

The pattern of genetic and environmental variation in relation to ageing in laying hens

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Summary – Data from a selection experiment with laying hens were used to study the structure of genetic correlations, as well as additive genetic and environmental variation over a period of 26–60 weeks of age. Genetic correlations were positive between all age periods for the 2 traits investigated, egg number and egg weight. Thus, the results do not support the pleiotropy theory of ageing which predicts negative genetic correlations between early and late fitness. For egg weight no trend with age was found for the 2 components of variance investigated. For egg number there was an increase in additive genetic variation as well as in environmental variation with age. The results support the mutation accumulation theory of ageing and other theories which postulate an increasing genetic variation with age.

genetic variation / environmental variation / genetic correlation / age changes

Résumé – Évolution avec l'âge de la variance génétique et de la variance de milieu chez des poules pondeuses. Les résultats d'une expérience de sélection de poules pondeuses ont été utilisés pour étudier, entre 26 et 60 semaines d'âge, l'évolution des corrélations génétiques et des variances génétiques et de milieu. Les corrélations génétiques entre différents âges étaient positives pour les 2 caractères étudiés, nombre d'œufs et poids des œufs. Ces résultats ne confortent pas la théorie de pléiotropie du vieillissement qui prédit des corrélations génétiques négatives entre différents âges. Pour le poids des œufs, aucune variation systématique avec l'âge des deux variances n'a été relevée. Pour le nombre d'œufs par contre, les 2 variances augmentaient. Ces résultats renforcent les théories (notamment celle de l'accumulation des mutations avec l'âge) qui prédisent une augmentation avec l'âge de la variance génétique.

variance génétique / variance due au milieu / corrélation génétique / changements dus à l'âge

INTRODUCTION

Increased knowledge about reproductive fitness and the fundamental causes of ageing is essential in order to be able to increase lifespan and lifetime production capacity in our domestic animals.

The pleiotropy theory of ageing (Williams, 1957) assumes that ageing is caused by pleiotropic or closely linked genes with beneficial effects at an early age, but unfavourable effects at a late age. This theory predicts negative genetic correlations between early and late fitness. Negative genetic correlations have actually been found in several investigations. Early fecundity decreased and late fecundity increased in response to selection for late fitness in selection experiments with *Drosophila melanogaster* by Rose and Charlesworth (1981b) and Luckinbill *et al* (1984).

Where genetic correlations have been calculated from pedigreed populations of *Drosophila melanogaster*, some estimates between early and late fecundity have been found to be negative (Rose and Charlesworth, 1981a; Tucic *et al*, 1988) while others have reported positive correlations (Giesel, 1986; Engström *et al*, 1989). When investigating part record production in laying hens, Clayton and Robertson (1966) found positive genetic correlations between early and late production, while Flock (1977) mainly found positive genetic correlations but negative correlations were also found. Fairfull and Gowe (1990) also found mainly positive genetic correlations between part record production in their literature review.

The mutation accumulation theory of ageing (Medawar, 1952) suggests that ageing is caused by late-acting mutations accumulating. These deleterious mutations accumulate due to their small effects on early fitness. The mutation accumulation theory predicts increasing additive genetic variation with age.

Rose and Charlesworth (1981a) did not find any trend in additive genetic variation with age when studying a population of *Drosophila melanogaster*. However, Liljedahl *et al* (1984) dealing with 2 populations of laying hens reported a positive trend in genetic variation with age for various egg production traits. An increase in additive genetic variation with age for fecundity traits in *Drosophila melanogaster* was found by Tucic *et al* (1988) and by Engström *et al* (1989).

Evidence for the 2 evolutionary theories described above both playing a role in the ageing process was found by Service *et al* (1988). Reverse selection was applied to lines previously selected for late fitness. Some of the fitness traits studied responded in accordance with the pleiotropy theory, while other traits showed no response, which supports the mutation accumulation theory.

In addition to the 2 evolutionary theories dealt with previously there are several other theories, one of which suggests that more and more inactive genes are turned on as needed during the course of ageing to counteract the negative effect of increased sensitivity to environmental stress (Liljedahl *et al*, 1984). Another theory postulates that genetic damage accumulates with age, causing different effects on the organism, the effect reflecting the individual capacity of DNA repair (Hart and Setlow, 1974). These 2 theories also predict increasing additive genetic variation with age.

The present study investigates the relationship between additive genetic as well as environmental variation and genetic correlations for egg production traits at different ages in laying hens.

MATERIAL AND METHODS

The 2 selected lines used in this investigation originated from a base population of laying hens which was formed by mating 7 commercial laying stocks in a diallel system. The resulting population was randomly mated for 3 generations before the formation of the different selected lines (Liljedahl *et al*, 1979).

Two selection lines were used in this experiment, one line selected for number of eggs (En) and the other line for egg weight (Ew). The selection was based on the performance during 20–42 weeks of age in both lines. The average rate of inbreeding was approximately 0.73% per generation. The environmental conditions were as usually recommended for commercial egg production except that the hens were fed a suboptimal diet (10.5 MJ/kg and 13% crude protein) and housed in single-hen cages. A more detailed description of the 2 lines and the environmental conditions can be found in Liljedahl and Weyde (1980).

The traits considered in this study were number of eggs (EN₁-EN₅) and egg weight (EW₁-EW₅) during 5 age periods (26–32; 33–39; 40–46; 47–53 and 54–60 weeks of age). Every second egg during the laying period was weighed.

Only hens surviving the entire experimental period (90.6%) are included in the data set. The results may possibly be slightly biased if hens who died early had a worse or better performance than the ones included in the analysis. In a similar study with *Drosophila melanogaster* the excluded group showed a very similar performance as compared with those included in the analysis (Engström *et al*, 1989). Individual records from an average of 419.8 hens per generation and line, bred from an average of 18.6 sires and 112.8 dams, were used for estimating genetic parameters and variance components within each line and generation. Data from 4 generations were used. Number of eggs laid decreased and egg weight increased with age. To take into account the dependence between the mean and the variance, data was transformed to a logarithmic scale.

The method used to calculate variance and covariance components for the 10 different traits was Multivariate Restricted Maximum Likelihood using an individual animal model (Meyer, 1986). The only factor in the model was the random effect of hen. The hens were kept under well controlled conditions which means that no environmental effects, such as differences between locations in the hen house, could be detected. The covariance structure among individuals was taken into account by a complete relationship matrix. The 2 variance components were estimated using an EM algorithm. As input to the multivariate analyses, variance component estimates from univariate analyses were used. The iterations were continued until the difference between 2 successive rounds was less than 0.01% for the 2 variance components estimated. The variance component between hens was used as an estimate of the additive genetic variation, whereas the component within hens was used as an estimate of environmental variation, ignoring other effects.

RESULTS

Because there were only small differences between generations for the variances and covariances estimated and to get reasonably small standard errors for the parameters involved, values presented are means and standard errors calculated over generations. Table I shows mean values and standard errors for egg number and egg weight at the 5 different age periods. Number of eggs laid decreased and egg weight increased during the laying period as expected.

The additive genetic component of variance and the environmental component increased with advancing age for the trait egg number, as shown in figures 1 and 2. The slope of the linear regression for the environmental component was significant in both the En and Ew lines ($P < 0.001$). The fit for the additive genetic component of the Ew line was also significant ($P < 0.03$); however, for the En line, the slope of the additive genetic component only approached significance ($P < 0.1$). For egg weight there was no significant trend in either of the 2 variance components estimated, as can be seen from figures 3 and 4.

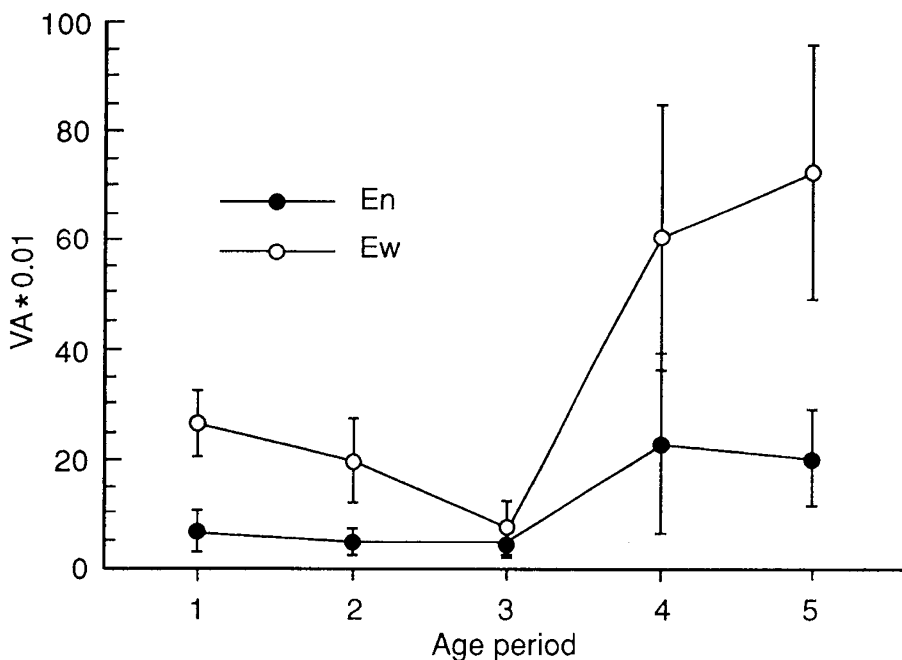


Fig 1. Additive genetic variance (VA) of the trait egg number at different ages (period 1 = 26–32 weeks, period 2 = 33–39 wk, period 3 = 40–46 wk, period 4 = 47–53 wk, period 5 = 54–60 wk) for a line selected for egg number (En) and another line selected for egg weight (Ew).

Selection may have resulted in a decrease in the magnitude of the genetic correlation between the early and late periods for both egg number and egg weight,

Table I. Descriptive statistics for egg number and egg weight at different ages.

Line ^a	Trait	Trait									
		EN1 ^b	EN2	EN3	EN4	EN5	EW1 ^c	EW2	EW3	EW4	EW5
En	Mean	40.72	40.40	38.50	36.25	36.30	47.68	50.88	53.12	54.48	56.00
En	SE	1.97	1.10	1.22	1.42	1.44	1.30	1.33	1.31	1.35	1.30
Ew	Mean	33.98	34.88	33.22	30.52	30.88	55.88	59.70	62.28	63.75	65.62
Ew	SE	0.96	0.91	0.96	1.80	0.90	1.36	1.45	1.56	1.62	1.82

^a Line En = line selected for number of eggs; Line Ew = line selected for egg weight. ^b Egg number recorded at 5 age periods; period 1 = 26-32 wk, period 2 = 33-39 wk, period 3 = 40-46 wk, period 4 = 47-53 wk, period 5 = 54-60 wk. ^c Egg weight recorded at the same age periods as egg number.

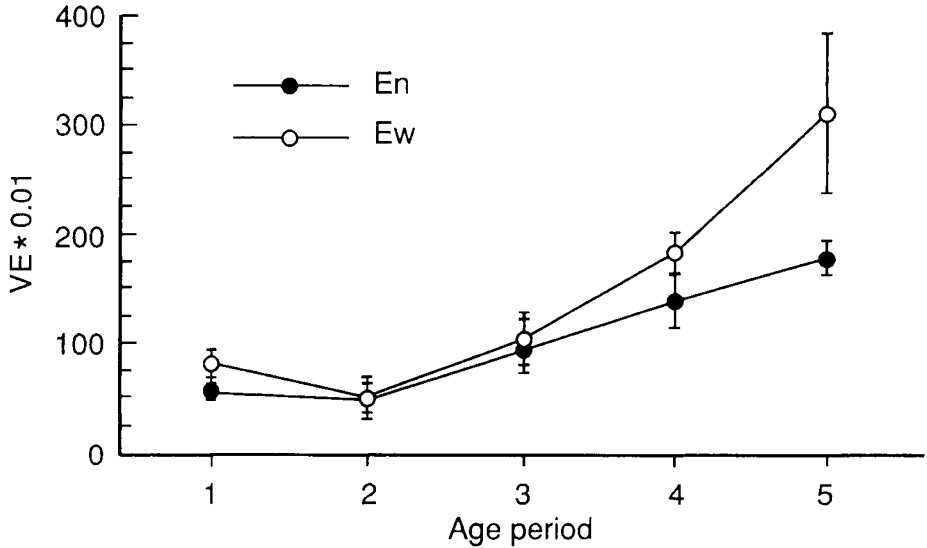


Fig 2. Environmental variance (VE) of the trait egg number at different ages (period 1 = 26–32 weeks, period 2 = 33–39 wk, period 3 = 40–46 wk, period 4 = 47–53 wk, period 5 = 54–60 wk) for a line selected for egg number (En) and another line selected for egg weight (Ew).

but especially for egg number (data not shown). Genetic and phenotypic parameters for egg number are presented in tables II and III. All phenotypic correlations between different age periods were significantly positive. The genetic correlations were also positive, and half of them differed significantly from zero. Tables IV and V present the same parameters for egg weight. All of these correlations were highly significant, positive values.

Table II. Genetic correlations (below), phenotypic correlations (above) and heritabilities (diagonal) for egg number at different ages in line En^a.

Trait	Trait				
	EN1	EN2	EN3	EN4	EN5
En1	0.10 ± 0.06	0.31 ± 0.05	0.24 ± 0.02	0.19 ± 0.02	0.23 ± 0.04
En2	0.48 ± 0.43	0.10 ± 0.06	0.49 ± 0.04	0.35 ± 0.04	0.23 ± 0.06
En3	0.33 ± 0.37	0.80 ± 0.19	0.04 ± 0.02	0.43 ± 0.08	0.30 ± 0.07
En4	0.49 ± 0.25	0.12 ± 0.42	0.41 ± 0.45	0.10 ± 0.07	0.44 ± 0.08
En5	0.74 ± 0.13	0.34 ± 0.46	0.50 ± 0.47	0.82 ± 0.13	0.10 ± 0.04

^a Trait abbreviations are as described in table I.

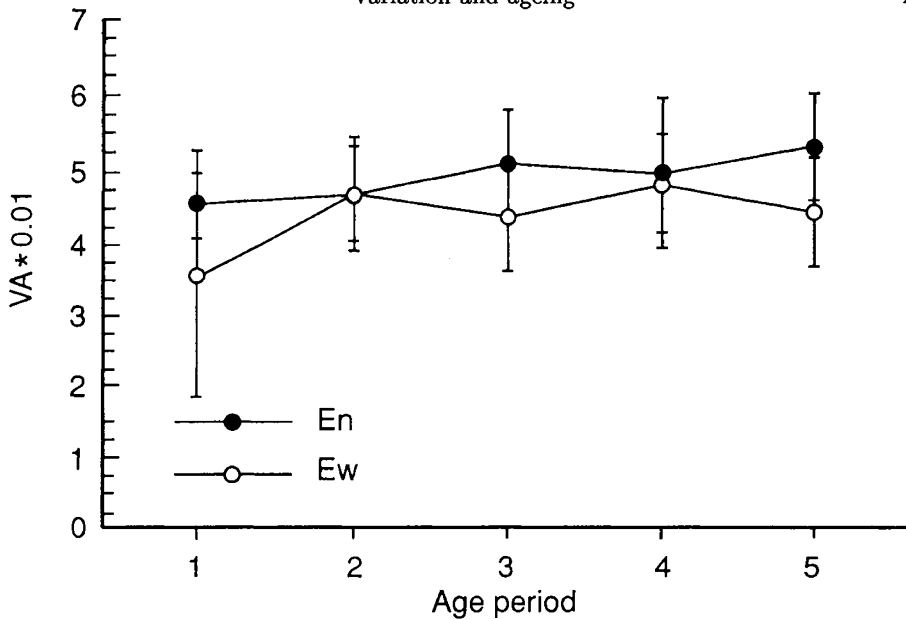


Fig 3. Additive genetic variance (VA) of the trait egg weight at different ages (period 1 = 26–32 wk, period 2 = 33–39 wk, period 3 = 40–46 wk, period 4 = 47–53 wk, period 5 = 54–60 wk) for a line selected for egg number (En) and another line selected for egg weight (Ew).

DISCUSSION

The present paper describes genetic parameters and variance components for egg number and egg weight within a population of laying hens. Estimates of genetic parameters can be affected by many factors, particularly linkage disequilibrium, genotype-environment interactions and inbreeding effects. In previous studies dealing with *Drosophila melanogaster* it has been argued that a population of wild-caught flies may show disguised genetic correlations between early and late reproductive fitness as a result of genotype-environment interaction arising from the change in environmental conditions when bringing them to a laboratory. When using populations of domestic animals, as in this study with laying hens, genotype-environment interaction should not be a problem.

Further, the population had undergone random mating before selection was applied and had a low level of inbreeding, which means that the parameters estimated should be practically unaffected by inbreeding. Positive genetic correlations can be caused by inbreeding (Rose, 1984). Inbreeding will result in a population that is homozygous for deleterious alleles, and its poor performance in both early and late fecundity will induce positive correlations.

Linkage disequilibrium arising from selection on early production in the 2 lines used could have affected the additive genetic variance. If there were such effects, the additive genetic variance should decrease predominantly in the early periods for the trait under direct selection. This would result in a pronounced increase in

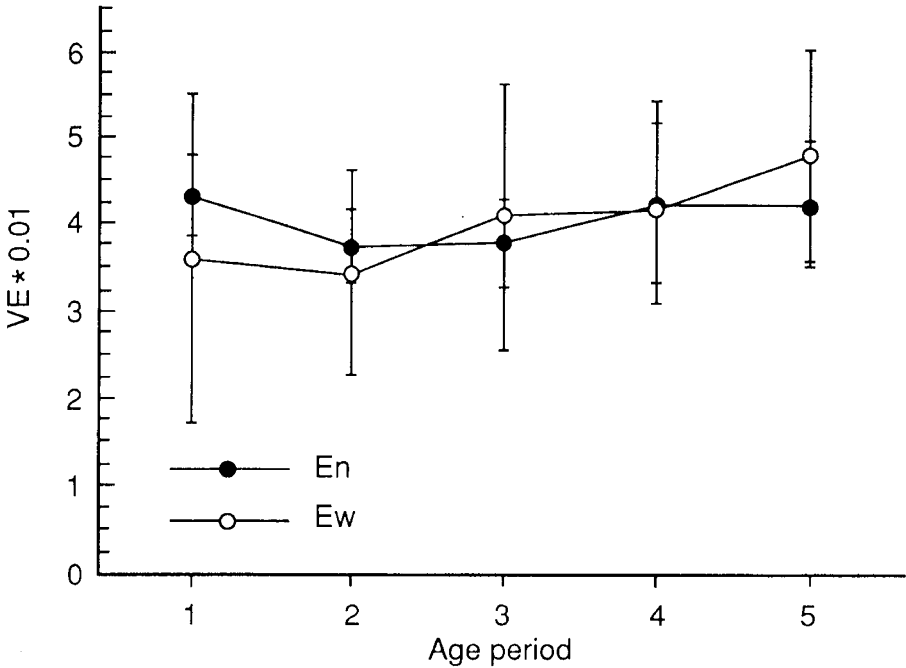


Fig 4. Environmental variance (VE) of the trait egg weight at different ages (period 1 = 26–32 wk, period 2 = 33–39 wk, period 3 = 40–46 wk, period 4 = 47–53 wk, period 5 = 54–60 wk) for a line selected for egg number (En) and another line selected for egg weight (Ew).

Table III. Genetic correlations (below), phenotypic correlations (above) and heritabilities (diagonal) for egg number at different ages in line Ew^a.

<i>Trait</i>					
<i>Trait</i>	<i>EN1</i>	<i>EN2</i>	<i>EN3</i>	<i>EN4</i>	<i>EN5</i>
EN1	0.26 ± 0.06	0.40 ± 0.05	0.21 ± 0.03	0.18 ± 0.02	0.15 ± 0.05
EN2	0.72 ± 0.15	0.26 ± 0.03	0.42 ± 0.03	0.32 ± 0.06	0.26 ± 0.05
EN3	0.57 ± 0.23	0.91 ± 0.08	0.28 ± 0.02	0.40 ± 0.05	0.22 ± 0.05
EN4	0.28 ± 0.23	0.76 ± 0.12	0.82 ± 0.16	0.16 ± 0.05	0.34 ± 0.07
EN5	0.24 ± 0.36	0.60 ± 0.27	0.40 ± 0.32	0.64 ± 0.19	0.14 ± 0.07

^a Trait abbreviations are as described in table I.

additive genetic variance with age for this particular line and trait combination. Accordingly, a larger increase in additive genetic variance for egg number would be expected in the En line than in the Ew line. However, no such pattern was found for egg number or egg weight in the 2 lines investigated.

Table IV. Genetic correlations (below), phenotypic correlations (above) and heritabilities (diagonal) for egg weight at different ages in line En^a.

<i>Trait</i>					
<i>Trait</i>	<i>EW1</i>	<i>EW2</i>	<i>EW3</i>	<i>EW4</i>	<i>EW5</i>
EW1	0.52 ± 0.04	0.79 ± 0.01	0.75 ± 0.01	0.70 ± 0.02	0.70 ± 0.02
EW2	0.98 ± 0.01	0.55 ± 0.07	0.87 ± 0.01	0.81 ± 0.01	0.79 ± 0.02
EW3	0.96 ± 0.01	0.99 ± 0.00	0.57 ± 0.07	0.87 ± 0.01	0.85 ± 0.01
EW4	0.91 ± 0.01	0.95 ± 0.00	0.98 ± 0.00	0.54 ± 0.11	0.87 ± 0.01
EW5	0.89 ± 0.01	0.92 ± 0.01	0.96 ± 0.01	0.97 ± 0.01	0.57 ± 0.08

^a Trait abbreviations are as described in table I.

Table V. Genetic correlations (below), phenotypic correlations (above) and heritabilities (diagonal) for egg weight at different ages in line Ew^a.

<i>Trait</i>					
<i>Trait</i>	<i>EW1</i>	<i>EW2</i>	<i>EW3</i>	<i>EW4</i>	<i>EW5</i>
EW1	0.52 ± 0.12	0.77 ± 0.03	0.74 ± 0.02	0.70 ± 0.02	0.69 ± 0.03
EW2	0.95 ± 0.02	0.56 ± 0.08	0.83 ± 0.04	0.80 ± 0.02	0.78 ± 0.03
EW3	0.94 ± 0.02	0.98 ± 0.01	0.52 ± 0.08	0.82 ± 0.02	0.82 ± 0.04
EW4	0.92 ± 0.02	0.98 ± 0.01	0.97 ± 0.01	0.54 ± 0.04	0.83 ± 0.02
EW5	0.91 ± 0.03	0.97 ± 0.01	0.96 ± 0.02	0.98 ± 0.00	0.48 ± 0.07

^a Trait abbreviations are as described in table I.

The 2 lines originated from the same cross of various commercial lines. But all original lines had been selected in similar ways, which means that crossing may not have removed all effects of long-term selection for number of eggs and egg weight on linkage disequilibrium.

The genetic correlations estimated between different age periods for egg number and egg weight were mainly significant and positive. The pattern of genetic correlations even though in the present experiment the hens were not very old, considering the biological lifespan of a hen, does not support the pleiotropy theory, which predicts negative correlations between early and late reproductive fitness.

The results of this investigation show a systematic increase in additive genetic and environmental variation with age for the trait egg number, although the heritability estimates vary very little with age. The slightly higher estimates for the 2 variance components in the early age periods is probably an effect of age at sexual maturity influencing the variance at this early age. The increased additive genetic variation could be explained by X-linked effects, epistasis and dominance contributing more to the total genetic variation at a late age than at an early age. This investigation does not consider variation caused by these factors; however, they will be dealt with in a later study.

For egg weight there was no significant age trend. This is to some extent expected because of the short age period considered in the present experiment compared to

the biological lifespan of a hen, as mentioned earlier. A similar pattern was found by Liljedahl *et al* (1984) when variance components were expressed as coefficients of variation to take into account the dependence between mean and variance. The difference in the results obtained for egg number and egg weight can be explained by egg weight not being as closely related to reproductive fitness as egg number. Egg weight is a trait with an intermediate optimum with regard to fitness, whereby intermediate values of the trait have maximum fitness.

Increasing environmental or phenotypic variation has been found in several studies investigating animal's reaction to increasing age or stressful environments (Clayton and Robertson, 1966; Flock, 1977; Liljedahl *et al*, 1984 in laying hens; Rose and Charlesworth, 1981a; Burla and Taylor, 1982; Engström *et al*, 1989 in *Drosophila melanogaster*). This pattern is probably due to the impairment of the individual's ability to cope with environmental stress due to increasing difficulties in maintaining their physiological homeostasis (Lerner, 1954).

The results of this investigation mainly support theories such as the mutation accumulation theory, more genes turned on as needed during the course of ageing and individual differences in DNA-repair capacity. The results also indicate that it is possible to improve life-time production without any negative effects on early reproductive fitness.

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