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COMPETITION IN REPRODUCTION OF MALES OF SMALL MOUSE STOCKS DIFFERING BY EFFECTIVE SIZE[1]

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Summary. Mice from two closed stocks bred with maximum avoidance of inbreeding throughout 30 generations were used for the study. The stock A (35 - 37% of inbreeding) consisted of 10 pairs, while the stock C (63 - 65% of inbreeding) consisted of 4 pairs in each generation. After the initial period of isolation, the A and C males were kept in pairs without and in the presence of mating females. The behaviour of males (previously isolated), the number of copulations and copulation plugs, the number of delivered litters in successive deliveries mated with the above two kinds of males under the conditions of sexual competition were analysed. It was shown that the A males significantly exceeded the C males in the number of copulation plugs (in the stock A — 42, i.e. 64.6%), in the stock C — 23, i.e. 35.4%). Similarly, the A males significantly exceeded the C males in the number of litters (the A males — 156 — 69%, the C males — 69 — 32%) in four successive deliveries. On the other hand, the mean time of producing copulation plugs by the A males was lawer (($\bar{x}$—6.69±4.58 min) in comparison to that of the C male s($\bar{x}$—9.23±±6.27 min). No significant correlation between the male heterozygosity and their increased aggressiveness was observed. Comparing the results obtained by other authors, it was suggested that there is a strong relationship between the degree of genetic variability and the capacity to get reproduction excess under the conditions of sexual competition with a common mating female.

As early as in the forties of our century, the relationship between domination and aggressiveness of males and the level of androgens, mostly in rodents, was found. At present, such a positive correlation is observed also in people (O'Carroll, Bancroft 1985). According to Gandelman (1984) in the years 1975 - 1981, 101 papers illustrating correlation between the hormone level and aggression degree were published, whereas as many as 407 published papers were dealt with correlation between the androgen level and reproduction success. At the same time Garten (1976) published very detailed papers concerning field mouse, showing that there is almost a linear correlation between the heterozygosity level and aggressiveness increase. According to this author, heterozygosity may facilitate the performance concerning many important features of a specimen. Åslund (1977) and Kyriacon et al. (1978) paid their attention to a high relationship between heterozygosity of a specimen and its significant superiority, particularly under conditions of sexual competition. Ac-

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cording to these authors, one of the most important mechanisms maintaining polymorphism in natural environment is heterozygote superiority in mating behaviour. Success in mating constitutes an important adaptable factor that can be evaluated by tests under conditions of competitions between males for a common female.

In the light of the above results, one may believe that all these parameters are somehow correlated. Therefore, a question arises, is it possible under conditions of sexual competition to evaluate the degree of heterozygosity of the used males on the basis of their behaviour and reproduction capacity? Is the sequence of the following relationship true: a higher level of genetic variability — a higher level of androgens-domination and increased aggressiveness, success in reproduction? In the previous paper of sexual competition (Musiałek, 1986 in print) no significant differences were found either in the behaviour or reproduction capacity of males from three closed stocks differing by the size and, in consequence, by the heterozygosity increase rate (Musiałek 1980). It may be suggesed that in the examined generation F_{15} - F_{17} the experimental material was not sufficiently differentiated in the genetic aspect.

At present, these investigations have been undertaken again, but the males used for the experiment originated from the stocks extremaly differing in the size and after the successive 17 generations.

MATERIAL AND METHODS

The experimental material consisted of mice from two closed stocks A and C obtained from crossing four inbred strains KE, KP, C57BL/Kw and CBa/Kw bred with maximum avoidance of inbreeding, with the same representation of each family in the successive generations (Musiałek 1980). The stock A comprised 10 pairs per each generation (N_e=40), the stock C — 4 pairs (N_e—16). Mice from the A stock belonged to F_{34-36} generation and theoretically could reach 35 - 37% of inbreeding. Mice from the C stock belonged to the F_{30-34} generation and the theoretically calculated inbred factor should be equal to 63 - 65%. Two groups of sexually mature males from the stocks A and C at the age from 8 to 10 weeks were used for the experiment. The first group consisted of males which were kept separately in cage for two weeks prior to the experiment, while the second group consisted of males kept in 4 in one cage. Similarly two groups of males, isolated and kept in groups, were used for examining the weight differences in the body, testicle, coagulating glands and seminal vesicle of mice from the stock A and C.

In each competition cage, one A and one C males were placed with one or two females from the C stock. The mice from the C stock were homozygous with regard to recessive pink eye dilution genes. The presence of pigment or its absence in the newborn eyes indicated the male that produced a given litter. A larger number of delivered litters after a given male evidenced the success in reproduction under conditions of competition for a common female. The significance of differences between the examined parameters was analysed using the Student's t-test and χ^2-test.

RESULTS

I SERIES OF EXPERIMENTS — BEHAVIOUR OF MALES FROM THE STOCKS A AND C WITH NO FEMALES IN COMPETITION CAGES

The males from the stocks A and C, after a two-weeks isolation were placed for 15 minutes in a plastic cage (33×23×12 cm) covered with a wire net giving a possibility of a thorough observation of male behaviour. According to a degree of aggressiveness of the males A and C, all observations (15 min.) were divided into 4 groups (Table 1).

Table 1. Behaviour of mouse males in competitive cage with no female (for 15 min)

Group	Degree of aggressiveness of A* and C**males	No. of male pairs
I	A aggressive — C submissive	36
II	A submissive — C aggressive	34
III	A submissive — C submissive	21
IV	A aggressive — C aggressive	24

* A — stock with 35 - 37% of inbreeding
** C — stock with 63 - 65% of inbreeding

Group 1 — consisted of 36 pairs, where the A males as soon as in the first minutes attacked the C males and during further periods were still very aggressive, injuring usually submissive partners from the C stock in numerous fights.
Group 2 — included 34 pairs, where the C males were the first to attack the A males, often injuring them in fights, however, it was also observed that the A males changed their attitude showing sometimes significant aggressiveness.
Group 3 — consisted of 21 pairs selected on the basis of a complete lack of conflict between the A and C males during the whole period of their co-existence.
Group 4 — had 24 pairs, where both A and C males showed the same behaviour, i.e. were aggressive, whereas the A males injured most often their adversaries.

II SERIES OF EXPERIMENTS — RESULTS OF SEXUAL COMPETITION BETWEEN THE A AND C MALES IN THE PRESENCE OF ESTRUS FEMALE

One female from the C stock at the stage of estrus was placed in a cage containing previously isolated males A and C. The behaviour of the males and their reaction to the female were observed, and the number of copulations with a given male resulting in ejaculation and copulation plugs was counted. The time from placing the female in the competition cage to the formation of the plug were measured. Table 2 illustrated the behaviour of males (during 15 minutes) classified in four groups and

Table 2. The number and time of copulations in A and C mouse males in 4 groups differing by the behaviour of both competitors

Groups	Behaviour of males in competitive cage with an estrus females		No. of pairs (%)	No. of plugs of males		test probability	
	Male A*	Male C**		A	C	t	p
I	Aggressive	submissive	12 (18.5%)	12 (100%)	—	—	—
II	Submissive	aggressive	16 (24.5%)	6 (37.5%)	10 (62.5%)	1.0	n.s.
III	Submissive	submissive	31 (47.8%)	22 (71%)	9 (29.%)	5.45	<0.001
IV	Aggressive	aggressive	6 (9.2%)	2 (22.2%)	4 (66.7%)	0.7	n.s.
		totally	65	42 (64.6%)	23 (35.4%)	5.55	<0.001
Mean time of producing the copulation plug by males: A — 6.69±4.58 min C — 9.23±6.27 min							

* A — stock with 35 - 37% of inbreeding
** C — stock with 63 - 65% of inbreeding

the number of plugs after each of the competing males. As it is seen the per cent share of each group was slightly different as compared to that of the I series of the experiment with no estrus female in the cage. The largest number of pairs, i.e. 31 (47.8%) consisted of males, both significantly aggressive and not preventing each other from getting the estrus female (group III). As a result of such a pattern of the behaviour, the A males copulated and produced the plug twice as often (71%) as did the C males. In 12 cases (18% — group I), where the A males were aggressive and prevented the C males from copulating, all plugs originated from the A males. In 16 cages (24.5% — group II), where more intensive aggressiveness of the C males was observed, and in 6 cages (9.2% — group IV), where both the A and C males were aggressive to the same extent, the excess of plugs after the C males was not high and statistically not significant. The total number of plugs after the A males in these four groups was nearly twice as higher as that after the males from the stock C ($\chi^2=5.55$, $p<0.02$). Table 2 shows also the mean time counted from placing the female in the competition cage with males to the formation of the plug. It is clearly seen that the A males start to copulate sooner and produce the plug in a shorter time (males A $\bar{x}=6.69\pm4.58$, males C $\bar{x}=9.23\pm6.24$, $p<0.02$).

III SERIES OF EXPERIMENTS — THE NUMBER OF LITTERS DELIVERED AFTER THE A AND C MALES IN FOUR SUCCESSIVE DELIVERIES

One male from the A stock, one male from the C stock and two C females were placed in each competition cage. Prior to the experiment, both A and C males stayed in one cage for two weeks. After the initial period of fights and often injuries, both males get used to each other and showed no more aggression, except a very weak aggression showed when being placed in the cage of estrus female. The males and females from the C stock were recessive homozygotes as to the pink eye dilution gene (pp), that was a suitable marker indicating the affiliation of the litter to a given farther. If a litter consisted only of newborns with pigment-free eyes it had to originate after C males, in another case, the litter was after the A male, who was a dominant homozygote regarding the gene marker (PP).

Table 3 shows the number of litters delivered in 60 competition cages. It appeared that in the first deliveries after the male from the A stock as many as 81 deliveries occurred (67.5%) and after the C males only 39 (32.5%), which consitutes a very significant difference ($\chi^2=14$, $p<0.001$). The prevalence of litters after the males

Table 3. Number of litters of A and C mouse males delivered in 60 competition cage in four successive deliveries

Litters of A and C males	Successive deliveries of C females				Totally
	I	II	III	IV	
A*	81 - 67.5%	38 - 79.2%	26 - 65%	13 - 68.4%	158 - 69%
C**	39 - 32.5%	10 - 20.8%	14 - 35%	6 - 31.6%	69 - 31%
Totally	120	48	40	19	227
Significant differences in the number of litters of A and C males (χ^2)	14.7 $p<0.001$	16.2 $p<0.001$	3.6 $0.05<p<0.10$	2.5 n.s.	15.7 $p<0.001$

* A — stock with 35 - 37% of inbreeding
** C — stock with 63 - 65% of inbreeding

from the A stock was maintained in the second, third and fourth deliveries. Totally, out of 227 deliveries, as many as 156 originated from the A males (69%), and only 69 (31%) from the C males, which constitutes highly significant differences ($t=15.7$, $p<0.001$).

Table 4 illustrates the number of delivered newborns after the A and C males in

Table 4. Number of delivered newborns and the mean litter size of the A and C mouse males in first deliveries (in competitive cage)

Males from the stock	Number of		Mean litter size	
	litters	newborns	$\bar{x}$	$\pm sd$
A*	81	627	7.72	2.55
C**	39	289	7.41	2.47
Totally	120	916		
Significant differences in the number of litters and delivered newborns (χ^2)	24.7 $p<0.001$	124 $p<0.001$		

* A — stock with 35 - 37% of inbreeding
** C — stock with 63 - 65% of inbreeding

the first deliveries and the mean size of litters. It is seen that the number of litters and deliveries after the A males was over twice as large as that after the C males ($p<0.001$), whereas the size of the litters showed no differences ($t=0.66$).

Table 5 shows the body, testicle, coagulation gland and seminal vesicle weights of the males from the A and C stocks (it was tried to select males with the same body

Table 5. The means of body, testicle, coagulation gland and seminal vesicle weights of the mouse males from the A and C stock: kept in 4 to 6 in one cage (a), kept separately in cages (b)

Stock	No. of males	Males kept in groups (a) mean weights			No. of males	Males kept separately (b) mean weights		
		Body (g) $\bar{x} \pm sd$	testicle (mg) $\bar{x} \pm sd$	coagul. gland and semial vesicle (mg) $\bar{x} \pm sd$		Body (g) $\bar{x} \pm sd$	testicle (mg) $\bar{x} \pm sd$	coagul. gland and seminal vesicle (mg) $\bar{x} \pm sd$
A*	25	25.6±1.7	199.2±26.6	247.3±60.1	25	27.2±2.4	227.2±25.4	283.6±107.2
C**	23	27.7±1.5	160.9±21.3	208.4±38.2	30	29.3±2.4	175.3±20.9	225.3±53.9

Significant differences[1] between mean weights:		Body	Testicle	Coagulation glands and seminal vesicle
A (a) and	C (a)	4.2 $p<0.001$	5.5 $p<0.001$	2.7 $p<0.01$
A (b)	C (b)	3.1 $p<0.001$	7.5 $p<0.001$	2.7 $p<0.01$
A (a)	A (b)	2.8 $p<0.01$	3.5 $p<0.001$	1.5 n.s.
C (a)	C (b)	2.4 $p<0.02$	2.5 $p<0.02$	1.0 n.s.

[1] Test *t*-Student's
* A — stock with 35 - 37% of inbreeding
** C — stock with 63 - 65% of inbreeding

weight within one stock, i.e. A and C): a) males kept in 4 to 6 in one cage for two weeks, and b) males kept separately in cages for the same period of time. It was found that: 1) in the both experimental groups (a and b) the body weights of the A males were significantly lower as compared to those of the C males ($t=4.18$, $p<$ <0.001), 2) the body weights of the A and C males kept in the group b prior to copulation were lower as compared to those of the males kept separately (for the A stock, $t=2.8$ $p<0.01$; for the C stock, $t=2.4$ $p<0.02$).

In contrast to that, the relationship between the weight of testicles, coagulating glands and seminal vesicles was as follows: 1) the weights of testicles and coagulating glands plus seminal vesicles of the males from the A stock were always significantly higher than those of the males from the C stock. For the testicles of males in the group a), $t=5.47$ $p<0.001$, in group b), $t=7.51$ $p<0.001$. For the coagulating glands and seminal vesicles in group a), $t=2.72$ $p<0.01$, in group b), $t=2.72$ $p<$ <0.01. The testicle weights of males isolated in the both stocks were higher than those of specimens kept in groups. In the A stock, $t=3.45$ $p<0.001$, while in the C stock, $t=2.45$ $p<0.001$. Similar relationship occurred in the weight of coagulating glands and seminal vesicles, however it was not found that the differences were statistically significant, probably due to a large deviation from the mean value.

DISCUSSION

Investigations using skin transplantation technique (Musiałek 1985 revealed that the males from the C stock were characterized by a higher level of inbreeding as compared to the males from the A stock. These results confirmed the expectations as the theoretically calculated inbred coefficients for the C stock were 63 - 65%, and those for the A stock were 35 - 37%. In the stock of the size $N_e=40$, the homozygosity increase was slightly higher than 1% per generation and enabled the genetic variability to be maintained nearly at the level of the initial stock for many generations (Krzanowska 1974, Musiałek 1980). In further generations it may be considered that the A stock is a highly heterozygous population, and in consequence, the males of this stock are more aggressive (Garten 1967, Ebert, Hyde 1976, Baker 1981) containing more testosterone (Rose et al. 1971, Buhl et al. 1978) and are more efficient in reproduction (De Fries, McClearn 1970, Dewsbury 1984) in comparison to the C stock males with higher level of inbreeding. Bronson (1973), Buhl et al. (1978), Benton and Brain (1979) revealed that males characterized by a higher sexual excitability are more aggressive, dominant as compared to submissive males, with a higher gonad activity, increased level of androgenes, higher weights of testicles, seminal vesicles, prostate glands and prepuces. Initial and preliminary studies on testosterone content in the testicles of males from the A and C stocks revealed a considerably higher level of this hormone in the A males (A=57.9 μg, C=23.15 μg). Similarly, the A males were found have a very high, statistically significant excess in the weight of the testicles coagulating glands and seminal vesicles (both in isolated males and in males kept in groups). In the light of these results it might be expected that males from the A stock should be more aggressive and should be the first to attack male from the C stock.

Meanwhile, even such procedures as a temporary isolation of males, usually causing an increase in the weights of their testicles, seminal vesicles (Brain, Nowell 1971), which was also shown in the present papers, and an increase in their aggression (De Catanzaro, Gorzalka 1979, 1980), or the presence of on estrus female in the competition cage (De Catanzaro 1981, Terman 1984) increasing aggressiveness equally effectively and increasing conflicts between the competitors, caused no evidently larger dominance and aggression of the A stock males (I and II series of the experiments). No marked difference in the aggressive behaviour of males like that observed between the F_1 hybrids and specimens belonging to one of the parental inbred strains of KP (Musiałek 1986 — in print) was detected. Probably differences in the level of heterozygosity between the males from the A and C stocks are not so large as those between the F_1 hybrids and the inbred strain (Musiałek 1986). Of interest are results of the II series of the experiments, showing that the lack of aggressiveness in the C males in the first group related with a complete lack of a successful reaction to the C estrus female odour (no copulations). Probably it was caused by an insufficient increase of testosterone level in these specimens. Hormone release depends on sexual motivation — the males which are not interested in estrus female odour do not rise androgene level during meeting (Kamel, Frankel 1978). On the other hand, a similar lack of aggressive symptoms in the males from the A stock (group 2) did not exclude their sensibility to the presence of a female, proved by the number of copulations and plugs, which was not much lower than that characteristic of more aggressive males from the C stock (nonsignificant differences), or by a very high excess (statistically significant) of plugs after the A male in group 3, where antagonistic behaviour was not observed at all. Despite the lack of markedly aggressive behaviour of males from the A stock, persistant copulations, prolonged and longer ejaculation were observed, which according to Price (1980), Dewsbury and Hartung (1980) may facilitate success in reproduction. Lanier et al. (1979) defined such a behaviour as a prolonged copulatory behaviour, due to which males have the largest chances to become fathers under conditions of sexual competition.

It seems, that even a considerable prevalence of male in reproduction should not be always accompanied by a marked aggresisveness and often fights between them (Dewsbury and Hartung 1980), which was observed in the present study. Moreover, Hart (1983) and Dewsbury (1984) had doubts whether laboratory tests truly reflect natural populations where, as a rule, each female is inseminated by more than one male, and, on the other hand, one male inseminates more than one female (McClintock, Anisko 1982). Competition in natural populations is less dramatic, since dominant males with an increased testosterone level engaged in fighting would loose a chance to inseminate an estrus female surrounded by a larger number of competitive males (Price 1980, Dewsbury 1981). Moreover, submissive males in natural populations may escape from attacking an adversary, avoiding in that way an injury from the side of an aggressive male (Fairbairn 1978). Hahn and Haber (1982) suggested that in natural populations, rather a moderate, not extreme aggre ssiveness should be favoured by natural selection.

It is known that strong conflicts between males may be weakened or eliminated by changing their living conditions (Winslow, Miczek 1984). Males staying with females after a certain time settle their proper social position without fighting and simply get used to the smell of sex attractants marking the cage (III series of the experiments). According to Butler's suggestions (1980) an antagonistic interaction in wild populations of mice is necessary rather to settle social hierarchy, after which the aggressiveness of dominant males usually decreases.

In wild populations of rodents, competition for an estrus female is concentrated rather on an increased number of copulations than on fights and antagonistic attitudes (Hart 1983, Dewsbury 1984). Dominanting males with an increased androgene level without aggressive symptoms can be more effective sexually, eliminating the fertility or their more submissive adversary through copulation with a female immediately after that copulation. Domination manifested by injuring or by preventing the adversary to get the estrus female would be less effective (McClintock et al. 1982). As it is known, the priority of a given male does not assure its fatherhood (Dewsbury, Hartung 1980, Dewsbury, Baumgardner 1981). The sequence of mating has no influence on increased number of delivered litter (Lanier et al. 1979). The composition of a delivered litter is an effect of competition between spermatozoa of copulating males (Dewsbury 1984). Thus, sexual competition between males differing by sexual behaviour be may transferred to spermatozoa competition (Lanier et al. 1979, McClintock et al. 1982), which according to Hart (1983) and Dewsbury (1984) is a very common phenomenon in natural populations. Mating with more than one male protects a female against sterile copulations, improves selection of genes with higher adaptive properties for their progeny and in consequence offers larger chances to a more vigorous male (Cox, Le Boeuf 1977). In the present experiments, in most of the competition cages (III series of the experiments), after a period of adaptation, mutual aggressiveness disappeared completely, but, reproduction excesses remained (regardless the sequence of delivery) only in the males from the A stock.

It may be suggested that in the process of evolution, aggressiveness and fighting capacity of dominant males, particularly under conditions of reproduction competition, did not offer so large adaptation values as a reproduction prevelance of males with a higher level of heterozygosity (Åslund 1977, Kyriacou et al. 1978) constituting an important factor in maintainning genetic variability, especially in small, closed populations.

The initial period of strong conflicts between dominating and submissive males facilitate settlement of their social hierarchy (Butler 1980), which plays an important role in the case of excessive density, since submissive males eliminated or limited in the process of reproduction (even to 10%, Horn 1971) migrate and become pioneers of new colonies (Smith 1974, Butler 1980). Christian (1970) suggested that submissive, less aggressive specimens are agents of mammalian adaptive radiation.

A conclusion arises, that after over 30 generations of breeding with maximum avoidance of inbreeding the A stock (N_e=40) specimens, still had a large amount of genetic variability which was revealed previously with the use of skin transplantation technique (Musiałek 1985), and in the present paper, it was evidenced by a very high prevalence of male reproduction under conditions of sexual competition.

Further studies on females will be dealing with the effects of a higher level of heterozygosity on some parameters of maternal behaviour (Strózik 1985).

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WSPÓŁZAWODNICTWO W REPRODUKCJI SAMCÓW MYSZY POCHODZĄCYCH Z MAŁYCH POPULACJI RÓŻNIĄCYCH SIĘ EFEKTYWNĄ WIELKOŚCIĄ

Streszczenie

Materiał do badań stanowiły myszy pochodzące z dwu zamkniętych stad, prowadzonych z maksymalnym unikaniem wsobności przez ponad 30 pokoleń. Stado A (35 - 37% wsobności) składało się z dziesięciu par, a stado C (63 - 65% wsobności) z czterech par w każdym pokoleniu. Po okresie izolacji umieszczono parami samce ze stada A i C obserwując ich zachowanie. Na podstawie przeprowadzonych badań stwierdzono, że procent samców agresywnych był w obu stadach podobny. Po umieszczeniu w klatce konkurencyjnej samicy estrusowej zaobserwowano, że częściej kopulował z nią samiec ze stada A niż ze stada C, a czas wyprodukowania czopa kopulacyjnego przez samca A był krótszy niż przez samca C. W przypadku stałego przebywania pary samców A i C z samicą (przeciętnie do czwartego wykotu) otrzymano aż 69% miotów po samcach ze stada A.

Wprawdzie nie wykazano powiązania pomiędzy stopniem heterozygotyczności samców a ich agresją, jednakże uzyskane wyniki wskazują, że im samce były bardziej heterozygotyczne, tym ich zdolność reprodukcyjna w warunkach konkurencji seksualnej była wyższa.

КОНКУРЕНЦИЯ ПРИ РАЗМНОЖЕНИИ МЕЖДУ САМЦАМИ НЕБОЛЬШИХ ПОПУЛЯЦИЙ, ОТЛИЧАЮЩИХСЯ ЭФФЕКТИВНОЙ ВЕЛИЧИНОЙ

Резюме

В исследованиях использовались мыши, принадлежащие к двум замкнутым стадам, проводимым при максимальном избежании инбридинга через более 30 поколений. Стадо А (35 - 37% инбридинга) складывалось из 10 пар, а стадо С (63 - 65% инбридинга) складывалось из 4-х пар в каждом поколении. После предварительной изоляции, самцы из стада А и С помещались парами и проводились наблюдения их поведения. Процент агрессивных самцов в обоих стадах был одинаковый.

Однако, когда в конкурентной клетке находилась самка estrus, то чаще всего копулировал с ней самец из стада А (64,6% пробок по самцу А), а время производства копуляционной пробки самцом А было меньше от времени, необходимого для производства такой пробки, у самца С (А—$\bar{x}$ 6.69 ± ± 4.58 мин., С — $\bar{x}$ 9.23 ± 6.27 мин.). В случае постоянного пребывания пары самцов А и С с самкой (в среднем до 4-го окота) было получено аж 69% помётов по самцах из стада А.

Хотя не удалось нам установить связи между степенью гетерозиготности самца и его агрессией, было отчётливо видно, что чем более гетерозиготными были самцы (из стада А), тем большей репродуктивной способностью характеризовались они в условиях половой конкуренции.