10 day fecundity showed no significant differences.

Mortality

Figure 4 shows the percent mortality for the control and selected lines for the 100 day lines, and A and CA F3. A two-way ANOVA on B and CB showed a significant

effect of generations (P <.05) (table F,appendix I). However a regression analysis showed that there is no significance, indicating that the variation between generations is not consistent. A one-way ANOVA was performed comparing percent mortality at 92 days of B and CB F3 with A and CA F3. There was no significant difference, although in Fig. 4 it can be seen that A and CA mortality is generally higher then B and CB lines in the F3 generation.

Heritability

Heritability of fecundity was estimated using a half sib design (Becker, 1975; Pirchner, 1983). Tables G and H in appendix 1 show the ANOVA for 10 day and 100 day heritability, respectively. Heritability for 10 day fecundity was .53 + .35. The estimated heritability for 100 days was a -0.2634 + 0.0574 using the sire component and a positive 0.27922 + 0.3389 using the dam component. Realized heritability was estimated from the selection experiments by regression of selection response on cumulative selection differential (Falconer, 1981) for both 100 and 10 day selected lines. None were significantly different from zero in the 10 day lines, and two, B2 and B3, were slightly above zero in the 100 day lines.

Discussion

The age specific fecundity curve of an organism can be thought of as a polygenic character, unique to a certain environment. Environmental factors that influence fecundity could have permanent or reversible effects on the shape of this curve. The effect these environmental factors have depends on the genetic and acquired characteristics of the individual. Fig. 5 shows fecundity and survivorship curves for *T. castaneum* derived from Young (1970). The shapes of these types of curves differ from study to study; fecundity curves from Sonleitner (1961) and Howe (1962) differ from each other and from Young (1970). Values for fecundity at 10, 20 and 100 days after eclosion for ORCS are shown on fig. 5. ORCS values are for 2 day egg lay, and Young's are for 3 day egg lay, showing that ORCS has higher fecundity at these ages than Young's population. Howe (1962) feels that these differences are due to the different husbandry techniques employed by researchers. Egg laying in *T. castaneum* is affected by many factors such as condition of flour and temperature (for a complete summary see Sokoloff,1974).

Fecundity curves such as the one in fig. 5 are generated by averaging the values of many females together and using that average as an indicator of

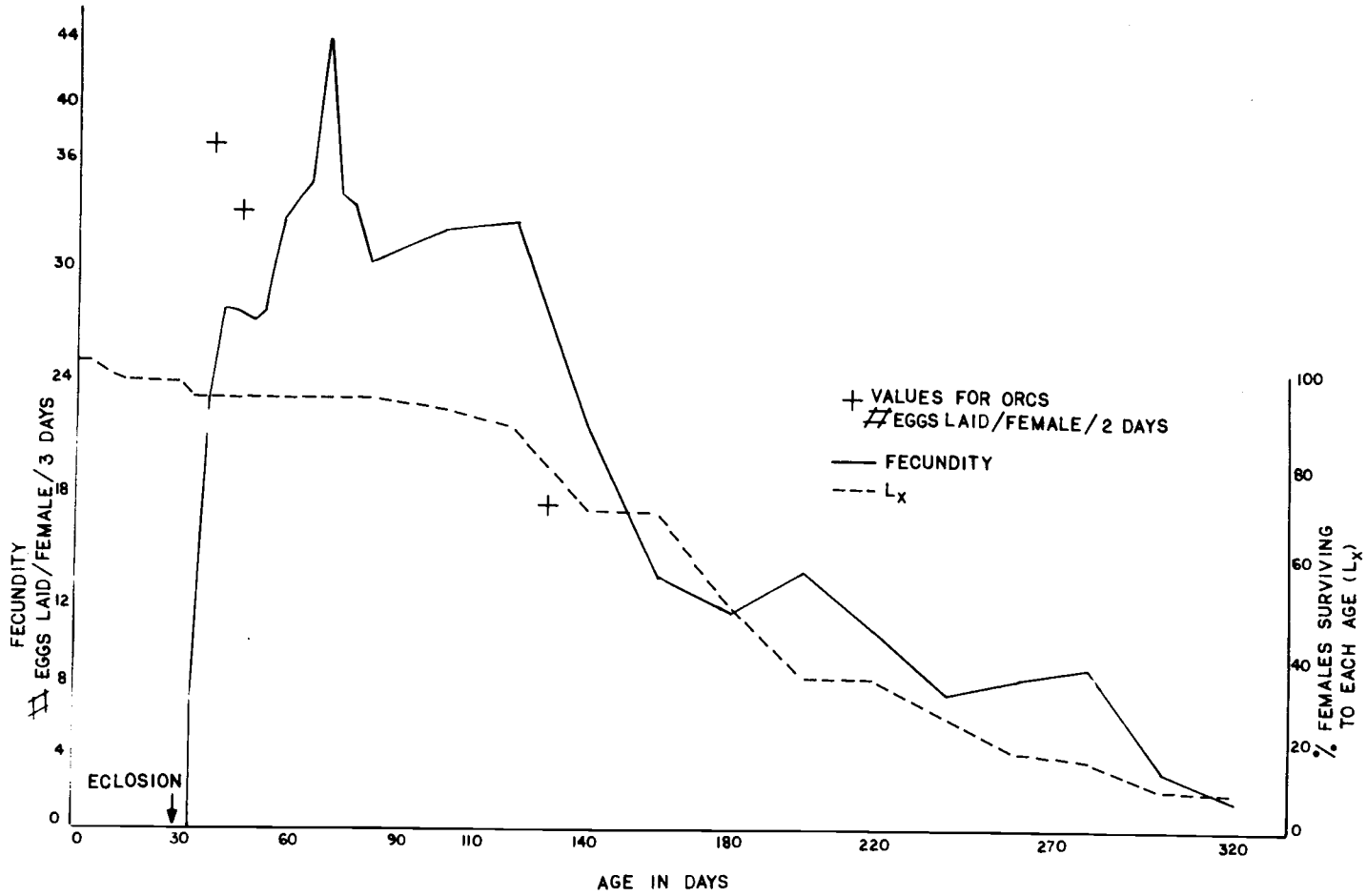

Fig. 5. Fecundity and survivorship curves of I. castaneum. (after Young, 1970)

fecundity at that age. It should not be assumed that individual beetles all possess curves with shapes similar to the one produced by averaging. As mentioned earlier, Geisel (1974) through computer simulations showed that populations with polymorphism in fecundity curves should be more successful in randomly fluctuating environments than monomorphic ones. If individual beetles within a population have fecundity curves with different shapes, the picture supplied by an average curve may not be the best description of that life history trait. Since polymorphism of this type is shaped by selective forces in the environment, averaging conceals information which could shed light on these forces.

Fig. 6 depicts how several different fecundity curves could produce the "average". The dashed line represents the composite average curve. Drawn above it and below it, curves A through D are specific for individual genotypes. They represent points on a continuum where all possible curves between them may exist within the population. The shape of the average curve would be determined by the frequencies of the different types of individual curves.

Curve A could be called the "burn out" curve. Individuals possessing A curves have a large number of +- alleles which impart high benefits early in life, but quickly lower the fitness of the organism as it ages. A

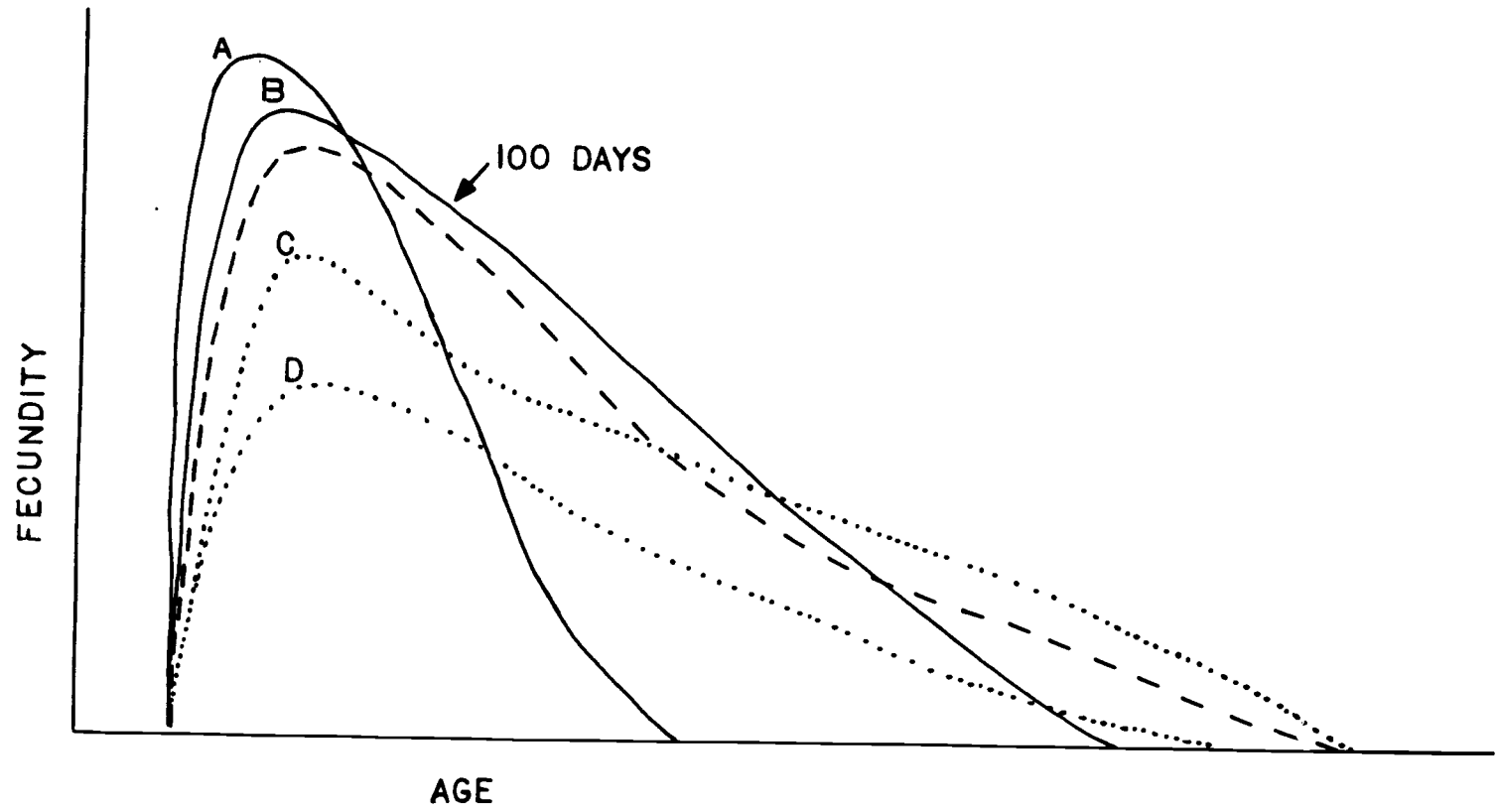

Fig. 6. Hypothetical set of fecundity curves found in one population. (100 days in the life cycle of I. castaneum is indicated).

types have the highest maximum early reproduction but die early. Evidence of their presence has already been discussed in the introduction, from studies where selection for early fecundity decreased late fecundity and lifespan (Rose, 1984; Lukinbill, 1984; Sokal, 1970).

Type B individuals have fewer of the +- alleles and many ++ alleles, which impart vigor throughout the life span. They die before the C and D genotypes. This type of curve was found in D. melanogaster by Giesel and Zettler (1980) who measured the age specific fecundity of individual flies in homozygous and heterozygous lines. Flies that had high reproduction in the first third of life were reproductive to a later age and had higher peak fecundities. These positive correlations indicate the presence of ++ alleles for fecundity in these populations. Flies with extremely high early fecundity had shorter life spans and lower late fecundity, showing the existence of A type curves. In the same study lines of flies were subjected to several non-optimal diet regimes, and a positive correlation between the ability to survive on different types of foods and survival under optimum conditions was found. This would indicate that lines with the highest rate of increase on an optimum diet were also the most efficient at resource utilization. Rose (1984c) criticized this interpretation, arguing that the positive correlations found between

fitness components were due to inbreeding depression since homozygous lines were used. Lines of this type were used, as were lines made from crosses of homozygous lines, i.e. F1 lines with a high percent of heterozygous loci. Both types of lines exhibited the characteristics described above.

Genotypes with shapes like curve C have the highest fitness late in life and have the longest life spans. Genes which act in this manner have been found in *D. melanogaster*: the *black* and *speck* loci (Gonzales, 1923). The experiments done by Rose (1984) and Luckinbill (1984) produced lines from stock populations with this type of curve.

The type D curve can be thought of as "genetic load"; the allelic combinations present in D individuals impart a shorter life span than B and C genotypes and low fecundity. D genotypes will be found in a population if the alleles they carry impart A, B, or C curves when recombined in different genotypes. Epistasis or heterozygote superiority are possible genetic mechanisms for the maintenance of these alleles in the population. If this type of curve is found in a population, especially one which is under intense selection, then heterozygote superiority may be a factor in producing fecundity curves. Competitive ability in *Tribolium* behaves in this manner (Dawson, 1983); selection for

increased competitive ability produced no response, whereas as selection for reduced ability was successful. The fact that there was an increase in the number of pairs with low reproductive ability in the B and CB F1 lines, and a reduction of pairs in this category in subsequent generations indicates the presence of alleles of this type. Although individuals with high reproductive ability were used as parents of the F1 there was an increase in the number of pairs that produced few or no eggs. This supports the idea that there are alleles present in the population which in the combinations of the parental generations give high reproductive ability, though the process of recombining to produce the F1 combinations are produced which give low reproductive ability at that age.

The data from this experiment indicate that within the ORCS population there exists polymorphism for fecundity curves. This can be seen in the fact that selection at both 10 and 100 days of age produced a rise in fecundity at 100 days of age. Selection for high fecundity at 10 days of age will produce a population of individuals with A and B type curves. Although A dies out before 100 days, B types do not, and therefore an increase in fecundity at 100 days in 10 day lines is seen. Fig.6 indicates where 100 days of age falls in *T. castaneum's* reproductive schedule; it is only 1/3 of the

possible lifespan. This being the case, selection at 100 days would not select for individuals with type C curves, but type B curves. This hypothesis would explain why 100 day fecundity is higher than the base population in all lines. The B genotypes were selected for under both selection regimes. Because the life span of *T. castaneum* is much longer then that of *D. melanogaster* only selection much later in life such as 200 or 250 days would be likely to produce a significantly longer life span and a decrease in early fecundity coupled with a rise in late fecundity.

There was no significant difference between selected and control lines in either treatment. Although beetles were randomly selected in control populations natural selection was as successful as artificial selection in producing a response. By randomly choosing pairs in the CB lines as parents of the next generation several pairs with low or no egg production were probably included. However the beetles with significant contributions to the next generation would have average or above average fecundity. In other words there was not as much difference between control and selection treatments as that suggested by the experimental design. All the A and CA lines had significant increases in 100 day fecundity as compared to ORCS. The distributions of fecundity/pair for these lines has very few pairs that produce few or

zero eggs. This could be because of the fact that the genotypes present in these F3 populations are either of the A or B variety. The A's have died before 100 days and those left have fairly high fecundity (B). Again, in the control populations natural selection, although weaker, produces this same effect. The lack of difference between selected and control lines may indicate some direct genetic pleiotropy involving longevity and fecundity.

The heritability estimate for fecundity at 100 days was zero. Fig. 1 shows base population (P) distributions at 100 days; there is a large number of pairs that produce no eggs. These beetles may have been close to death, and the removal of these zeros from the heritability estimates could show significant Va. This however was not the case; an ANOVA performed after removing these zeros still yielded a heritability value of zero. This procedure also lowered the sample size. Because there was a response to selection in 3 out of 4 B lines and one CB line it is probable that Va was present, but the sample size was too small to detect it.

The combination of high heritability of 10 day fecundity and lack of response to selection is not consistent with Fisher's fundamental theorem; that the response to selection will be proportional to the amount of additive genetic variance existing for that trait. It

is possible that there was a response to selection but the wrong measurements were taken and so it was not detected. Referring again to fig. 6 it can be seen that the time of maximum egg production is earlier for A and B curves than it is for the population as a whole. Selection favoring A and B individuals would shift the day of maximum reproduction ahead. The actual fecundity at 10 days of age may not increase, because 10 days now falls on a part of the curve which is lower then the maximum reproductive value occuring earlier in life. Selection here is for a certian curve shape, and therefore the shape of the curve is what responds to selection no an isolated age specific fecundity. This shifting of the fecundity curve is seen in Rose (1984) and Luckinbill (1984) in D. melanogaster.

This raises a problem when selection is performed at a fixed age for high fecundity. Selection will shift the curve so that in each generation selection will be on a different section of the population and will favor different genotypes with each generation. Again, referring to fig. 6; selection at 10 days of age will select both A and B curves. If selection went on for enough generations, the B curves may eventually be selected for, if the point where the A crosses under the B curve occurs at that age in life for the population under selection.

Selection at 100 days for *T. castaneum* is not at an age of severe fecundity reduction. Because the regime imposed by husbandry conditions prior to this experiment on ORCS would select for high fecundity at from 19 to 30 days of age, and possibly also at 4 and 56 days of age, fecundity curve polymophism could be maintained. The fact that mortality did not decrease significantly in the 100 day lines, or increase significantly in the 10 day lines does not contradict the notion of antagonistic pleiotropy between fecundity and longevity proposed by Williams (1957) and Rose (1983,1984). Because of the nature of *T. castaneum*'s survivorship and fecundity schedules selection was not performed on "old" beetles. There was actually a very low percent mortality at the age of 92 days (the highest was 26% in a parental population, and the lowest was 5% in an F3 100 day line) and there was high variability between lines. Selection needs to be at a much older age, and mortality recorded for samples of the population through the whole life span.

It is clear that the highly cannibalistic nature of flour beetles creates an environment with high juvenile mortality once there are larvae and adults in substantial numbers in a colony. However cannibalism in a newly colonized environment is quite low. This is coupled with the fact that adults may disperse to new habitats.
In view of the ideas presented here the iteroparity and

long life span of Tribolium are the result of an environment in which sporadic reproductive success occurs and there is low adult mortality compared to juvenile stages. At high densities beetles undergo fecundity depression (Sonleitner, 1961) and increased cannibalism rates, producing non-optimum environments. This type of situation is predicted to select for fecundity curve polymorphism at both intra- and interindividual levels. Studies of age specific fecundity curves of individuals in populations of T. castaneum undergoing selection for high fecundity at a variety of ages must be done to substantiate the hypothesis proposed here.

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APPENDIX

Appendix 1

Table A: Anova for 100 day selected and control lines.

source	df	SS	MS	F
Blocks	1	124.68	124.68	11.06 **
Treatments	3	73.16	24.39	2.16 ns
control vs selection	1	0.01	0.01	0.00 ns
within	2	73.15	36.58	3.25 ns
Generations	3	411.42	137.14	12.17 **
Generation X Treatment	9	12.12	1.35	0.12 ns
Error	15	169.02	11.27	

* significant to alpha level P=.05
**significant to alpha level P=.01

Table B: Anova for F3 B and CB vs parental B and CB 100 day egg lay

source	df	SS	MS	F
subgroups	3	203.51	67.84	
generations	1	148.59	148.59	7.69 *
blocks	1	29.80	29.80	1.54 ns
interaction	1	25.12	25.12	1.30 ns
error	12	231.64	19.30	

Table C: Anova for F3B1* vs. F3 A1 100 day egg lay

source	df	SS	MS	F
Treatments	1	93.23	93.23	3.24 ns
error	6	172.54	28.76	

*1 indicates block 1; i.e. block 1 holds B1-CB2, block holds B3-CB4.

Table D: Anova for F3 A1 vs Parental B1 100 day egg count

source	df	SS	MS	F
treatments	1	217.05	217.05	36.39 **
error	6	35.78	5.963	

Table E: Anova of 10 day lines: A1, A2, CA1, CA2

source	df	SS	MS	F
subgroups	7	104.95	14.99	4.34 ns
selection	1	18.11	18.11	5.25 ns
generations	3	83.91	27.97	8.11 *
interaction	3	2.94	0.98	0.28 ns
error	8	27.62	3.45	

Table F: Anova for regression of % mortality in 100 day lines

Source	df	SS	MS	F
subgroups	7	143.64	20.52	3.62 ns
blocks	1	2.52	2.52	0.44 ns
generations	3	95.71	31.90	5.62 *
regressions	1	4.80	4.80	0.10 ns
deviations	2	90.91	45.45	8.00 ns
interaction	3	45.41	15.14	2.66 ns
error	8	45.72	5.68	

Table G: Anova on half sib design for heritability of 10 day fecundity of single pairs of age.

Source	df	SS	MS	F
Blocks	1	1802.77	1802.67	23.42 **
Sires	8	3289.89	411.24	2.52 *
Dams	20	2473.74	123.69	1.61 ns
error	120	9238.70	76.98	

Table H: Anova on half-sib design for heritability on fecundity at 100 days of age.

Source	df	SS	MS	F
Blocks	2	2338.86	1169.43	6.71 *
Sires	8	499.78	62.47+	0.36 ns
Dams	22	5178.67	235.39	1.35 ns
error	132	23009.20	174.31	

+note that MS sires is smaller then MS dams.