Original article

Effects of selection for early and late reproduction in low and high larval density populations of the bean weevil (Acanthoscelides obtectus)

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Summary – This study concerns an analysis of one-generation selection for early and late reproduction in populations maintained for 10 generations at low and high levels of larval density. We have obtained direct responses to selection in both the early and late reproducing parents. There was, however, no correlation between fecundity and longevity. Phenotypic responses suggest that parental age could change the fecundity schedule in the way predicted by antagonistic pleiotropy theory. However, the absence of statistically detectable negative genetic correlation between early and late fecundities made our study inconclusive with respect to possible genetically based trade-off among fecundity indices.

Acanthoscelides obtectus / larval density / parental age effect / fitness components

Résumé – Effets de la sélection pour une reproduction précoce et tardive dans des populations de bruche du haricot (Acanthoscelides obtectus) à haute et faible densité larvaire. *Cette étude concerne l'analyse d'une génération de sélection pour une reproduction précoce ou tardive de populations maintenues pendant 10 générations à une densité larvaire faible ou élevée. Nous avons obtenu des réponses directes à la sélection, chez les parents à reproduction précoce et à reproduction tardive. Il n'y avait cependant pas de corrélation entre la fécondité et la longévité. Les réponses phénotypiques suggèrent que l'âge des parents pourrait modifier l'évolution de la fécondité au cours de la vie comme le prédit la théorie de la pléiotropie antagoniste. Cependant, l'absence de corrélation négative statistiquement détectable entre les fécondités précoces et tardives ne nous permet pas de conclure quant à des oppositions de nature génétique entre ces 2 fécondités.*

Acanthoscelides obtectus / densité larvaire / âge des parents / valeur adaptative

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INTRODUCTION

Since natural selection operates on several traits simultaneously the optimal life history has been seen as "the best compromise given a set of options" (Sibly and Calow, 1986). Starting from this point, a great deal of the theory of life history evolution (see *eg* Charlesworth, 1980; Reznick, 1985; Scheiner *et al*, 1989) is based on the assumption of "trade-offs" or negative genetic pleiotropy among life history fitness components (fitness components are largely synonymous with life history parameters; see *eg* Istock, 1983). For example, according to the best-known evolutionary theory of senescence (Williams, 1957), senescence is envisaged most accurately as a by-product of genes with pleiotropic effects on the fitness components, such that increases early in the life span in one set of fitness components are accompanied by decreases in other fitness components later in life.

Despite the central position of antagonistic pleiotropy in life history theory, experimental demonstrations of genetic trade-offs were until very recently almost absent. Several recent studies (*eg* Rose and Charlesworth, 1981a, b; Rose, 1984; Luckinbill *et al*, 1984; Tucić *et al*, 1988) have provided evidence of negative genetic correlations among traits at early and late stages of life history. However, Giesel *et al* (1982), Stearns (1983), Mitchell-Olds (1986) and Engstrom *et al* (1989), for example, found no evidence of negative genetic correlations among fitness components.

Independently of any mechanism of genetic control proposed, the fundamental question of the evolutionary theory of senescence is "how do long and short life spans evolve?" (Luckinbill and Clare, 1985). Having in mind the suggestion provided by MacArthur and Wilson (1967) that density dependent selection could be responsible for much of the observed diversity of life history strategies among taxa, Luckinbill and Clare (1985) used 2 experimental treatments of larval density in a long-term selection study for increased longevity of *Drosophila melanogaster*. By selecting for late reproduction when larval density was held low, they were unable to detect a significant increase in longevity. However, populations with high and uncontrolled numbers of the developing larvae responded strongly to selection for late reproduction, with the longevity increasing by ≈ 50%. Thus Luckinbill and Clare demonstrated, showing that the larval environment could alter the expression of genes for adult longevity, existence of genetic variation for sensitivity of fitness to density. Service *et al* (1988) have corroborated these findings. Indeed, low rearing density seems to reduce response to selection for increased longevity in *Drosophila* populations.

Motivated by these studies on *Drosophila*, as surprisingly little experimental work on genetic variation for response to conspecific density exists, we conducted an experiment to examine the phenotypic and genetic responses in bean weevil *(Acanthoscelides obtectus)* life history traits that occur when density dependent selection is acting. Specifically, in this paper we present the results of a study of one-generation selection for early and late reproduction in populations maintained for 10 generations at low and high levels of larval density.

MATERIALS AND METHODS

Life history of Acanthoscelides obtectus

The bean weevil, *Acanthoscelides obtectus* (Say), is a well known leguminous-feeding beetle of the family Bruchidae (Coleoptera). The females lay eggs on the surface of host seeds. The eggs hatch, and the first instar larvae bore into the seed where they feed. The final instar larvae excavate a chamber just below the seed testa, and the presence of a larva may be detected by a small "window". Pupation occurs in this chamber and adults must chew a hole through the testa in order to emerge. Larval stages feed entirely within a single seed. Competition among larvae in overcrowded circumstances can be severe; from a single bean seed (about 20 mm sized) as many as 45 adults can emerge (personal observation). The adults do not require to feed in order to mate and oviposit. This feature (non-feeding adults) of the bean weevil life history is particularly attractive for the analysis of genetic trade-offs since adults have a finite amount of resource that may be allocated between fecundity and maintenance.

The population used here was "synthetic", originating from different local populations of Yugoslavia. It was maintained in culture ≈ 3 yr prior to these experiments. In all experiments *Phaseolus vulgaris* cv "gradistanac" beans were used. The size of all seeds used in the present experiment was ≈ 20 mm. All the beans were brought in bulk at one time from one source.

Density dependent selection

The following summarizes the method of selection used to obtain the low density, high density and control populations.

The low density regime was designed to be uncrowded for the developing larvae. At the start of this treatment, 320 beetles were chosen randomly from the base population and reared in 10 separate bottles with 100 bean seeds (*ie* each bottle contained 32 weevils whose sex ratio has been determined by chance). After ≈ 3 wk these bottles were monitored daily until the first eclosion of adults began (the eclosion is recognized by getting "windows" black; otherwise windows at the seed testa are grey). At that time beans with 1 to 3 windows (which indicate low larval density) were separated. Since the probability of larvae from same bean being sibs is higher when the number of larvae per bean is small (which could cause inbreeding depression over generations) we employed the following procedure. Beans with low larval density from all 10 bottles were kept together in a single bottle. The seeds with higher larval density were discarded. From the newly emerged adults (usually $\approx 1\,000$ individuals), in the batch of low larval density seeds we chose, again randomly, 10 groups with 32 beetles, in order to establish a new generation. This procedure was repeated for 10 generations.

A high density population was maintained under high larval density. The procedure and propagule size (*ie* 32 beetles per bottle) were as described above, except that new generations were founded from beans containing 10–20 (rarely more) windows. Thus, the only difference between the 2 selection regimes was the higher degree of larval crowding in the high density population.

In the control treatment we did not control larval density. In all other aspects the experimental procedures were identical to those in the previous 2 treatments.

Analysis of the parental age effects

After 10 generations 200 pairs of beetles were chosen randomly from each treatment. Individual females were put into separate Petri dishes containing 3 beans and an unrelated male, for oviposition. These Petri dishes were checked daily. Upon death of the female, her life span and daily fecundity were recorded. In order to demonstrate parental age effects in the population selected for different larval density, the following 1-generation artificial selection for age-specific modification of fecundity was imposed.

This selection proceeded by choosing the females with highest 3-day fecundity record, from 1–3 as the "young" parents, and from 7–10 as the "old" parents. According to our previous results (Tucić *et al*, 1990) these 2 periods are the most convenient for analysing age-specific pattern of reproduction in the non-feeding bean weevils. Thus, within the population selected for different larval densities, the experiments were designed to enforce an early *versus* late age-specific pattern of reproduction. The best 25% of females laying were chosen. However, for late reproduction more intense selection was imposed ($\approx$ 15% of females laying were chosen as the parents) because of the low fecundity of the old females or some other reason.

Daily fecundity was measured on 4 newly emerged adult females, chosen at random from each selected female, in separate Petri dishes with 3 bean seeds and a male sib. The number of beetles which died was counted every day. Upon death of the female, her longevity and different fecundity indices have been recorded. We chose the following indices of fecundity: egg-laying d 1–3, egg-laying d 7–9, egg-laying d 10 or more; total fecundity (over life span), first day of egg laying, last day of egg laying, age of peak fecundity and laying rate (total fecundity/last day of egg laying).

All cultures were maintained in an incubator at 30°C and $\approx$ 70% humidity. Experimental adults were subjected to starvation.

Narrow sense heritability for each trait was estimated by regression analysis of mean offspring values and maternal values (Falconer, 1981). In general, it is desirable to regress offspring values of the male parents, because the estimated covariance between mother and offspring can be inflated by maternal effects. Unfortunately, regression on male parent is impossible here because we analysed age-specific fecundity pattern in females. Thus, the confounding of maternal and genetic covariance in the parent–offspring regression is unavoidable. In addition, broad sense heritability was also calculated using a least squares analysis of variance model (Sokal and Rohlf, 1981).

RESULTS

In table I the means and standard errors of different life history traits for each density selected population in the first generation of reproduction at young or old age are given. For each trait pairwise comparisons between means were made

Table I. Means $(\overline{X})$ and standard errors (SE) for longevity and 8 fecundity indices in offspring of young and old parents within populations selected for low and high larval density.

Trait	Control				Low density				High density			
		Young		Old		Young		Old		Young		Old
	n	$\overline{X} \pm SE$	n	$\overline{X} \pm SE$	n	$\overline{X} \pm SE$	n	$\overline{X} \pm SE$	n	$\overline{X} \pm SE$	n	$\overline{X} \pm SE$
Longevity	201	15.56 ±0.28	51	15.71 ±0.42	199	14.65 ±0.23	25	15.20 ±0.71	216	12.83 ±0.18	51	13.47 ±0.41
Fecundity												
Days 1–3	201	28.45 ±1.39	51	26.22 ±2.71	199	32.53 ±1.26	25	24.40 ±4.57	216	35.36 ±1.10	51	24.37 ±2.94
Days 7–9	199	3.48 ±0.53	51	5.16 ±1.24	199	3.67 ±0.45	25	4.04 ±1.52	214	2.83 ±0.42	51	6.57 ±1.47
Days ≥ 10	194	6.61 ±0.79	51	8.16 ±1.34	191	5.52 ±0.67	23	10.77 ±2.17	173	2.71 ±0.52	45	4.67 ±1.05
Total	201	52.00 ±1.79	51	52.73 ±3.16	199	55.95 ±1.58	25	49.04 ±4.74	216	57.37 ±1.29	51	44.96 ±3.49
First day	197	2.43 ±0.19	51	2.51 ±0.40	198	2.11 ±0.16	25	4.12 ±0.88	215	1.69 ±0.10	50	3.18 ±0.53
Last day	197	10.49 ±0.32	51	10.84 ±0.53	198	9.76 ±0.28	25	10.88 ±0.66	215	7.79 ±0.20	50	9.56 ±0.41
Age of peak fecundity	197	4.79 ±0.32	51	5.58 ±0.73	198	4.41 ±0.29	25	6.84 ±1.04	215	3.41 ±0.19	50	5.73 ±0.63
Laying rate	197	6.62 ±0.32	51	5.97 ±0.56	198	7.07 ±0.28	25	5.47 ±0.74	215	8.51 ±0.25	50	5.74 ±0.58

using Tukey's test. The high larval density population for both parental ages shows lower average longevity relative to the corresponding parental age in the low density groups, as well as in control populations. These differences are significant at the 0.01 level in all but 1 case (low density, young parents vs high density, old parents). In all other cases the differences between average longevities are insignificant. In the high larval density population all fecundity indices, except the fecundity 7–9 days, were significantly different between the offspring of the young and old parents. However, when the same comparisons are made within low density or control populations, the picture which emerges is quite different. Here Tukey's test has shown that fecundity indices of the differently aged parents, except for the first day of laying within the low density population, are not detectably different from each other (table I). All the other comparisons show that fecundity indices of the young parent offspring in the high density population are most frequently statistically different from the other treatment.

It is worth considering the effect of larval density on the longevity and fecundity irrespective of the parental age. Table II compares the means of these life history traits, obtained after pooling of early and late-reproduced parents within

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Table II. Pooled (early and late reproduced parents) average and standard errors ($\overline{X} \pm SE$) within low and high density populations. The signs of the t-test denote agreement (+) or disagreement (−) with prediction of r- and K-selection theory.

Trait	Low density		High density		t-test
	n	$\overline{X} \pm SE$	n	$\overline{X} \pm SE$	
Longevity	224	14.71 ±0.22	267	12.96 ±0.17	− 6.43**
Fecundity					
Days 1–3	224	31.63 ±1.22	267	33.26 ±1.05	− 1.02
Days 7–9	224	3.71 ±0.43	265	3.55 ±0.44	− 0.26
Days ≥ 10	214	6.02 ±0.63	218	3.11 ±0.46	− 3.72**
First day	223	2.33 ±0.17	265	1.97 ±0.13	− 1.68
Last day	223	9.89 ±0.26	265	8.12 ±0.18	− 5.59**
Age of peak fecundity	223	4.69 ±0.29	265	3.85 ±0.19	− 2.43*
Laying rate	223	6.89 ±0.26	265	7.99 ±0.23	− 3.16**

$^*P < 0.05;$ $^{**}P < 0.01.$

populations with low and high larval densities. The average longevity, fecundity ≥ 10 d, last d of egg laying, age of peak fecundity and laying rate were higher in the low density population than in the high density population. In all above cases the differences between traits at low and high density were significant, as shown by the t-test. The observed pattern among life history traits, for weevils selected for different larval density, is quite opposite to that predicted by r- and K-selection regimes (see Pianka, 1970). An outcome such as we obtained is expected in models of life history in which the effects of variable environment are relatively greater on mortality of juveniles than adults. Stearns (1976) discusses these predictions under the heading of "bet-hedging".

It seems from table I that parental age at the time of reproduction can also affect the analysed traits. To test for significance between early and late-reproduced parents, taking simultaneously into account the effects of larval density, a 2-way analysis of variance was made (since we had an unbalanced data set, we used the method described in Steel and Torrie, 1960). The results of such an analysis of variance for longevity and different fecundity indices are presented in table III. In all these cases there was a small, statistically insignificant "parental age × density" interaction, suggesting that these 2 variables are largely independent in moulding the observed pattern among analysed traits. Interestingly enough, the effects of

parental age and population density on longevity and fecundity seem to be different. For all fecundity indices we found significant influence of parental age (table III). Significant effects of larval density have been found for longevity, as well as for several fecundity indices (see table III).

Table III. Mean squares (MS) from 2-way ANOVA. Control population is not included. df_e = error degrees of freedom; dfs for all other MSs are 1.

Trait		Source of variation			
		Parental age	Population density	Interaction	Error
Longevity	MS	20.45	393.18	0.12	8.91
$df_e = 487$	F	2.29	44.14***	0.01	
Fecundity					
Days 1–3	MS	5 278.09	711.45	118.09	315.28
$df_e = 487$	F	16.74***	2.26	0.38	
Days 7–9	MS	243.73	16.27	163.87	47.12
$df_e = 485$	F	5.17*	0.35	3.48	
Days ≥ 10	MS	571.25	1 088.69	93.62	66.84
$df_e = 485$	F	8.55**	16.29***	1.40	
Total	MS	5 383.51	50.03	435.16	450.82
$df_e = 487$	F	11.94***	0.11	0.97	
First day	MS	175.75	29.03	3.88	5.43
$df_e = 484$	F	32.36***	5.35**	0.71	
Last day	MS	119.83	423.00	6.06	11.67
$df_e = 484$	F	10.27***	36.24***	0.52	
Age of peak	MS	323.70	123.44	0.17	13.95
fecundity	F	23.21***	8.85**	0.01	
$df_e = 484$					

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Figure 1 shows the overall pattern of survivorships in different treatments. In order to compare different survivorship curves we have employed the test suggested by Rose (1984). This test is based on the comparison of mortality rates. Concerning mortality rate differences there are 2 hypotheses to test. First, statistical significance of the average mortality rate differences between paired groups. Second, analysis of trend with respect to age in mortality rate differences. The raw data for testing both hypotheses have been obtained as follows: (1), age specific mortality rates were calculated for each of 5 4-d intervals, from d 1 to d 20 of the assay (after d 20 there were too few individuals); (2), mortality rate differences between the paired groups have been divided by the total mortality rate in that age-interval; (3), the obtained data were then used to calculate the mean mortality rate differences between paired groups. Through each pair's mortality rate data the least square linear regression was calculated as well.

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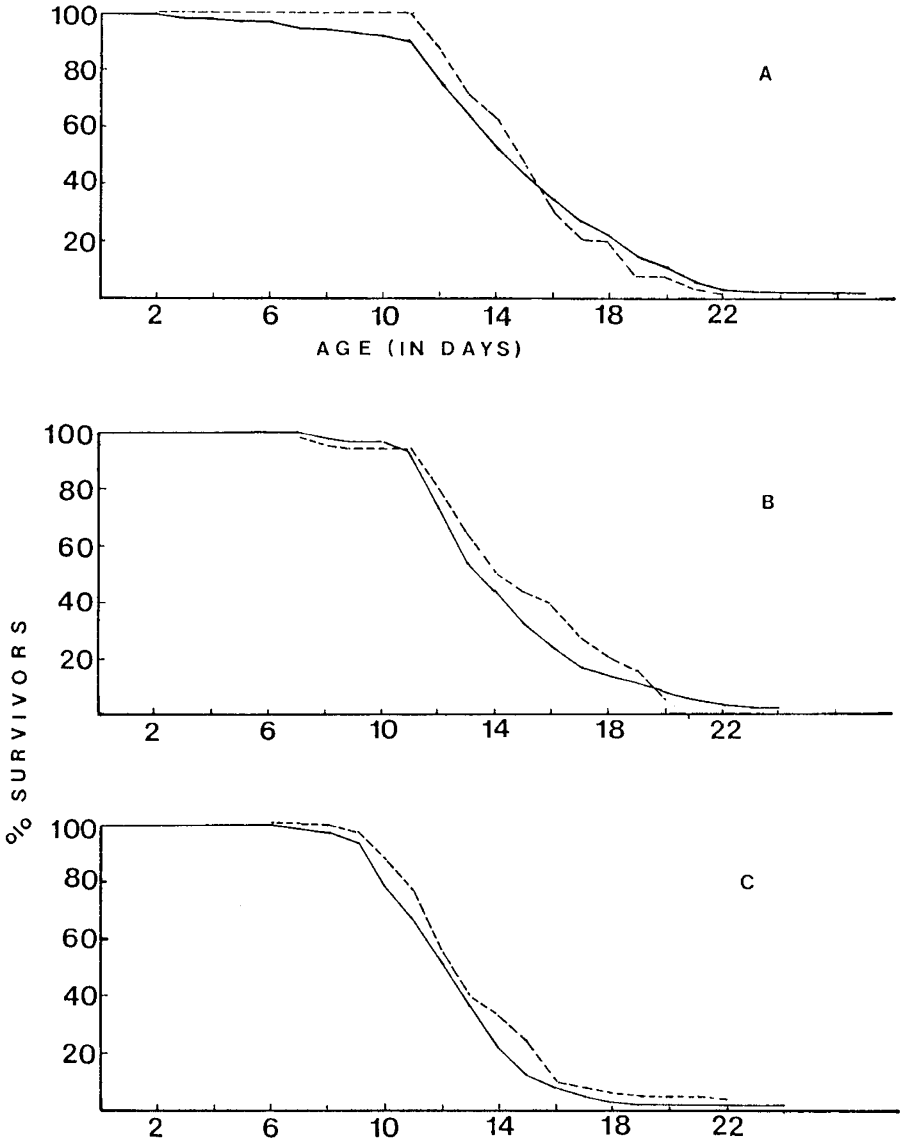
Fig 1. Survivorship of females selected for early and late (dashed lines) reproduction in control (A), low density (B) and high density (C) populations.

None of the estimated average mortality rate differences between any pair of compared populations is significantly different from zero. In addition, except for the comparison within control population (between offspring of young and old parents) there is no apparent age specificity in mortality rate differences between compared groups. (Space considerations preclude the detailed presentation of these results, but they are available from the senior author.)

The overall patterns of the mean daily fecundity in all treatments are shown in figure 2. Although there is no appropriate statistical test for the entire fecundity pattern, it seems that postponement in reproductive output is present in the offspring of old relative to young parents in all treatments.

The magnitudes of the actual responses to one-generation selection for early and late fecundity in terms of the intensity of selection (i), selection differentials (S), selection response (R) and realized heritability (h^2) are given in table IV. The change in the expected phenotypic value in offspring as a result of one-generation selection that chiefly interests us here is the realized heritability. The patterns for both traits (early and late fecundities) suggest that realized heritabilities are greater in the high density population. A comparison of realized heritabilities between early and late reproduced groups indicates that realized heritabilities are higher for early fecundity in all experimental populations.

Table IV. Direct responses to 1-generation selection for early and late reproduction within 3 populations. Early fecundity=fecundity 1–3 d; late fecundity=fecundity 7–9 d; i = intensity of selection; S = selection differential; R = selection response; h^2 = realized heritability.

Population	Parental age	Fecundity	i	S	R	h^2
Control	Young	Early	1.253	15.410	4.367	0.2834
	Old	Late	1.843	8.962	1.618	0.1806
Low density	Young	Early	1.265	13.612	9.824	0.7217
	Old	Late	2.040	9.125	1.265	0.1386
High density	Young	Early	1.219	11.288	15.056	1.3339
	Old	Late	1.843	13.071	3.2018	0.2449

Narrow and broad sense heritability estimates for longevity and fecundity data for early reproduced weevils within each population are given in table V. The heritabilities for late reproduced parents have been omitted, since a valid estimation of genetic variation with a small number of families (here 10–16 per population) is not possible. Only 2 traits, both within the low density population, showed significant narrow sense heritabilities (table V). Among all full-sib estimates of heritability 7 were significantly different from zero.

Genetical variation is a necessary prerequisite for the existence of genetic correlation between different traits. Since we found no significant heritabilities in most analysed traits, there was a small possibility of finding a significant genetic correlation among them. Nevertheless, we calculated the additive genetic correlation matrix (by means of the parental–offspring regression method; see Falconer, 1981)

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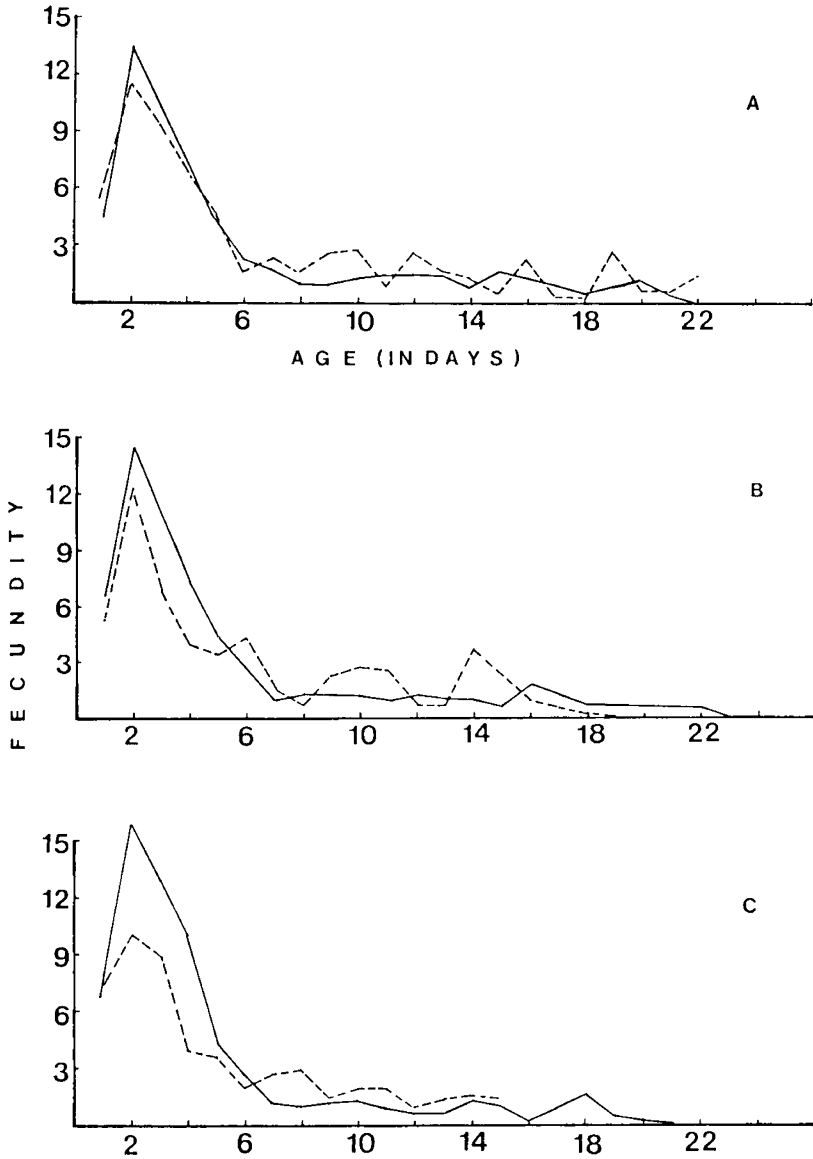
Fig 2. The mean daily fecundity of females selected for early and late (dashed lines) reproduction in control (A), low density (B) and high density (C) populations.

Table V. Narrow (h_N^2) and broad sense (h_B^2) heritabilities and their standard errors (SE) for early-reproduced weevils in the control, low- and high-density populations. Negative h^2 estimates are indicated by -0. N = No of families.

Trait	Control (N = 52)		Low density (N = 50)		High density (N = 54)	
	$h_N^2 \pm SE$	$h_B^2 \pm SE$	$h_N^2 \pm SE$	$h_B^2 \pm SE$	$h_N^2 \pm SE$	$h_B^2 \pm SE$
Longevity	0.21 ±0.29	0.39** ±0.15	0.59* ±0.22	0.41** ±0.15	0.22 ±0.21	0.50** ±0.15
Fecundity						
Days 1–3	0.90 ±0.48	0.14 ±0.13	1.06 ±0.83	0.30* ±0.14	−0	0.08 ±0.12
Days 7–9	−0	−0	0.43 ±0.29	−0	0.47 ±0.52	0.25 ±0.14
Days ≥ 10	−0	−0	0.94 ±2.08	0.12 ±0.14	2.53 ±3.53	0.11 ±0.15
Total	−0	0.17 ±0.14	0.12 ±0.36	0.45** ±0.15	−0	0.09 ±0.12
First day	−0	0.06 ±0.13	0.75 ±0.59	0.11 ±0.13	0.38 ±0.41	−0
Last day	0.22 ±0.54	0.36* ±0.15	0.66 ±0.37	0.40 ±0.15	0.35 ±0.23	0.23 ±0.13
Age of peak fecundity	0.43 ±0.97	−0	−0	−0	0.65 ±0.53	0.40 ±0.12
Laying rate	0.16 ±0.31	0.09 ±0.13	0.95* ±0.41	0.42 ±0.15	−0	0.25 ±0.14

$^*P < 0.05$; $^{**}P < 0.01$.

among traits for offspring of young parents within each of 3 populations. As predicted, none of the estimated correlations are significantly different from zero (for this reason we omitted their presentation, but they are available from the authors).

DISCUSSION

According to Luckinbill and Clare (1985) specific change in the external environment during preadult stages (*ie* high larval density) and the internal environment during adult stages (*ie* reproduction at the later stages) give rise to increased longevity in *Drosophila melanogaster*. The results of long-term selection for delayed senescence obtained by Rose and Charlesworth (1981b), Rose (1984), Mueller (1987) and Service *et al* (1988), also with *D melanogaster*, are in qualitative accord with the above-cited expectation regarding the effects of parental age and larval density. It is to be expected, therefore, that 1-generation selection for late reproduction in a population selected 10 generations for high larval density will show higher longevity relative to a population selected for low larval density and early reproduction. In this experimental design with the bean weevil, *Acanthoscelides*

obtectus, we, however, have not been successful in detecting significant response to combined effects of late parental age and high larval density with respect to adult longevity (table I).

In fact, we have obtained only direct responses to 1-generation selection in both early and late reproducing parents (table IV). However, there was no correlation between the fecundity responses and longevity. Though the average longevities in late reproduced parents suggest some enhancement in longevity, the overall effects of this treatment do not reveal significant differences (table III). Finally, mortality rate differences between treatments were not observed either.

The outcome of our previous study with the bean weevil (Tucić *et al*, 1990), in which long-term selection for early and late reproduction was imposed, has been consistent with the present results. Moreover, these findings are in agreement with the observation of Møller *et al* (1989), who found a similar relationship between longevity and fecundity in another weevil species, *Calosobruchus maculatus*. The absence of the direct link between fecundity and longevity in our experiments implies, therefore, that differences in fecundity of the bean weevils need not involve genes with pleiotropic effects on longevity.

Though quantitative genetic analyses seem futile when selection experiments fail to detect a cost of reproduction trade-off, we have found, at least, 2 reasons for such analyses. First, besides the predictive value, analyses of the genetic variation and covariation among fitness traits have important descriptive value. Second, and of more interest in the present context, there is a possibility that observed trade-offs between early and late fecundity have a genetic basis. Indeed, the results in tables I and III suggest that parental age could really change the fecundity schedule in the way predicted by antagonistic pleiotropy theory (*ie* that offspring of the young parents have higher early fecundity than offspring of the old parents, and *vice versa*). But the absence of statistically detectable negative correlations between early and late fecundities made our study inconclusive with respect to the possible genetically based trade-off among fecundity indices. There is another argument against antagonistic pleiotropy between early and late fecundity. Having in mind our selection regimes, it is very likely that offspring of the young parents lack some genetic variants, increasing the late reproduction, which are present in offspring of the old parents. Similarly, the high late reproduction in offspring of the old parents would not be causally related to their low early reproduction effort (Partridge, 1987, has used the same arguments against negative genetic pleiotropy in the interpretation of the above-cited long term selection studies with *Drosophila*).

Hence, the simplest interpretation of our results is in terms of phenotypic plasticity for longevity and fecundity. It means that every bean weevil female may face a phenotypic (physiological) trade-off in the allocation of limited resources between fecundity and longevity, but in the absence of genetic variation in this allocation, the genetical trade-off is undetectable by long-term selection experiments or by genetical analyses. We could say then that differences between individuals are based on phenotypic plasticity (which is a short-term, contingent response of an individual to immediate circumstances which may increase fitness), and a genetical trade-off need not exist.

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