

Selection for fertility in mice – the selection plateau and how to overcome it

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Summary. A long-term experiment for increasing the traits first day litter size (LS1) and litter weight (LW1) was conducted with two populations for 33 generations. The selection plateau was reached in population DU-C (selection and estrus synchronization ($h^2 = 0.02 \pm 0.01$); in population DU-K (selection) the plateau ($h^2 = 0.05 \pm 0.2$) was nearly reached. Selection progress per generation was in LS1 $b = 0.11 \pm 0.02$; $b = 0.12 \pm 0.04$ (1st to 18th generation DU-K, DU-C) and $b = 0.10 \pm 0.03$; $b = 0.07 \pm 0.05$ (19th to 33rd generation, DU-K, DU-C) in LW1 $b = 0.16 \pm 0.04$ g; 0.19 ± 0.07 g (DU-K, DU-C) $b = 0.20 \pm 0.09$ g; 0.001 ± 0.09 g (DU-K, DU-C). Reverse and relaxe selection as well as systematic inbreeding was applied for 10 generations. Reverse selection yielded $h^2 = 0.28 \pm 0.11$ (R-DU-K) and $h^2 = 0.17 \pm 0.05$ (R-DU-C) and showed that there was still additive genetic variance. Relaxe selection did not cause alterations in the selection parameters, whereas inbreeding lead to inbred depressions ($b = LS1 = -0.42 \pm 0.15$; -0.45 ± 0.12 ; $b = LW1 = -1.13 \pm 0.20$; -0.82 ± 0.18 I-DU-K, I-DU-C). The plateau was based upon the heterozygote advantage. Several methods for overcoming the plateau were applied. A new selective useful variance could be created by crossing the plateau populations ($h^2 = 0.14 \pm 0.04$). A short-term progress in overcoming the plateau (1st to 3rd generation) could be obtained by litter size standardization (LS=8). Tandem selection (selection for body weight – BW42) as well as crossing of inbred strains were not suitable for overcoming the selection plateau. Altering the environmental conditions as a possibility for overcoming the plateau has been discussed.

Key words: Mice – Selection experiments – Plateau – Fertility

Introduction

Long-term selection experiments within a population has shown that selection response decreases in the course of selection until, eventually, no further progress can be obtained. In such cases it can be said that the selection plateau of the population has been attained. The following factors influence the time required to reach the plateau: environmental conditions, effective population size, and the effects of genetic drift and degree of inbreeding, selection intensity, selection parameters, direction of selection, gene frequencies in the base population.

Selection experiments with laboratory animals yielded a plateau after 10 to 40 generations, the above mentioned factors causing this variation width. Roberts (1966a,b, 1967a,b, 1974) conducted theoretical studies regarding the occurrence of the selection plateau for a given effective population size, and these investigations were continued by Kress (1975) and Eisen (1980).

Genetic causes of the plateau have been discussed by Falconer (1971) and Al-Murrani (1974) who both described possible ways of overcoming it. If the plateau is reached because the additive genetic variance has been exhausted, it should be possible to overcome it by introducing new genetic variances. This method has been applied successfully by crossing (mouse) and X-ray exposure (*Drosophila*) by Falconer and King (1953); Falconer (1953, 1960) and Roberts (1967b). If the plateau is caused by overdominance or heterozygote advantage recurrent selection (RS) or reciprocal recurrent selection (RRS) should lead to success. Experiments with *Drosophila* (Bell et al. 1955; Brown and Bell 1980) however, failed to confirm this.

Bell (1982 a, b) using *Tribolium*, the mouse and the hen, showed that the success of RRS depends on both whether or not the selection criterion is determined by non-additive gene effects and on the environmental conditions (optimal or suboptimal) under which selection is conducted.

Falconer (1971) found an experimental solution to the "One Strain Problem" by systematic inbreeding selection and crossing. As Eklund and Bradford (1977) later confirmed, it is

Table 1. Methods for analysing and overcoming the selection plateau

Plateau analysis	Designation	Generations	Start of investigation
Reverse selection	R-DU-K	10	20th generation
	R-DU-C	10	20th generation
Relax selection (randomised mating)	Re-DU-K	10	21th generation
	Re-DU-C	10	21st generation
Inbreeding (sibling mating)	I-DU-K	10	22nd generation
	I-DU-C	10	22nd generation
<i>Overcoming the plateau</i>			
Crossing of populations DU-K and DU-C and selection	DU-K × C	5	33rd generation
Selection for BW42	DU-K-6	8	28th generation
Selection with the aid of litter size standardization	DU-Ks	5	33rd generation
	DU-Cs	5	33rd generation
Crossing of inbred populations I-DU-K × I-DU-C	I-F ₁	–	–
	I-F ₂	–	–

possible by this method to overcome the litter size plateau, but Barria-Perez (1976) had no success when he tried to use it to overcome the plateau while selecting for growth (gain from the 21st to the 42nd day of life). Abplanalp (1962), by altering the environment (feeding regime), was able to pass the selection plateau with respect to egg production.

The objectives of the present investigations were to analyse the genetic background to the plateau for fertility selection and to test various experimental methods of overcoming it.

Material and methods

The investigations were carried out on an outbreeding line Fzt:DU. The selected populations were kept under conventional conditions until the 18th generation and under semi-barrier conditions from the 19th to the 33rd generation. In the 18th generation, in which no selection took place, the population was transferred with the aid of hysterioectomy to a new laboratory with better environmental conditions. As the two environments are not comparable, the selection data were analysed separately for each environment. Selection for fertility consisted of selecting with the aid of a basis index made up of the characters litter size (LS1) and litter weight (LW1) on the first day of life of the first offspring ($I = LW1 + 1.6 \times LS1$). Selection was performed in two populations (DU-K and DU-C) with an effective population size $N_e = 40.3$ animals using a mean selection quota of 27%. Litter sizes were not standardized. In population DU-C, selection up to the 23rd generation was accompanied by estrus synchronization with gestagen chlormadinon acetate prior to mating for the first litter, but in the generations 24 to 33 there was only selection without synchronization. Details of the environment and of the selection and estrus synchronization procedures have been previously given by Schüler (1976, 1979) and Schüler and Bachnick (1977, 1978).

A selection plateau was observed in the course of selection. The methods used to analyse and overcome the plateau are outlined in Table 1. Further particulars regarding these methods are described in the "discussion".

The following traits were recorded in each generation.

Litter traits: litter size and litter weight (g) on the 1st and 21st day of life (LS1, 21; LW1, 21); implantation rate (IR); post-natal losses L1-21).

Parameters of puberty: age (days) and body weight (g) at first estrus (A1E, BE1E); *growth parameters:* body weight on 21st and 42nd day of life (BW21, 42).

Statistic analysis

The data were analysed by calculating the linear regression coefficients (b) and the standard deviations of b (s_b) for the character (generation means) of the generation number describing the direct and the correlated selection progress. The h^2 and sh^2 values were estimated by Hills's (1972) procedure for the selection criterion. The level error for the first risk was $\alpha = 0.05$ for all statistical tests.

Results and discussion

Direct results of selection

Figures 1 and 2 show the development of the trait selection index for 33 generations: the index increased by 20.8 (DU-K) and 23.6 (DU-C) index units corresponding to 2.70 (DU-K) and 3.06 (DU-C) times the phenotypic, and 9.0 and 10.2 (DU-K, DU-C) times the genetic, standard deviations in the base population ($s_p = 7.71$; $s_g = 2.31$). This result is an overestimate for there was no selection between the 18th and 19th

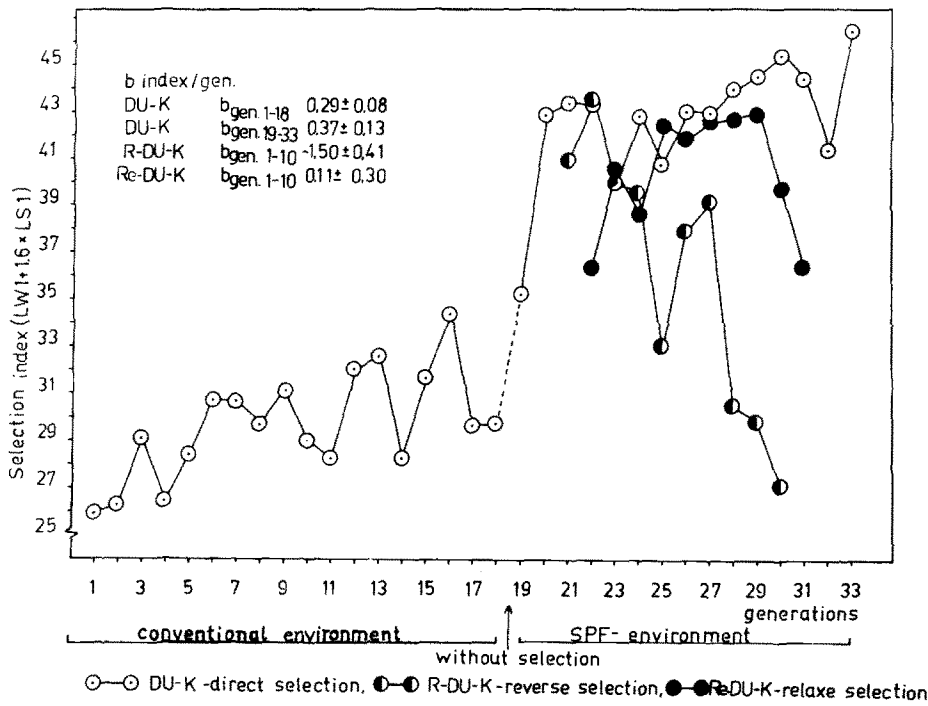


Fig. 1. Direct response to selection in populations DU-K, R-DU-K and R-DU-K

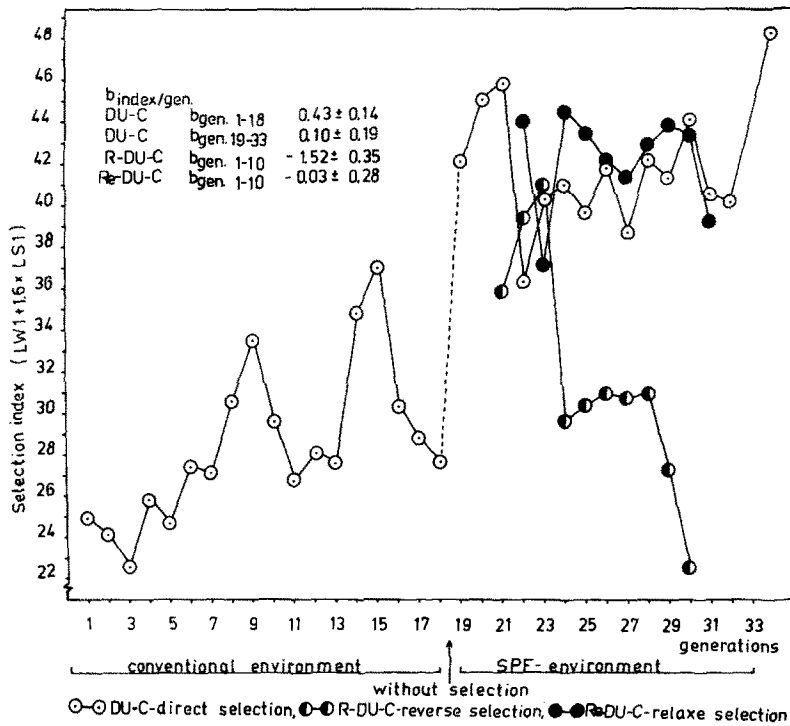


Fig. 2. Direct response to selection in populations DU-C, R-DU-C and Re-DU-C

generations and the phenotypic improvement of the traits was due to environmental influences.

If this effect was taken into account, the index would increase by 15.4 and 9.1 units, respectively, which corresponds to 2.0 and 1.2 times the phenotypic, and 6.7 and 3.9 times the genetic, standard deviations

(DU-K, DU-C). The heritability coefficients obtained for the two populations differed, and this has been attributed to the effects of gestagen-induced estrus synchronization (Schüler 1976).

It was higher for population DU-K ($h^2=0.16$; 1st to 6th generation) than for population DU-C ($h^2=0.10$;

1st to 6th generation). In the new environment no selection progress was achieved with population DU-C ($h^2=0.02$; 19st to 33rd generation), whereas a value of 0.05 was estimated for h^2 in population DU-K. In the first selection period (1st to 18th generation), selection success decreased through the course of generations in population DU-K, but not in population DU-C. The heritability coefficients and the linear regression coefficient are shown in Table 2.

This table also shows values of index traits LS1 and LW1 since, in view of the phenotypic correlation of $r_p < 0.9$ to the index, these traits can be considered as a direct selection success.

Analysis of the selection plateau

As shown in Table 2 and Figs. 1 and 2 no selection progress was obtained in population DU-C and only a little success was achieved in population DU-K after the 19th generation.

The height of the selection plateau was estimated in the two populations by calculating the mean trait values of generations 28 to 33. Selection progress was only obtained randomly in this period of selection. Thus, the level of the plateau was 44.4 and 42.9 units for the selection index, and LS1 = 13.95 and 13.56 and LW1 = 22.12 g and 21.27 g (DU-K, DU-C), respectively. Reverse and relaxe selection as well as inbreeding was applied in the two populations for 10 generations to analyse the genetic causes of the selection plateau.

Reverse selection. Eighty males and 80 females were chosen randomly in the 20th generation and selected for reducing the index (mass selection). Selection values corresponded to those of populations DU-K and DU-C. The results of selection for 10 generations are shown in Figs. 1 and 2 and Table 3. Selection yielded to a success corresponding to a realized heritability of 0.25 ± 0.11 (R-DU-K) and 0.17 ± 0.05 (R-DU-C). The

Table 2. Realized heritability coefficients (h^2) and regression coefficients (b) of the mean trait values for the generation number (selection index, litter size (LS1) and litter weight (LW1) on the 1st day of life)

Traits	Generation	DU-K				DU-C			
		h^2	$\pm s_{h^2}$	b	$\pm s_b$	h^2	$\pm s_{h^2}$	b	$\pm s_b$
Index	1.- 6.	0.16	0.31	0.81	0.33*	0.10	0.05	0.51	0.36
	1.-12.	0.09	0.03*	0.39	0.13*	0.12	0.03*	0.57	0.11*
	1.-18.	0.02	0.01*	0.29	0.08*	0.08	0.02*	0.43	0.14*
	19.-33.	0.05	0.02*	0.37	0.13*	0.02	0.01	0.10	0.19
LS1	1.-18.			0.11	0.02*			0.12	0.04*
	19.-33.			0.10	0.03*			0.07	0.05
LW1	1.-18.			0.16	0.04*			0.19	0.07*
	19.-33.			0.20	0.09*			0.001	0.09

* $P \leq 0.05$

Table 3. Linear regression coefficients of the generation means on the generation number for the reverse (R-DU-K; R-DU-C), relaxe selection (Re-DU-K, Re-DU-C) and inbreeding over 10 generations (I-DU-K, I-DU-C)

	R-DU-K		R-DU-C		Re-DU-K		Re-DU-C		I-DU-K		I-DU-C	
	b	$\pm s_b$	b	$\pm s_b$	b	$\pm s_b$	b	$\pm s_b$	b	$\pm s_b$	b	$\pm s_b$
Index	-1.50	0.41*	-1.52	0.35*	0.11	0.30	-0.03	0.28	-2.10	0.42*	-1.57	0.36*
LS1	-0.49	0.09*	-0.46	0.10*	0.04	0.08	-0.03	0.08	-0.42	0.15*	-0.45	0.12*
LW1 (g)	-1.04	0.21*	-0.80	0.18*	0.04	0.17	-0.01	0.18	-1.13	0.20*	-0.82	0.18*
LS21	-0.35	0.10*	-0.37	0.11*	-0.04	0.10	0.02	0.10	-0.55	0.10*	0.56	0.14*
LW21 (g)	-3.43	1.24*	-3.43	1.28*	-0.38	1.45	2.10	11.74	-6.65	1.40*	-4.14	1.65*
L 1-21	0.10	0.07	0.02	0.10	-0.02	0.13	0.05	0.08	0.67	0.19*	0.42	0.21
AIE	-0.27	0.38	-0.27	0.25	0.10	0.23	0.25	0.25	0.36	0.28	0.59	0.41*
BW1E (g)	-0.07	0.11	-0.07	0.03	-0.02	0.10	-0.08	0.07	0.03	0.23	-0.12	0.11
OR	-0.03	0.30	-0.60	0.10	-0.31	0.02*	-0.24	0.13	0.05	0.26	0.14	0.26
IR	-0.46	0.34	-1.08	0.24	-0.07	0.18	-0.38	0.13*	0.09	0.21	0.09	0.25

* Significant regression coefficients

basis index decreased by -1.50 ± 0.41 and -1.52 ± 0.35 units per generation (R-DU-K; R-DU-C). Hence, it could be suggested that there was still additive genetic variance not being used in selection for LS1 and LW1.

Table 3 shows the direct (LS1, LW1) and correlated effects of the reverse selection as regression coefficients of the generation number. As correlated effects, LS21 and LW21 decreased in the two populations, but the ovulation rate (OR) and implantation rate (IR) decreased only in population R-DU-C. Body weight and age of animals at first estrus decreased over several generations.

The linear regression coefficients were not significant statistically.

Relaxe selection. Eighty males and 80 females were taken for relaxe selection from the 21st generation and kept by random mating for 10 generations. Sib- and half-sib mating was avoided. Results are represented in Figs. 1 and 2 as well as in Table 3. The following traits were not altered by relaxe selection over the period of 10 generations: index (b index = 0.11 ± 0.30 , Re-DU-K; -0.03 ± 0.28 , Re-DU-C) litter traits development and puberty (Table 3).

The ovulation rate (OR) (b -0.31 ± 0.02) in population Re-DU-K and the implantation rate (IR) (b -0.38 ± 0.13) decreased significantly. These data were only obtained from generations 1, 4 and 8. Results of random mating exclude natural selection as the cause of the plateau. The correlated effects of the ovulation and implantation rate in the populations show that despite a similar selection intensity and criteria, different gene combinations were achieved by selection in the populations DU-K and DU-C.

Similar results have also been recorded by Schüler (1979) for the response to endurance stress and they were estimated as the influence of the estrus synchronization.

Inbreeding. Ten full sibs per population were taken from the 22nd and 23rd generations and inbred for 10 generations (brother and sister matings). Results of this method are presented in Table 3. Modifications in the generations for the traits – LS1 and LW1 – are shown in Fig. 3. Inbreeding resulted in a significant decrease in litter traits (LS1, LW1, LS21, LW21, L 1-21). Ovulations- and implantations rates as well as traits of puberty were not influenced (Table 3). Thus, post-implantative and post natale mortality have increased by inbreeding. Body weight (BW42) was reduced (b = -0.85 ± 0.20 ; -0.48 ± 0.20) in population I-DU-K in comparison with population I-DU-C (Fig. 3).

Investigations on the genetic causes of the selection plateau show that it was due to an overdominance and that heterozygote animals were selected. Falconer (1971) and Eklund (1976) also confirmed these plateau causes in selection for LS1, but they also showed that recessive alleles were important.

Overcoming the selection plateau. The cross population (DU-K \times C) derives from animals of the 33rd generation of the selection populations DU-K and DU-C. Forty males and 40 females of each population were crossed reciprocally (F1) and mated randomly to F2. Mass selection was conducted for 5 generations starting in the generation F3; population size and selection quota corresponded to those of populations DU-K and DU-C. Results of reverse selection showed that additive genetic variance was still existing in the two "Plateau Populations", but was not useful for increasing the index. New additive genetic variance was created by crossing the populations DU-K and DU-C, for by com-

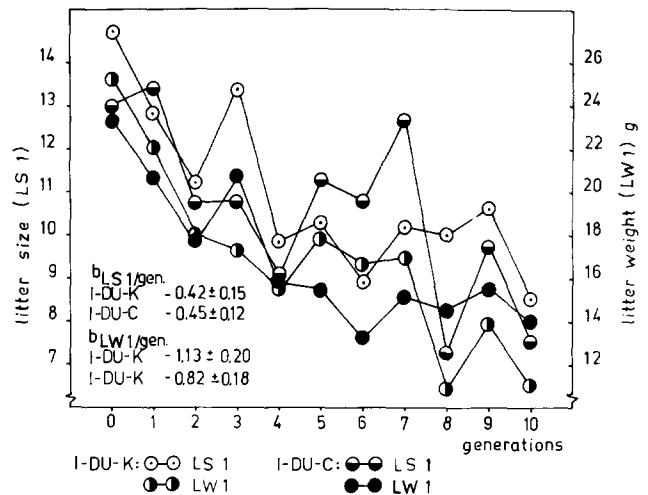


Fig. 3. Influence of inbreeding for 10 generations on the parameters of the selection index – litter size (LS1) and litter weight (LW1) – in the populations I-DU-K and I-DU-C

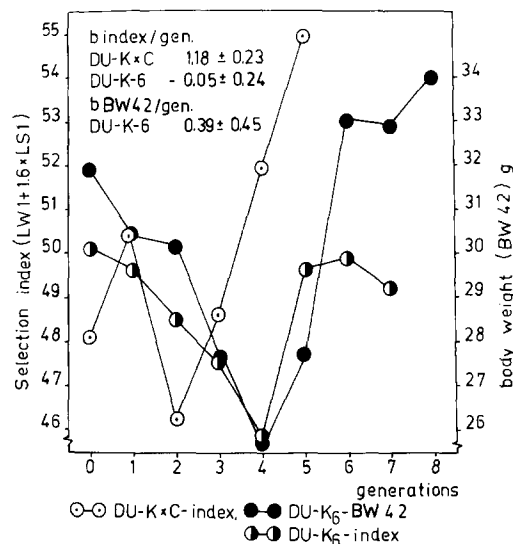


Fig. 4. Direct response to selection in population DU-K \times C and direct BW42 and correlated response (index) in population DU-K-6

Table 4. Direct and correlated selection progress in the cross population (DU-K×C) and in the populations with litter size standardization (DU-Ks, DU-Cs), heritability coefficients and linear regression coefficients of the generation means on the generation number

Traits Index	DU-K×C		DU-Ks		DU-Cs	
	h^2	$\pm s_{h^2}$	h^2	$\pm s_{h^2}$	h^2	$\pm s_{h^2}$
	b	$\pm s_b$	b	$\pm s_b$	b	$\pm s_b$
Index	1.18	0.23*	0.14	0.17	-0.74	0.72
LS1	0.37	0.04*	-0.06	0.17	-0.12	0.19
LW1	0.82	0.06*	-0.08	0.32	-0.47	0.41
LS21	0.28	0.04*	-0.01	0.05	-0.02	0.06
LW21	4.93	0.80*	-3.28	0.91*	-7.50	1.37*
L 1-21	0.23	0.63	-0.05	0.11	-0.11	0.16
AIE	-0.29	0.53	0.12	0.71	0.04	0.17
BW1E	0.41	0.03*	0.60	0.74	-0.01	0.22
BW21 ♀	-0.15	0.29	-	-	-	-
BW21 ♂	0.22	0.01*	-	-	-	-
BW42 ♀	0.62	0.08*	-1.71	0.92	-0.75	0.50
BW42 ♂	0.30	0.10*	-2.60	1.14	-1.25	0.64

parison of the direct and correlated selection progress it was known that selection in the two populations had influenced other gene combinations (Schüler 1979, 1982). Crossing resulted in heterotic effects of litter traits in F_1 and in F_2 -population as well. The index amounted to 48.52 and 48.04 units, respectively, a value significantly above the plateau level. Differences in the plateau in LS1 was 1.32 (F_1) and 1.24 (F_2) animals, respectively; in LW1 there were 3.23 g (F_1) and 2.34 g (F_2), respectively. In F_3 to F_7 , selection was conducted with the aid of the index (5th generation). Results of this selection are given in Fig. 4 and Table 4.

Selection increased the trait selection index by 11.07 units with an increase in LS1 by 2.82 animals and LW1 by 6.49 g. This selection progress corresponded to a realized heritability (h^2) of 0.14 ± 0.04 (Table 4). Apart from this direct selection progress, LS21 and LW21 increased, as did postnatale losses. It was typical that the growth potential of the pups increased, which was to be seen in an increase of body weight at the beginning of puberty as well as in the weights of the individual animals (BW21, BW42).

This was due to a higher milk yield of the mothers which can be characterized indirectly by postnatale losses. The mean rates of losses in the plateau population were 31.4% and 18.3% (DU-K, DU-C), respectively, whereas losses in the cross population only amounted to 15.1% from the 1st to the 21st day of life. Hence, the creation of the new applicable variance by crossing was a suitable method for overcoming the selection plateau.

Falconer and King (1953); Roberts (1967 a, b) reported on similar results in overcoming the plateau by crossing for growth traits, and Falconer (1971) for litter size.

Growth selection (tandem selection)

An increase of litter size was obtained as a correlated effect of selection for growth. This effect is based on the positive phenotypic and genetic correlations between these traits as Eisen et al. (1970: $r_p=0.24$; $r_g=0.64$), Hanrahan and Eisen (1978: $r_p=0.34$; $r_g=0.36$), and Eisen (1978: $r_p=0.27$; $r_g=0.63$) reported.

Consequently, there is the opportunity to use the genetic correlations for also overcoming the plateau. A sibling selection for body weight on the 42nd day of life was conducted in the 34th generation of population DU-K with the aid of litter size standardization (LS=8) for 8 generations. A detailed description of this selection quota was 45% in a mean population size of 80 males and 80 females. Figure 4 shows the direct selection progress in the trait "body weight" (BW42) and the correlated success in "selection index". As a result of selection, body weight per generation increased by $b=0.39$ g/generation. This success corresponded to a realized heritability of 0.15 ± 0.19 . The trait "selection index" was not influenced by growth selection ($b=-0.05 \pm 0.24$). Thus, the plateau could not be overcome by growth selection. Fertility selection for 34 generations reduced the genetic variability for growth traits as well as the genetic correlation between BW42 and the index traits.

Bünger et al. (1982) obtained a selection progress of 0.94 g per generation and an increase of litter size of 0.19 per generation without having selected for fertility—they selected only for body weight (BW42) in the outbreeding population Fzt: DU. On the average, LS1 with 0.4 animals exceeded the plateau in the experiment recorded. This result is more likely due to litter size standardization than to growth selection. Further investi-

gations on the nonselected population Fzt:DU showed an increase of LS1 in standardized litters (LS=8) by 0.32 animals on the average (Bünger et al. 1983). Due to the positive correlation between body weight at mating (BWM) and LS1 of $r=0.33$ and the positive regression (BWM and LS1) of $b=0.36$ in the population Fzt:DU, a correlated selection progress could be expected in LS1. Indeed, LS1 remains unchanged by selection for growth. The estimated selection coefficient of the selected population was only 0.2; it was considerably smaller than in the population Fzt:DU.

Selection with litter size standardization

The traits of the selection indices LS1 and LW1 are influenced by prenatal effects. Selection without litter size standardization influences the body weight of the offsprings and with it the fertility performance of these animals. The ups and downs of the selection progress in populations DU-K and DU-C in the course of generations is the result of these correlations. Due to these results and the higher litter sizes of females from standardized litters (LS=8) of 0.32 animals, it could be tested, by eliminating maternal effects, if the plateau could be overcome by selection with litter size standardization.

Selection with litter size standardization (LS=8) was therefore conducted for 5 generations with animals of the 33rd generation (80 males and 80 females). Results of this selection are presented in Table 4 and Fig. 5.

Regression coefficients as well as estimated realized heritability ($h^2=0.02 \pm 0.03$ DU-Ks, -0.09 DU-Cs) show that there was no progress during the total selection period.

It was typical for the two populations that a selection progress was obtained in generations 1 to 2 (DU-Ks) and 1 to 3 (DU-Cs), but it declined again in the generations 4 to 5. Level of the populations DU-K and DU-C was reached again after 5 generations. Figure 5 shows the deviations from contemporary generations in the populations DU-K and DU-C in the trait "selection index".

These differences were significant (generation 1, 2 – DU-K; generation 1, 2, 3 – DU-C). It should also be considered that selection progress also includes the influence of litter size standardization.

On the supposition that the standardizing effect in LS1 of 0.32 animals in the population Fzt:DU is also valid for the populations DU-K and DU-C, a correction of the selection progress may be possible. The result of 0.32 animals corresponds to an index value of 1.02 units. If this effect is subtracted from the selection progress of the populations DU-Ks and DU-Cs and the deviations from the corresponding generations are tested, selection progress in the 1st and 2nd generations (DU-Ks) and in the 1st and 3rd generation (DU-Cs) will remain statistically reliable. Thus the plateau could

be overcome by selection with litter size standardization within a very short time.

Crossing of inbred populations

Recessive allele reducing fitness of the populations were eliminated from the populations by inbreeding. The two inbred populations were crossed reciprocally to I-F₁ and I-F₂ after 10 generations of brother and sister matings. A mean LS1 of 10.87 animals and LW1 of 14.48 g were obtained in the two reciprocal I-F₁ crossings and a LS1 of 13.67 and LW1 of 21.12 g in I-F₂. Values of I-F₁ were significantly below the plateau, whereas in I-F₂ the plateau was reached again (13.67 vs 13.76; 21.12 vs 21.70). On the average, the traits of I-F₁ were 30% above those of the inbred parents and those of I-F₂ were 26% (LS1) and 45% (LW1) above the level of I-F₁.

Consequently, the plateau level could be reached but not overcome by crossing. A comparison with Falconer (1971) and Eklund (1976), who were able to overcome the plateau by crossing, was not possible, because no further selection was conducted. Barria (1976) and Barria and Bradford (1981) were not able to overcome the plateau in the trait "growth" with the aid of the method mentioned above. Experiments for overcoming the plateau show that supplying new genetic variability into the plateau generation by crossing and

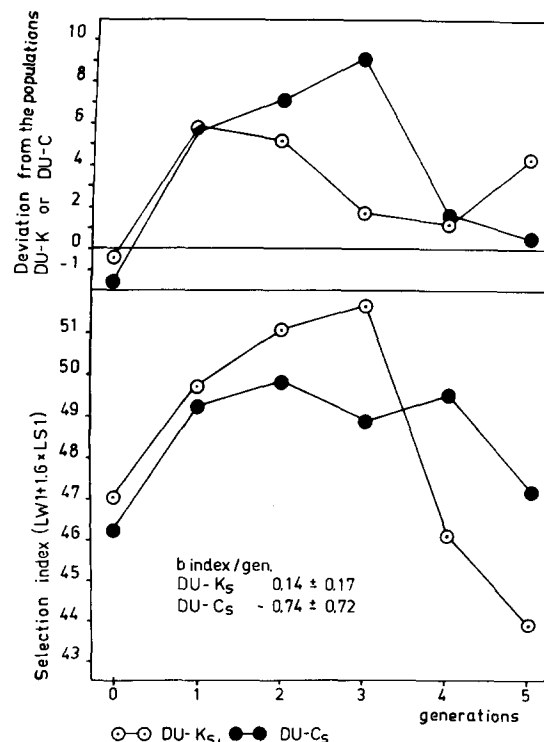


Fig. 5. Direct response to selection with litter size standardization

following selection was able to overcome the plateau successfully.

Short-term effects can also be obtained by eliminating maternal effects. Selection for growth (tandem selection) as well as crossing of inbred populations were not suitable for overcoming the plateau.

Results of selection under conventional and semi-barrier conditions refer to the fact that improving the environmental conditions is a suitable method for overcoming the plateau. The increase of phenotypic trait determination by improving the environment was higher than the selection progress for 18 generations in the first selection period. Provided that population DU-K approximated the plateau considerably (h^2 1st–18th gen. = 0.02), the plateau could be overcome successfully. This possibility for overcoming the plateau has already been discussed by Falconer (1971) and Al-Murrani (1974). It is based on the effect of genotypical environmental interactions, that means that the same trait should be considered as two different ones under the conditions of two different environments (Falconer 1952). Experimental evidence of this theory was given by Abplanalp (1962) in hens, overcoming the plateau in the trait "laying performance" by deprivation of feed for 24 h. Selection criteria (LS1 and LW1) applied in the experiment also show a different genetic determination under endurance stress. Thus it could be observed that a common and specific suitability for combination, estimated with the aid of diallele crossings, changes under the conditions of the physical stress cages (Schüler et al. 1983).

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