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LIFETIME, FERTILITY AND FECUNDITY IN THE SMALL STOCKS OF MICE BRED WITH MAXIMAL AVOIDANCE OF INBREEDING[1]

BARBARA MUSIAŁEK[2]

Department of Genetics and Evolution, Institute of Zoology Jagiellonian University, Kraków

Summary. Mice from three closed stocks A, B and C were examined for lifetime, fertility and fecundity throughout the whole life. These stocks originated from crosses of four inbred strains (KE, KP CBA and C57) and were bred with maximal avoidance of inbreeding and with equal representation of families in each generation.

Mice from the stock A (10 pairs) belonged to generations F_{23}-F_{25} and theoretically reached the inbreeding coefficient 0.25 - 0.27. Mice from the stock B (6-pairs) were from generations F_{23} - F_{24} with the theoretical inbreeding coefficient 0.40 - 0.43, and mice from the stock C (4 pairs) from generations F_{23} - F_{26} with the inbreeding coefficient 0.51 - 0.56.

Females A showed significantly longer mean lifetime ($\bar{x}$ — 489,6 days), than females C ($\bar{x}$ — 424.8 days). The mean reproductive period of females A averaged 325 days, that of females B and C only about 270 days.

Females A had the largest number of litters ($\bar{x}$ — 9.31) and the young per one female ($\bar{x}$ — 52.59). Females B and C had a smaller number of litters ($\bar{x}=7.0$ and 6.4) and the young ($\bar{x}=44.5$ and 44.4).

The time interval between mating and first delivery was lower in the stock A ($\bar{x}$ — 28.0 days) than in the stock B ($\bar{x}=53.2$ days) and C ($\bar{x}=34.7$ days). Mothers from stock A were younger than mothers from the stocks B and C on the birthday of successive litters.

Stocks B and C were noted to have high mortality of the young from birth until eight weeks.

The results of the present study indicate that in populations consisting of 10 pairs the equilibrium could be stable and may effectively prevent the population from gene fixations. But the above parameters of stocks B and C manifested inbreeding depression. In these stocks the equilibrium could be unstable.

Several studies have demonstrated that small natural populations of wild *Mus musculus* do possess large amounts of genetic variability (Dunn et al. 1960, Braden 1960, Dunn 1967). It could be suggested that natural selection favours heterozygosity (Hamilton et Helström 1978). The role played by "heterozy-

[1] Received for publication: August 1983.

[2] Docent dr hab. Present address: Krupnicza 50, 30-060 Kraków, Poland.

gote selection" in maintaining genetic variability of natural populations was often discussed, and the resulting controversy has contributed substantially to the population genetics theory and experimentation (Cain and Sheppard 1954, Dobzhański 1955, Falconer 1960a, Krzanowska 1974, Musiałek 1980, 1982, in press).

It is difficult to determine directly the effect of heterozygote advantage because of a variety of obstacles complicating factors, e.g: linkage of alleles potentialy favored by selection, the environmental specificity of any selection advantage and other problems discussed by Barry (1978).

In order to examine quantitatively heterozygote advantage many authors used systematic inbreeding as an indirect method. Performance of populations undergoing systematic inbreeding enables one to compare theoretical and real inbreeding coefficients. If natural selection favours heterozygotes at individual loci then the rate of homozygote production should be lower than that predicted by the theoretical inbreeding coefficient F (Wright 1965).

Experiments with populations having known inbreeding coefficients (Connor and Bellucci 1979) showed that effects of inbreeding were delayed in comparison with those which could appear normally, and there was no selection for heterozygotes. The above authors call this situation a "selection inbreeding equilibrium" model, since selection and inbreeding occur simultaneously and produce opposite effects.

It has been shown that when the population is large this equilibrium may be stable. A stable equilibrium occurs when balancing selection is sufficiently large. On the other hand, when balancing selection are weak in relation to inbreeding in large population, or if breeding populations are small, "unstable equilibrium" results, gene fixation possibly occurs but it is delayed in relation to an unselected population with the same inbreeding intensity (Connor et Bellucci 1979).

In the previous investigations on laboratory mice (Musiałek 1980, 1982, in press) we tried to establish the minimal size of a closed population which still prevents the occurrence of inbreeding depression, with respect to fertility and fecundity.

It was shown that after previous elimination of genetic load from the initial material, even a population consisting of 6 or 4 pairs equally represented in each generation, was adequate to maintain fertility and fecundity parameters at a fairly constant level. The only sign of depression was lengthening of the time lapse between mating and delivery. In a population consisting of 10 pairs the fertility and viability was preserved for 25 generations at the level of the foundation stock. Falconer (1960b) and Krzanowska (1974) demonstrated a similar phenomenon with respect to litter size. It seems that in populations consisting of 10 pairs ($N_e=40$) the equilibrium could be stable.

The aim of the present study was to determine the role of heterozygote selection in preserving the following parameters: lifetime, fertility throughout the whole life, mean number of litters, mean litter size at birth, mortality during the first 8 weeks of life. To reveal the influence of population size, three closed stock of mouse were used: A (10 pairs), B (6 pairs) and C (4 pairs).

MATERIAL AND METHOD

Three closed stocks of mouse A, B and C were used. They originated from crosses of four inbred strains, and were bred with maximal avoidance of inbreeding, every family being equally represented in each generation (Musiałek 1980). The used experimental design gave the lowest homozygosity rise to be obtained with a given number of individuals.

Experimental mice from the stock A (10 pairs, $N_e=40$) belonged to generations F_{23} - F_{25}, and had the theoretical inbreeding coefficient 0.25 - 0.27. Mice from the stock B (6 pairs, $N_e=24$) were from generations F_{23} and F_{24}, and reached the theoreticaly calculated inbreeding coefficient 0.40 - 0.43, and mice from the stock C (4 pairs, $N_e=10$) were of generations F_{23} - F_{26} with the inbreeding coefficient 0.51 - 0.56.

Virgin females, 7 - 8 week old and mature males were used. Females were paired with males from the same stock. All young were eliminated on the first day after birth, except one experiment when the young were kept till the 8-th week of life.

The experimental material consisted of 32 pairs from the stock A, 21 pairs from the stock B and 32 pairs from the stock C. The following parameters were examined: 1) lifetime of females, 2) reproductive period in days (throughout the whole life of females, 3) number of litters, 4) number of the young, 5) litter size in successive generations, 6) mortality of the young from birth until the 8th week of life, 7) age of females on the day of delivery, 8) time interval between mating and delivery. Differences in above parameters between experimental stocks were examined using the Student's *t*-test.

RESULTS

The mean lifetime (Table 1) was calculated only for females because males in most cases survived longer (Roberts 1961). Females from the stock A showed the longest mean lifetime averaging 489,56 days (range 845 - 221 days). Females from the stock B lived on average 412.01 days (726 - 141), and females from the stock C — 424.78 days (652 - 99). Differences in lifetime between mice from the stocks A and B or C were significant ($p<0.05$).

The mean reproductivity period of females (Table 1) was calculated as the number of days from pairing till delivery of the last litter. This period was the longest for females A and average 325.47 days (range 725 - 161); for females B it was only 263.33 days (525 - 91), and for females from the stock C — 270.66 (508 - 68). Differences in the reproductive period between females A and B ($p<0.05$), and between females A and V ($p<0.05$) were significant.

The mean number of litters per female (Table 1) was the highest in the stock A: $\bar{x}=9,31$ (range 17 - 5). Females B and C had a smaller mean number of litters:

Table 1. Lifetime and fertility parameters of females from stocks A (10 pairs), B (6 pairs) and C (4 pairs).

Parameter investigated	A (32)[1]			B (21)			C (32)			Significance of differences between stocks
	$\bar{x}$	±sd	CV	$\bar{x}$	±sd	CV	$\bar{x}$	±sd	CV	
Lifetime (days)	489.56	±149.9	30.6	412.09	±168.3	40.8	424.78	±166.1	39.1	A – C $p<0.05$ A – B $p<0.05$ C – B N.S.
Period of fertility (days)	325.47	±112.8	34.5	263.33	±121.9	46.3	270.66	±118.0	43.6	A – C $p<0.05$ A – B $p<0.05$ C – B N.S.
Mean number of days: from pairing till first litter	28.03	± 13.9	49.7	35.24	± 16.5	46.7	34.69	± 21.6	62.2	A – C $p<0.05$ A – B $p=0.10$ B – C N.S.
Mean number of days: between two last litters[2]	37.58	± 13.5	36.1	36.95	± 21.9	59.4	45.41	± 23.1	50.9	A – C $p=0.10$ A – B N.S. B – C N.S.
Mean number of litters per female	9.31	± 2.9	31.7	7.0	± 2.8	40.6	6.44	± 2.3	35.7	A – C $p<0.001$ A – B $p<0.01$ C – B N.S.
Mean number of young per female	52.59	± 13.9	26.5	44.52	± 20.1	45.1	44.47	± 15.9	35.9	A – C $p<0.05$ A – B $p=0.10$ C – B N.S.

[1] in parentheses the number of pairs mated originally
[2] the last litter was 17th in stock A, 14th in B and 10th in C.

$\bar{x}=7.0$ (range 14 - 3) and $\bar{x}=6.44$ (10 - 2), respectively. Significant differences appeared only between the stocks A and C ($p<0.001$) and A and B ($p<0.01$).

The mean number of young per female (Table 1) was also higher in the stock A ($\bar{x}=52.59$ range 78 - 28) than in the stock B ($\bar{x}=44.52$, 94 - 17) or C ($\bar{x}=44.47$, 73 - 11). Significant differences were found only between A and C ($p<0.05$).

The mean time interval between mating and the first delivery (Table 1) was lower in the stock A ($\bar{x}=28.0$ days) than in the stock B ($\bar{x}=35.2$ days) or C ($\bar{x}=34.7$ days). Significant differences were found only between the stocks A and C ($p<0.05$).

The mean number of days between the last two deliveries (Table 1) was the largest in stock C ($\bar{x}=45.41$ days) than in B (36.95) or A (37.55). However, the differences were not significant. It should be stressed that the last litter was the 17th for the stock A, the 14th for B and 10th for C.

Tables 2, 3 and 4 show the mean age of mothers from A, B and C stocks at the birth of successive litters. Almost each mother A was younger than mothers from the stocks B and C at successive delivery. For example: at the birth of 10th successive litter the mean age of mothers from stock A was 385.12 days whereas that of mothers from stock B — 403.33 days and that of mothers from stock C — 432.33 days.

Fecundity calculated as the litter size in successive litters was the lowest in stock A (Table 2) and decreased after 6th litter in which the mean number of young was 6.41. The stock B (Table 3) and particularly the stock C (Table 4) showed higher fecundity. Frequently differences in the litter size of respective litters were sta-

Table 2. Mean litter size and age of mother at birth of successive litters in stock A

Successive litters	No. of pairs	Age of mother (days)			Litter size			Per cent of litters size=8	Significance of differences between stocks A – C (litter size)
		x̄	±sd	CV	x̄	±sd	CV		
1	32	87.56	±11.4	13.0	6.22	±2.44	39.2	22.6	$t=2.41$ $p<0.02$
2	32	123.03	20.7	16.8	5.94	2.39	40.2	37.9	$t=1.98$ $p<0.05$
3	32	158.53	31.7	20.0	7.44	2.60	34.9	44.8	N.S.
4	32	192.63	34.9	18.0	5.90	2.35	39.8	31.0	$t=3.47$ $p<0.001$
5	32	225.63	35.4	15.7	6.81	2.96	43.4	48.3	N.S.
6	29	259.76	41.4	15.9	6.41	2.44	38.0	50.0	N.S.
7	26	294.19	45.6	15.5	4.92	2.15	43.7	18.2	$t=2.30$ $p<0.02$
8	23	322.0	51.8	16.1	4.61	2.10	45.5	5.3	N.S.
9	17	351.71	53.8	15.3	3.23	1.77	54.7	0	$t=4.71$ $p<0.001$
10	14	383.12	76.9	20.1	4.28	2.25	52.6	0	
11	10	423,60	86.3	20.3	3.82	2.16	56.5	12.5	
12	8	438.12	91.2	20.8	4.0	2.50	62.5	0	
13	6	447.33	25.6	5.7	2.50	0.96	38.4	0	
14	2	468.50			3.67	2.49	67.8	0	
15	2	508.50			1.0				
16	1	496			2				
17	1	527			2				

Table 3. Mean litter size and age of mother at birth of successive litters in stock B

Successive litters	No. of pairs	Age of mother			Litter size			Per cent of litters size = 8	Significance of differences between stocks A – B (litter size)
		x̄	±sd	CV	x̄	±sd	CV		
1	21	99.52	24.4	24.5	7.66	2.69	35.1	52.4	$t=1.97$ $p<0.05$
2	21	141.95	40.0	28.2	7.38	3.03	41.0	47.6	$t=1.9$ $p<0.05$
3	21	178.14	42.01	23.6	6.43	2.08	32.3	33.3	N.S.
4	19	207.68	35.18	16.9	6.79	2.37	34.9	31.6	N.S.
5	16	238.50	42.23	17.7	5.0	2.15	43.0	25.0	$t=2.13$ $p<0.01$
6	13	273.23	62.92	23.0	5.92	2.02	34.1	15.4	N.S.
7	13	316.46	72.82	23.0	6.07	2.78	45.7	38.5	N.S.
8	10	365.80	82.79	22.6	6.40	2.01	31.4	20.0	$t=2.72$ $p<0.02$
9	5	397.80	98.82	24.8	5.0	1.79	35.8	0	
10	3	403.33	43.08	10.7	6.33			33.3	
11	3	439.66	53.19	12.1	6.0				
12	1	411			2				
13	1	449			7				
14	1	498			4				

Table 4. Mean litter size and age of mother at birth of successive litters in stock C

Successive litters	No. of pairs.	Age of mother			Litter size			Per cent of litters size = 8	Significance of differences between stocks C – B (litter size)
		x̄	±sd	CV	x̄	±sd	CV		
1	32	95.31	20.9	21.9	7.62	2.10	27.5	50	N.S.
2	32	137.72	33.5	24.3	7.41	3.33	44.9	46	N.S.
3	29	172.79	33.8	19.5	7.45	2.39	32.0	48	N.S.
4	27	204.25	35.75	17.5	7.70	2.49	32.3	44	N.S.
5	26	241.34	39.12	16.2	5.61	2.63	46.9	23	N.S.
6	21	287.81	59.17	20.5	6.24	1.99	31.9	24	N.S.
7	17	301.30	81.32	22.5	6.65	2.62	39.5	47	N.S.
8	10	378.40	58.73	15.5	5.70	3.32	58.2	20	N.S.
9	8	410.25	60.89	14.8	6.75	1.48	21.9	25	N.S.
10	3	432.33	35.44	8.2	6.67	1.70	25.5	33	N.S.

tistically significant (Table 2, 3 and 4). In the stock A the percentage of litters containing 8 or more young dropped rapidly after the 6th litter, while in stock C it remained at a high level till the end of the reproductive period.

The young from ten pairs of the stocks A, B and C were kept (3 females, 3 males) from birth until the 8th week. The mortality in the stock C was 33.3% and in the stock B — 30.6%, when calculated from birth until eight weeks. In the stock A the mortality was very low amounting to 8%.

DISCUSSION

The fact that after many generations, important parameters connected with viability and fertility are only slightly lower than those of the heterozygous basic populations, may indicate that the population in spite of the theoretically increasing inbreeding coefficient is less homozygous than could be expected. This might be due to a simultaneous action of inbreeding and selection favouring heterozygosity, which could result in a „selection inbreeding equilibrium". This equilibrium may be stable when a population is large enough (Conner and Bellucci 1979) and may effectively prevent the population from gene fixations. The fitness of members of such a population is not lowered and the overall heterozygosity may be relatively high for many generations (Krzanowska 1974, Musiałek 1980, 1982).

The results of the present study indicate that stable equilibrium was reached only in the stock A, each generation of which consisted of 10 pairs ($N_e=40$). When compared with the stocks B and C, the stock A showed significantly higher values the of following parameters: 1) lifetime; 2) length of the reproductive period; 3) number of litters per female; 4) litter size. Stock A also showed a lower mortality of the young from birth till the age of 8 weeks. The fact, that in respect to the measured characteristics the two stocks B and C (with generations consisting of 6 and 4 pairs, $N_e=24$ and $N_e=16$, respectively) performed worse than did the stock A, suggests that the selection most probably could not prevent the rise of homozygosity. So, after 20 generations the results of increased homozygosity were apparent in the stocks B and C. It seems, however, that even during the strongest inbreeding (sibmating) selection favouring heterozygosity is unavoidable (Connor and Bellucci 1979). The stocks A and C differed significantly in the mean rejection time of skin transplants ($\bar{x}=27$ and $\bar{x}=90$) days, respectively: (Musiałek unpublished data), which indicates clearly that these two stocks differed in the amount of homozygosity. At the same time, the females from the stocks B and C showed a longer time interval between mating and delivery than did females from the stock A. Consequently, females from the two former stocks were always older at the time of delivery than females from the stock A. It means that females from the stocks B and C were much less fertile than females from the stock A. This lower fertility could be either a result of irregularity of sex cycles — a common feature in inbred lines, where females could not be stimulated effectively by males or by the lower libido of males (Musiałek in press). It can be believed that some alleles lowering the overall fitness could be fixed in small populations B and C, after several years of breeding.

Overall fitness depends not only on the number of progenies produced (which in fact was low in the stocks B and C), but also on the number of progenies, which survived till the reproduction age (Roberts 1961). The stocks B and C again showed a much higher mortality of the young between the birth and reproduction age (8 weeks) than did the stock A. Unexpectedly, the number of the young in a litter was often higher in the stock B and C than in the stock A, and what more, both males and females in the stocks B and C were significantly ($p<0.001$) heavier at the age of 8 weeks than animals of both sexes at the same age from the stock A (Musiałek — unpublished data). It is known that the litter size depends on many factors including the number of ovulated eggs. Since the number of ovulated eggs depends on the body weight and is not influenced by inbreeding depression in mice (Falconer 1960b, Roberts 1960), large litters in the stock C might be a result of a higher body weight in this group.

The results indicate that after 20 generations of breeding in small group (stock C), in spite of a clear evidence of inbreeding depression, the amount of homozygosity reached after 6 years of inbreeding was not as high as could be expected theoretically (the expected value of the inbreeding coefficient in the stock C should range from 51% to 56%). This is true also for the stock C, which consisted of the smallest possible number of animals can be bred without sibmating and in which even such a good indicator of inbreeding depression as the time interval between mating and delivery, has not changed much after 20 generations of breeding (Musiałek 1980). This can be explained only by the action of selection favouring heterozygosity.

The results of the investigations on both natural and experimental populations strongly suggested that selection favouring heterozygosity is a widespread phenomenon, which can effectively act as a mechanism preventing small isolated populations from genetic impoverishment due to inbreeding.

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DŁUGOŚĆ ŻYCIA, PŁODNOŚĆ I PLENNOŚĆ MYSZY W MAŁYCH POPULACJACH KOJARZONYCH Z MAKSYMALNYM UNIKANIEM WSOBNOŚCI

Streszczenie

Materiał doświadczalny stanowiły trzy zamknięte stada myszy wyprowadzone z poczwórnego krzyżowania 4 szczepów wsobnych (KE, KP, CBA i C_{57}), hodowane z maksymalnym unikaniem wsobności, przy jednakowej reprezentacji rodzin w każdym pokoleniu. Myszy ze stada A (10 par, $N_e=40$) należały do pokolenia F_{23} - F_{25} i ich teoretycznie obliczony współczynnik wsobności wynosił 25,2 - 27,1%: myszy ze stada B (6 par, $N_e=24$) należały do pokolenia F_{25} i F_{26}, współczynnik wsobności 40,4 - 42,7%: myszy ze stada C (4 pary, $N_e=16$) do pokolenia F_{23} - F_{26} współczynnik wsobności 51,5 - 55,9%.

Samice ze stada A charakteryzowały się najwyższą średnią długością życia ($\bar{x}=489{,}6$ dni), zaś najniższą, samice ze stada C ($\bar{x}=444{,}7$ dni). Podobnie samice A odznaczały się najdłuższym okresem reprodukcji ($\bar{x}=325{,}5$ dni), najkrótszym samice B i C ($\bar{x}=270{,}7$ dni). Samice A urodziły największą liczbę miotów ($\bar{x}=9{,}31$) i potomstwa na jedną samicę ($\bar{x}=52{,}59$), samice C — najniższą liczbę i miotów ($\bar{x}=6{,}4$) i potomstwa ($\bar{x}=44{,}5$).

Czas od skojarzenia do wykotu był najkrótszy u samic A ($\bar{x}=28{,}0$), najdłuższy u samic C ($\bar{x}=34{,}7$ dni).

Wiek matek w dniu urodzenia poszczególnych miotów był najniższy u matek ze stada A.

Natomiast plenność samic zwłaszcza w końcowych miotach okazała się w stadzie C wyższa niż w stadzie A.

Najwyższą śmiertelność młodych zanotowano w stadzie B i C. Powyższe wyniki sugerują, że w stadzie A (10 par) występowała „równowaga stała” w której nie ujawniły się skutki działania chowu wsobnego, gdyż był on w każdym pokoleniu równoważony nadwyżką selekcyjną heterozygot. Natomiast w stadach B (6 par) i C (4 pary) widać było wyraźnie skutki pogłębiającej się wsobności, średnie wartości prawie wszystkich analizowanych parametrów były niższe w porównaniu ze stadem A. Musiała więc występować tu „równowaga niestała”.

ПРОДОЛЖИТЕЛЬНОСТЬ ЖИЗНИ, ПЛОДОРОДНОСТЬ И ПЛОДОВИТОСТЬ МЫШЕЙ В НЕБОЛЬШИХ ПОПУЛЯЦИЯХ, СПАРИВАЕМЫХ ПРИ МАКСИМАЛЬНОМ ИЗБЕЖАНИИ ИНБРЕДИНГА

Резюме

Эксперментальный материал составляли три стада мышей, выведенные из четырехкратного скрещивания 4-х инбредных линий (КЕ, КР, СВА и C_{57}) и выращенные при максимальном избежании инбреднига, причем каждое поколение было представлено одинаковым числом семей. Мыши из стада А (10 пар, $N_e=40$) принадлежали к поколению F_{23}-F_{25} и их теоретически вычисленный коэффициент инбрединга составлял 25,2 - 27,1%; мыши из стада В (6 пар, $N_e=24$) принадлежали к поколению F_{25} и F_{26}, коэффициент инбрединга составлял 40,4 - 42,7%; мыши из стада С (4 пары, $N_e=16$) принадлежали к поколению F_{23}-F_{26} , коэффициент инбрединга составлял 51,5 - - 55,9%.

Самки из стада А характеризовались наивысшей средней продолжительностью жизни ($\bar{x}=489{,}6$

дней), а самки из стада C ($\bar{x}$=444,8 дней) — наинизшей. Самки A отличались самым долгим периодом репродукции ($\bar{x}$=270,7 дней). Самки A имели самое большое число пометов ($\bar{x}$=9,31) и потомства на одну самку ($\bar{x}$=44,5).

Самое короткое время от спаривания до окотов был у самок A ($\bar{x}$=28,0), а самое долгое — у самок C ($\bar{x}$=34,7 дня).

Возраст маток в день рождения отдельных пометов был наинизший у маток стада A.

Однако, плодовитость маток, особенно в последних пометах оказалась высшей в стаде C,чем в стаде A.

Наивысшая смертельность молодых была отмечена в стадах B и C.

Вышеупомянутые результаты позволяют предположить, что в стаде A (10 пар) выступало ,,постоянное равновесие'', в котором не отразились результаты инбрединга, так как в каждом поколении он уравновешивался селекционным излишком гетерозигот. Зато в стадах B (6 пар) и C (4 пары) результаты усиливающегося инбрединга были отчетливо видны: средние значения почти всех анализированных параметров были нисшие по сравнению со стадом A. Здесь, следовательно, должно было выступать ,,равновесие непостоянное''.