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Mating Frequency in Male Chickens: Long-term Selection*

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Summary. Twenty-three generations of bidirectional selection in male chickens (*Gallus domesticus*) for number of completed matings resulted in widely diverse mating behavior in the high and low lines. Selection caused a steady increase in cumulative number of completed matings (CNCMs) of the high line with a realized heritability of 0.18 ± 0.02. In contrast, selection for decreased CNCMs caused many males to pass a threshold below which they would not mate naturally. Changes in male mating behavior were not accompanied by changes in mating behavior of females.

Key words: Selection – Mating behavior – Chicken – *Gallus domesticus*

Introduction

Polygenic influences on the mating behavior of chickens have been based on estimates of genetic parameters and short-term selection experiments (Wood-Gush and Osborne 1956; Siegel 1959; Tindell and Arze 1965; Galpern and Dukhno 1974). Via bidirectional selection from a randombred control population, Siegel (1965) developed lines of chickens that were genetically divergent for high and low mating frequency of males. Short-term responses were asymmetrical, with genetic variation being primarily additive in the high line and a combination of additive, non-additive and sex-linked in the low line (Cook et al. 1972; Siegel 1972).

These populations have been used to examine various mechanisms associated with sexual behavior. McCollum et al. (1971) and Cook and Siegel (1974) postulated genetic influences on a two-system control (endocrine and neural) for adult mating behavior, and Benoff (1979) demonstrated that the systems could be activated in young chicks from these lines. While selection for mating frequency was assumed to affect both systems, it was hypothesized that the neural mechanisms were of primary importance and the endocrine secondary. Van Krey et al. (1977) showed that mating frequency of capons could be restored to the basal level of intact males by injections of testosterone, suggesting that such androgens regulate the expression of mating behavior. Combining their results with those of others (Barfield et al. 1975; Crawford and Glick 1975; Haynes and Glick 1974). They postulated an inhibitory mating center (IMC) dominant to a stimulatory mating center (SMC). This hypothesis, which states that the IMC is not affected by gonadal hormones and that androgens stimulate only a threshold response, is further supported by observations of Snapir et al. (1974) and Benoff et al. (1978).

This paper summarizes an experiment in which chickens were selected for high and low frequencies of completed matings over 23 generations. In addition to characterizing the lines with respect to realized genetic and phenotypic parameters, a relaxed (unselected) subpopulation was taken from each selected line in the 21st generation and maintained for two generations to further ascertain the results of past selection and prediction of future responses. In addition, data are presented on the mating behavior of females from these lines.

Materials and Methods

Selection Criterion

The selection criterion for males was the cumulative number of completed matings (CNCM). Each male was taken from his cage or home flock (all males) during the afternoon and placed singly with a tester flock of females for a 10-min period. Tester flocks consisted of randomly chosen groups of six to eight contemporary females from the selected and control lines. Numbers of courts, mounts, treads (Guhl 1961) and completed matings for each male were recorded and summed over eight observation periods. Data were obtained between 29 and 34 weeks of age, and no male was tested more than once per day. Testing and assignment to tester flocks were at random.

Chickens follow a definite sequence of mating behavior (Guhl 1961). Courtship of the female can be either a sexual or an aggressive act by the male. In response the female may

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either avoid him or assume a receptive, crouching position. Her crouch will usually encourage the male to mount her, tread and complete the mating, although he may ignore her. In this experiment, a cumulative scoring system was used, such that males which performed one part of the mating sequence were given credit for all previous behaviors in the sequence. For example, a male that mounted was assumed to have courted, one that completed a mating was assumed to have courted, mounted and treaded.

Stocks

The base population for the selected lines was a sample from the Athens-Canadian (AC) randombred population (Hess 1962; Merritt and Gowe 1962). From this parental population, males with the highest CNCMs were chosen as parents of the high mating line (HM) and males with the lowest CNCMs were chosen as parents of the low mating line (LM). In subsequent generations, individual selection for CNCMs within the HM and LM lines was used to perpetuate each line. A randomly chosen sample of the Athens-Canadian randombred population was maintained as a control.

Husbandry

Each generation chicks were obtained from hatches on the first and third Tuesdays in March. Chicks were removed from the hatcher on the 22nd day after incubation commenced, pedigreed and placed in floor pens with a hot-air brooding system. Temperature, humidity and length of photoperiod were controlled to provide environmental conditions as similar as possible among pens and generations. Cockerels were reared in heterosexual flocks until 8 to 10 weeks of age and thereafter, maintained either in all-male flocks or in individual cages. The same feed fomulation (Siegel 1962) was used in all generations.

Within each selected line, ten males were chosen to sire the next generation. Each male was assigned four females and reproduction was via artificial insemination. Females were randomly chosen from within the same line, avoiding full and half sib matings. Estimates of the rate of inbreeding per generation (F) were based on the effective number of sires (Nm) and dams (Nf) where $F = 1/(8Nm) + 1/(8Nf)$ (Wright 1931). The inbreeding coefficient in the 23rd generation was 0.412 for the HM line and 0.409 for the LM line. These values are slightly overestimated, since sib matings were avoided.

Female Data

Mating behavior of females in each selected line and the control line was recorded, including numbers of courts received, crouches and avoids (female's rejection of male's attention). Each value represented the summed scores of eight 10-min observation periods when females were between 29 and 34 weeks of age. The ratios of crouches/courts × 100 and avoids/courts × 100 were also calculated.

In generation 23, adult females from the HM and LM lines were tested in initial paired encounters to determine dominance-subordinance relationships. First, females from each selected line were randomly paired with similarly sized females from an unrelated stock (tester females) to ascertain which of each pair had higher social rank. Second, females of the HM line were randomly paired with females of the LM line to determine if individuals from one line were consistently dominant to those from the other line. Chi-square goodness of fit tests were used to analyze number of wins versus number of losses in each line.

Male Paired Encounters

In generation 23, sixteen roosters (27 weeks of age) from each selected line and the control line were randomly chosen to participate in paired encounters as a measure of relative aggressiveness. Each male took part in one encounter per day for six days. The experimental design ensured that each male was matched with two roosters randomly chosen from within each line. The system used for scoring the encounters was as follows:

Score	Activity
9	win by a fight
8	win by a peck
7	win by a threat
6	lose by a fight
5	no contest
4	avoid a peck
3	flee from a peck
2	avoid a threat
1	flee from a threat

The six scores for each rooster were summed and an analysis of variance on square root transformed data was used to determine if there were differences among lines in relative aggressiveness of the roosters.

Relaxed Lines

In the 21st generation, 10 males were randomly chosen from the HM and from the LM lines to create relaxed (i.e., unselected) lines. The semen of the 10 males within each line was pooled and used to inseminate 40 randomly chosen females from that line. The resulting progeny were hatched and reared contemporaneously with individuals of the control and the 22nd generation selected lines. Mating behavior (courts, mounts, treads and CNCMs) were obtained for the high and low relaxed populations. This procedure was repeated within the respective relaxed lines for comparison with the 23rd generation progeny from the selected lines.

Analyses

The response to selection for CNCMs was calculated after adjusting each selected line generation mean for fluctuations in the control line means. The realized heritability of CNCMs was calculated as the regression of the cumulative response on cumulative effective selection differential (Falconer 1960, 1981). Heritabilities of unselected traits (Siegel 1972) were estimated from full sib correlations (King and Henderson 1954). The statistical model was:

$$X_{hijk} = u + L_h + S_{hi} + D_{hij} + e_{hijk}$$

where X_{hijk} was the CNCMs of the kth offspring of the jth dam mated to the ith sire within the hth line. Product-moment correlations across generations and within each line were used to estimate the phenotypic association of CNCMs with unselected traits. Confidence intervals were obtained on the correlations transformed to Z values.

Genetic correlations (rGG′) between CNCMs and unselected traits were obtained by the method of Falconer (1954) in which:

$$rGG' = \Delta G' \, h \, \sigma p' / \Delta G \, h' \, \sigma p$$

where $\Delta G'$, h′ and $\sigma p'$ refer to the genetic change, square root of heritability and phenotypic standard deviation of the unselected trait and ΔG, h and σp refer to those values for the selected trait.

Mating efficiencies were calculated as the ratio of each mating behavior to the preceding behavior in the sequence × 100. These percentages were transformed to arc sine square roots before statistical tests were performed. Cumulative number of courts, mounts, treads and completed matings were transformed to square roots prior to analysis.

Results

The Selected Trait

Although dramatic changes in mean CNCMs occurred in the selected lines (Fig. 1), none was observed in the randombred control line where the regression of mean CNCMs on generation number (-0.04 ± 0.06) was not significantly different from zero. After adjusting the means of the selected lines for deviations from the control line means to correct for minor environmental fluctuations, the regressions of control-adjusted mean CNCMs on generation number were 0.95 ± 0.11 and -0.23 ± 0.05 for the high and low lines, respectively (Table 1). Thus, response to 23 generations of bidirectional selection for CNCMs was effective at the phenotypic level, being 0.17 and -4.07 phenotypic standard deviations in the HM and LM lines, respectively. The response in genetic standard deviation units was 0.40 in the HM and -4.30 in the LM line.

By comparing the expected and effective selection differentials within each line, one can ascertain the relationship between artificial and natural selection for the selected trait. The signs of the differences between expected and effective selection differentials were tested (chi-square sign test, Steel and Torrie 1960) among generations in both selected lines. No significant differences between the two types of selection differentials were found in either line.

Realized heritability (h^2) is a function of selection intensity and response to selection, providing an estimate of additive genetic variation (Falconer 1960; 1981). Twenty-three generations of selection for increased CNCMs resulted in a h^2 of 0.18 ± 0.02 (Fig. 2). The h^2 was essentially zero for the first several generations of selection. Since the selection differential averaged 1.5 standard deviation units for this period, the lack of response can probably be attributed to linkage. After the breakup of linkage groups, positive response in the HM line to selection was accompanied by gradual decrease in effective selection differential (-0.012 ± 0.006, $p < 0.05$, for 23 generations) until generation 20. In generations 20 to 23, negative responses in CNCMs occurred although an effective selection differential of 0.496 standard deviation units re-

Table 1. Regressions ± SE of control-adjusted means on generation for mating behavior

Trait	Line	
	HM	LM
Courts	1.92 ± 0.61*	-0.59 ± 0.61
Mounts	1.16 ± 0.11**	-0.31 ± 0.07**
Treads	1.02 ± 0.11**	-0.25 ± 0.06**
CNCMs	0.95 ± 0.11**	-0.23 ± 0.05**

* $P < 0.05$; ** $P < 0.01$

Statistical tests werre performed on square root transformed data

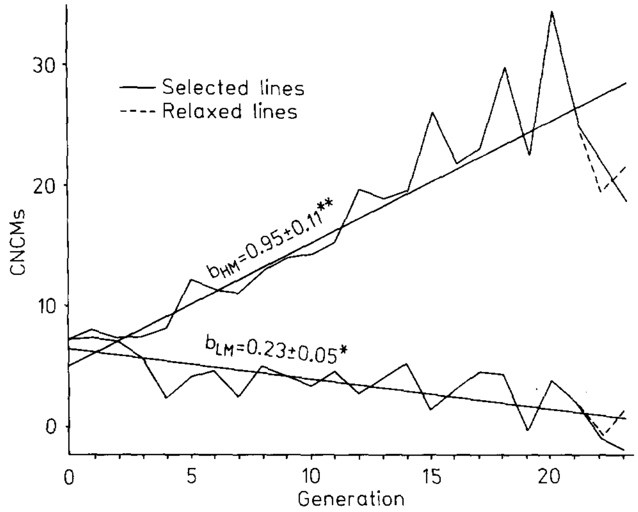

Fig. 1. Cumulative number of completed matings (control-adjusted) by generation for selected and relaxed lines

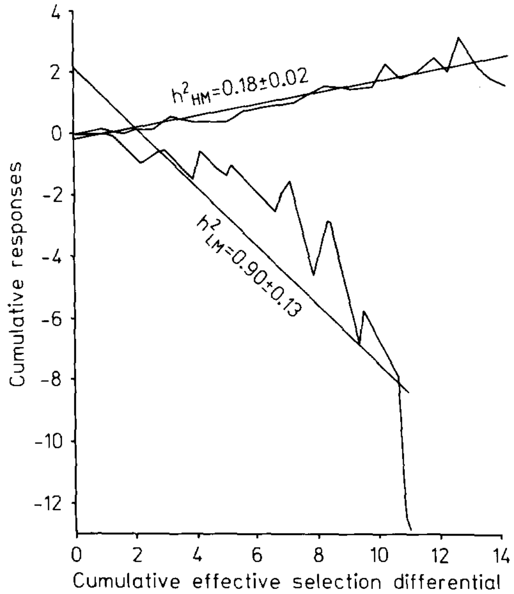

Fig. 2. Realized heritabilities of cumulative number of completed matings (CNCM) for 23 generations

Table 2. Regressions ± SE of coefficients of variation X 100 on generation for selected and unselected traits

Line	Courts	Mounts	Treads	CNCMs
HM	$-1.10 \pm 0.31^{**}$	$-1.72 \pm 0.37^{**}$	$-1.77 \pm 0.28^{**}$	$-1.79 \pm 0.28^{**}$
AC	-0.05 ± 0.35	$0.82 \pm 0.33^{*}$	0.80 ± 0.40	0.69 ± 0.40
LM	-0.45 ± 0.38	$6.09 \pm 0.98^{**}$	$7.25 \pm 1.16^{**}$	$7.83 \pm 1.26^{**}$

* $P<0.05$; ** $P<0.01$

mained in generation 23. This indicates that additive genetic variance for CNCMs has not been exhausted in the HM line. The decreasing coefficient of variation (Table 2), combined with the decreasing selection differential, suggest that individuals in this line may be approaching a physiological limit to selection, although it appears to be happening relatively slowly.

Selection for low CNCMs has resulted in an entirely different response. Inspection of Fig. 2 reveals that the h^2 for generations 0 to 23 (0.90 ± 0.13) does not accurately describe progress over the entire study. The h^2 reported by Siegel (1972) for generation 0 to 11 was 0.32 ± 0.07 and appears valid until generation 15. Thereafter, a considerable CNCM response occurred concurrently with little change in effective selection differential (regression coefficient of selection differential on generations $=0.007 \pm 0.012$). The coefficient of variation of CNCMs in the LM line increased significantly (Table 2), indicating that individuals were becoming less alike over time. In generations 21, 22 and 23, the males that never mated in the LM line made up 84, 89 and 60 percent of each generation, respectively (compared to 17, 7 and 9 percent in the control line). These results suggest that additive genetic variance still exists in the LM line but that reduction in CNCMs has progressed to the point that the threshold of the trait is not being attained.

Percentage of Nonmaters

Selection for increased and decreased CNCMs might change the percentage of males in each line that never mate although given the opportunity. Chi-square tests indicated that the incidence of nonmaters was significantly greater in generation 6 through 23 in the low than in the high line with the control line being intermediate. Regressions of percentage of nonmaters on generation are presented in Table 3. Lack of a significant time trend in the control line and significant negative and positive regressions in HM and LM lines, respectively, suggest that selection for CNCMs is modifying the threshold for both the elicitation of mating behavior and mating frequency.

Table 3. Regressions ± SE of percentage of nonmaters on generation for selected and control lines

Line	Regression ± SE
HM	$-0.35 \pm 0.09^{**}$
AC	0.17 ± 0.25
LM	$2.80 \pm 0.37^{**}$

* $P<0.05$; ** $P<0.01$
Statistical tests were performed on arc sine transformed data

Mating Behavior Traits

Courts, mounts, treads and CNCMs of males were recorded each generation. Since these behaviors were considered a definite sequence (i.e., each male which performed one behavior in the sequence was given credit for all previous behaviors), the high degree of associations among them is not surprising. In the early generations of selection, this was an accurate representation of events. However, after six generations it became obvious that, in some HM line males, the natural mating sequence was breaking down and that they were engaging in forced copulations (McKinnney 1975) without prior courtship activities. As selection progressed, the frequency of forced copulations increased (although it was not quantified). Hence, the information regarding courtship behavior in HM line males should be interpreted with caution.

While courting is often initiated as an aggressive behavior, and may lead to either a pugilistic or sexual encounter, mounting and treading are sexual (Kruijt 1966; Siegel 1972). Therefore, it is valid to discuss mounts and treads separately from courts. The regressions presented in Table 1 indicate that the regression of control adjusted means for mounts and trends on generation were significant and positive in the HM line and significant and negative in the LM line. When coefficients of variation of mounts and treads were regressed on generations, the only significant regression (Table 2) in the control line was for number of mounts. Individuals in the HM line became phenotypically more similar over the course of selection in frequencies of mounts and treads, while variability in mounts and treads increased among individuals in LM line (Table 2). Phenotypic and genetic correlations of CNCMs with mounts and with treads were positive and highly significant in both lines (Table 4). Thus, within each selected line, there were correlated responses in frequencies of mounts and treads to selection which corresponded to the changes in frequencies of CNCMs.

The association between courts and CNCMs is not as clear, however. The number of courts per generation increased significantly in the HM line (Table 1), while individuals within the line became progressively more alike (Table 2). The phenotypic correlation between courts and CNCMs in the HM line was positive and highly significant, but the realized genetic correlation was essentially zero (Table 4), suggesting large environmental influences on the association between courts and CNCMs, perhaps the females' reactions to males' advances. However, in the LM line the mean number of courts did not change during selection (Table 1), nor did the coefficients of variation of courts (Table 2). Both phenotypic and genetic correlations between courts and CNCMs were positive and high in line LM (Table 4). It is conceivable that courts in the HM line are primarily sexual i.e., often leading to completion of mating, while courts in the LM line are more often aggressive despite the high correlations between the two traits.

Another method of ascertaining relationships among the mating behavior is to evaluate mating efficiencies. Mating efficiencies (Table 5) were calculated as the ratio × 100 of each mating trait with the preceding traits (e.g., CNCM/courts, mounts/courts). The regressions of each ratio on generation are presented in Table 6. A significant positive regression in CNCM/treads was found in all lines, suggesting that males far enough in the mating sequence to tread also completed matings regardless of their genetic backgrounds (Table 6).

The regressions of ratios between courts and succeeding sexual behavior on generation increased in the HM line, indicating that over the course of selection, a higher proportion of courts led to sexual behavior than had previously been the case. In the LM line, however, negative regressions of sexual behavior to courts on generation occurred, suggesting that a smaller proportion of courts led to sexual behavior in this line as selection progressed.

In the 23rd generation the mean for the control line was intermediate to those for the selected lines (Table 4), suggesting that correlated responses in mating efficiency occurred with selection for CNCMs. It is apparent from comparing the mating efficiencies of the two selected lines that the HM line has significantly greater ratios of CNCMs to courts, mounts to courts and treads to courts (Table 5). That is, courts in the HM line generally lead to sexual encounters. Conversely, the LM males have significantly greater ratios of CNCMs to mounts, CNCMs to treads and treads to mounts which suggest that, once the LM line males progress beyond the court, i.e., to mounting, their activities become primarily sexual. Thus, courting has become more of a sexual display in the HM line and an aggressive act in the LM line.

Table 4. Estimates of phenotypic and genetic correlations between CNCMs and preceding mating behavior

Trait	Line			
	HM		LM	
	rPP′	rGG′	rPP′	rGG′
Courts	0.56	0.04	0.63	1.43
Mounts	0.93	0.82	0.96	1.83
Treads	0.97	0.98	0.98	2.13

Table 5. Percentage of mating efficiencies in the parental and 23rd generation in selected and control lines

Ratio	Mating efficiency (%)			
	Gen 0	Gen 23		
		HM	AC	LM
CNCM/Courts	14.7	24.5 c	11.6 b	3.5 a
CNCM/Mounts	68.4	69.8 a	72.6 b	83.9 c
CNCM/Treads	72.5	87.9 a	90.3 b	94.5 b
Mounts/Courts	21.4	35.1 c	16.0 b	4.2 a
Treads/Courts	20.2	27.9 c	12.9 b	3.8 a
Treads/Mounts	94.3	79.4 a	80.4 b	88.7 c

Any two means in a row for Gen 23 with the same letter are not significantly different ($P \leqq 0.05$)

Table 6. Regressions ± SE of mating efficiencies on generation in selected and control lines

Ratio	Regression ± SE		
	HM	AC	LM
CNCM/Courts	0.8 ± 0.1**	0.0 ± 0.1	−0.4 ± 0.1**
CNCM/Mounts	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.3
CNCM/Treads	0.4 ± 0.1*	0.4 ± 0.1**	0.4 ± 0.2*
Mounts/Courts	0.9 ± 0.1**	−0.0 ± 0.1	−0.5 ± 0.1**
Treads/Courts	0.8 ± 0.1**	−0.1 ± 0.1	−0.4 ± 0.1**
Treads/Mounts	0.0 ± 0.0	−0.1 ± 0.2	−0.3 ± 0.3

* $P<0.05$; ** $P<0.01$

Female Mating Behavior

Although selection was for mating behavior of males, data on the mating behavior of females were also analyzed, commencing in the 16th generation. Courts,

Table 7. Regressions ± SE of mating behavior on generations 21 to 23 for selected and relaxed lines

Trait	Line			
	HM	HMR	LMR	LM
Courts	-12.5±10.7	-9.5±12.9	-0.9±20.4	-8.5±11.7
Mounts	- 3.4± 1.2	-3.2± 3.7	0.0± 2.7	-2.9± 1.0
Treads	- 3.1± 0.1**	-2.0± 2.7	-0.3± 1.9	-2.3± 0.7*
CNCM	- 3.3± 0.1*	-1.9± 2.3	-0.3± 1.6	-2.0± 0.6

* $P<0.05$; ** $P<0.01$
Statistical tests were performed on data transformed to square roots

crouches, avoids, crouches/courts×100 and avoids/courts×100 were analyzed for the 16th through the 23rd generation. An analysis of variance with year, male line and female line as main effects plus all possible interactions indicated highly significant differences in both main effects and interactions, differing from the findings of Siegel and Cook (1975). However, when analyses were conducted within each generation, no consistent differences among lines were found for female mating behavior.

Social Ranking

Chi-square tests of paired encounters between females indicated that neither HM females nor LM females were consistently dominant or submissive to tester females. Also, HM and LM females did not differ from each other in dominance-subordinance rankings.

Paired encounters between roosters of the 23rd generation were analyzed to determine relative aggressiveness among the lines. Means and standard deviations of aggression scores were 35.7±8.5, 39.2±7.3 and 29.6±6.2 for the HM, control and LM lines, respectively. Although the difference between the high and control line males was not significant, the low line roosters had significantly lower scores than either the high or control line roosters.

Relaxed Lines

In the 21st generation of selection, random samples of individuals from the high and low selected lines were used to begin, respectively, high relaxed (HMR) and low relaxed (LMR) lines. These relaxed lines were maintained contemporaneously with the selected and control lines in generations 22 and 23. After adjusting the relaxed and selected lines for environmental fluctuations as measured by the control line (Fig. 2), means were regressed on generation in each line (Table 7). Since only three generations of data with a relatively small number of individuals were available for these regressions, the results were not, in most cases, statistically significant. It is instructive, however, to observe trends over time which might elucidate the characteristics of each relaxed line as compared to its corresponding selected line.

It was shown earlier (Fig. 1) that a sizeable drop in the control-adjusted mean of mating traits occurred in the high line after generation 20. The drop in the HMR line was not as precipitous (Table 7), suggesting that natural selection did not strongly oppose artificial selection for CNCMs. Further evidence of this is that the percentage of nonmaters in both the selected and relaxed HM line remained essentially at zero in generations 22 and 23.

The frequency of mating traits increased to some extent in the LMR line as compared to the low selected line (Fig. 1). This trend of the relaxed line means toward the original population mean indicates an opposition between natural selection and selection for reduced frequency of CNCMs. There was, however, no significant decrease in the percentage of nonmaters of the LMR line as compared to the selected low mating line. Thus, short-term relaxation of selection did not alter the threshold for elicitation of mating behavior in the LM line.

Discussion

Twenty-three generations of bidirectional selection for frequency of CNCMs in male chickens has caused extreme diversity in the two selected lines. After a few generations without phenotypic response in the HM line, CNCMs increased steadily through generation 20. Thereafter, an unexplained decrease in response to selection has occurred. Since a sizeable selection differential still remains, however, future response to selection may be expected to occur.

In the LM line, there was a fairly steady decrease in CNCMs through 15 generations of selection after which a precipitous drop in CNCMs occurred. It appears that this was because a behavioral threshold has been passed by many of the individuals below which they will not mate naturally, although they are still physiologically capable of reproduction via artificial means.

The concept of a threshold trait seems a paradox when dealing with a supposedly quantitative trait (Falconer 1960, 1965, 1967, 1981). One must assume that, underlying such an all or none situation (mating or not mating) are influences from one or more systems (e.g., neural, endocrine). When the underlying system(s) reach some level or particular combination of levels, mating does not occur, and one cannot ascertain by inspection of phenotype any further information regarding the genotype of the individual. In such cases, the selection intensity is necessarily reduced and response to selection is expected to decrease. In nature, this situation could be masked because these individuals would not be contributing to the gene pools of subsequent generations.

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