FEATURES OF BREEDING VALUE INHERITANCE SIRES OF HOLSTEIN BREED

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In our studies, the phenotypic manifestation of the additive form of inheritance of breeding value by milk yield (intermediate and parental dominance) was in 334 (82.2%) bulls, and non-additive form (over-dominance and regression) – in 72 (17.8%) including: over-dominance in 55 (13.5%) and regression in 17 heads (4.2%).

In the population assessment, for all forms of inheritance, there was a clear quantitative shift of the breeding value of sons of milk yield to positive (+) values, compared with the breeding value of their parents. This confirms that sons, selected after their evaluation, and recognized as milk yield improvers.

The variability of the breeding value of sons by milking depending on the forms of its inheritance has been established.

According to the group of bulls by intermediate type of inheritance, milk yield sign were found in 291 (71.7%) sons, whose pedigree value was 606.4 ± 11.6 kg and was higher than the half-sum of both parents (554 kg), which deviates from the action of intermediate inheritance at 52 kg (109%).

After all, the recognition of the intermediate nature of inheritance involves obtaining in the offspring of animals with the same set of chromosomes as their parents, and hence with the same phenotype. Therefore, from a theoretical point of view, genetic progress in the population should be not expected from this group of animals. However, in this case, the increase in breeding value was 9%, which is statistically significant (P > 0.99).

A rather high variability of the breeding value of sons from its level in their parents with an intermediate form of inheritance has been established. Thus, of the 159 bulls-breeders in which the breeding value was inherited by intermediate form, only 30 sons (7.3% of the total population) of the bull Duster 2147488 (BV +579 kg and mothers with an average BV +632 kg, half the amount of the BV of both parents was +605 kg), was +605.5 ± 30.8 kg and was equal to the half-sum of the BV of both parents, and 9 (2.2%) sons of the bull Manfred 2183007, whose breeding value was, on average, at the population level +856.3 ± 37.6 kg and was equal to the half-sum of the indicator of the parents’ BV (+851 kg).

The inheritance of breeding value of bulls on quantitative signs of milk productivity in highly consolidated breeds on these signs, at intra-breeding selection occurs by a combination of phenotypic display of action of additive and non-additive (super-dominance) forms of inheritance. The frequency of these forms of inheritance probably is determined by the number and quality of chromosome pairs in the karyotype of animals on the probable basis of their manifestation in the population [15].

The relative variability of breeding value by milk yield along the line "father – son" and "mother – son" depends on the form of its inheritance. The coefficient of phenotypic correlation between the breeding value of parents and sons in the intermediate form of inheritance is +0.524 – +0.560 and increases with parental dominance to +0.907 ± 0.040 and +0.985 ± 0.006, and over-dominance to +0.887 ± 0.044 and +0.905 ± 0.033, at high statistical significant.

Inheritance by non-additive form (over-dominance of both parents) is more effectively associated with increasing of breeding value by milk yield their sons than by the additive form.

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ОСОБЛИВОСТІ УСПАДКУВАННЯ ПЛЕМІННОЇ ЦІННОСТІ БУГАЇВ ГОЛШТИНСЬКОЇ ПОРОДИ
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В наших дослідженнях фенотипове проявлення адитивної форми успадкування племінної цінності за надоєм (проміжне та домінування батьків) було у 334 (82,2%) бугаїв, а неадитивна форма (наддомінування та регресія) – у 72 (17,8%), в тому числі: наддомінування у 55 голів (13,5%) та регресія – у 17 голів (4,2%).

При популяційній оцінці, за всіх форм успадкування, спостерігалось явне кількісне зміщення племінної цінності синів за надоєм до позитивних (+) значень, порівняно із племінною цінністю їхніх батьків. Це підтверджує, що сини, відселекціоновані після їх оцінки, визнані як поліпшувачі за надоєм.

Встановлено мінливість племінної цінності синів за надоєм від форм її успадкування. По групі бугаїв за проміжним типом успадкування ознаки надою виявлено у 291 (71,7%) синів, племінна цінність яких становила 606,4 ± 11,6 кг і була вищою від напівсуми обох батьків (554 кг), що відхиляється від оцінки проміжного успадкування на 52 кг (109%). Адже визнання проміжного характеру успадкування передбачає одержання в потомстві тварин з однаковим набором хромосом, тобто з однаковим фенотипом. Тому, з теоретичної точки зору, від цієї групи тварин не слід очікувати генетичного прогресу у популяції. Проте, в даному випадку, підвищення племінної цінності склало 9%, що статистично вірогідно.

Встановлено досить високу мінливість племінної цінності синів від її рівня у їхніх батьків за проміжної форми успадкування. Так, із 159 бугаїв-поліпшувачів, в яких племінна цінність успадковувалась за проміжною формою, лише у 30 синів (7,3%) до загального поголів'я бугаїв Дастера 2147488 (ПЦ +579 кг та матерів із середньою ПЦ +632 кг, напівсума показника ПЦ обох батьків склала +605 кг), становила +605,5 ± 30,8 кг і прирівнювалась до напівсуми ПЦ обох батьків, та у 9 (2,2%) синів бугаїв Манфреда 2183007, племінна цінність яких становила, в середньому, на популяційному рівні +856,3 ± 37,6 кг і прирівнювалась до напівсуми ПЦ батьків (+851 кг).

Успадкування по лінії «батько – син» та «мати – син» залежить від форми її успадкування. Коефіцієнт кореляції між племінною цінністю тварин за неадитивною формою успадкування становить +0,524 – +0,560 і підвищується за домінування батьків до +0,907 ± 0,040 та +0,985 ± 0,006 і наддомінування до +0,887 ± 0,044 та +0,905 ± 0,033, за високої статистичної вірогідності.

Успадкування за неадитивною формою (наддомінування батьків) більш ефективно асоціює із підвищенням племінної цінності за надоєм їх синів, ніж успадкування за адитивною формою (домінування).
ОСОБЕННОСТИ НАСЛЕДОВАНИЯ ПЛЕМЕННОЙ ЦЕННОСТИ БЫКОВ ГОЛШТИНСКОЙ ПОРОДЫ
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В наших исследованиях фенотипическое проявление аддитивной формы наследования племенной ценности по надою (промежуточное и доминирование родителей) было у 334 (82,2%) быков, а неаддитивной формы (сверхдоминирование и регрессия) — у 72 (17,8%), в том числе: сверхдоминирование у 55 голов (13,5%) и регрессия — у 17 голов (4,2%).

При популяционной оценке всех форм наследования наблюдалось явное количественное смещение племенной ценности сыновей по надою к положительным (+) значениям по сравнению с племенной ценностью их родителей. Это подтверждает, что сыновья, отселекционированные после их оценки, признаны улучшителями по удою.

Установлено изменчивость племенной ценности сыновей по удою в зависимости от форм ее наследования. По группе быков с промежуточным типом наследования признака удоя обнаружено у 291 (71,7%) сыновей, племенная ценность которых составляла 606,4 ± 11,6 кг и была выше полусуммы обоих родителей (554 кг), что отклоняется от ожидаемого на 52 кг (109%). Ведь признание промежуточного характера наследования предусматривает получение в потомстве животных с одинаковым набором хромосом, а значит, с одинаковым фенотипом. Поэтому, с теоретической точки зрения, от этой группы животных не следует ожидать генетического прогресса в популяции. Однако, в данном случае, повышение племенной ценности составило 9%, что статистически достоверно (Р > 0,99).

Установлено достаточно высокую изменчивость племенной ценности сыновей от ее уровня у их родителей по промежуточной форме наследования. Так, у 159 быков-улучшателей, у которых племенная ценность наследовалась по промежуточной форме, только у 30 сыновей (7,3% от общего поголовья) быка Дастера 2147488 (ПЦ +579 кг и матерей со средним ПЦ +632 кг, полусумма показателя ПЦ обоих родителей составила +605 кг), составила +605,5 ± 30,8 кг и приравнивалась к полусумме ПЦ обоих родителей, и у 9 (2,2%) сыновей быка Манфреда 2183007, племенная ценность которых составляла, в среднем, на популяционном уровне +856,3 ± 37,6 кг, и приравнивалась к полусумме показателя ПЦ родителей (+851 кг).

Наследование племенной ценности быков по количественным признакам молочной продуктивности в высоко консолидированных по этим признакам породах при внутрипородном разведении происходит путем объединения фенотипического проявления аддитивных и неаддитивных (сверхдоминирование) форм наследования. Частота проявления этих форм наследования определяется количеством и качеством пар хромосом в кариотипе животных на вероятной основе их проявления в породе.

Соотношение изменчивости племенной ценности по надою по линии «отец — сын» и «мать — сын» зависит от формы ее наследования. Коэффициент фенотипической корреляции между племенной ценностью отцов и сыновей по промежуточной форме наследования составляет +0,524—+0,560 и повышается при доминировании родителей до +0,907 ± 0,040 и +0,985 ± 0,006, и сверхдоминировании — к +0,887 ± 0,044 и +0,905 ± 0,033 при высокой статистической достоверности.

Наследование по неаддитивной форме (сверхдоминирование родителей) более эффективно ассоциируется с повышением племенной ценности по надою их сыновей, чем наследование по аддитивной форме доминирования родителей.

Ключевые слова: количественный признак, племенная ценность, форма наследования, промежуточное наследование, доминирование, сверхдоминирование, коэффициент корреляции

Introduction. The rate of genetic progress on selection signs in dairy farming by 90–95% depends on the level of breeding value of bulls-breeders [1]. Therefore, knowledge of the nature of
inheritance of their breeding value (BV) by selection signs in the generations of offspring is an important component of the correct selection pairs and selection progress in the breed.

In intra-breed selection, traditional methods of selection, their programming based on methods of population genetics, aimed at selection of animals by quantitative signs of productivity, are based on the additive action of genes and intermediate inheritance of signs [2, 3, 4].

However, in genetics there are two forms of inheritance – additive (intermediate, dominance of one parent) and non-additive (superdominance, epistasis, regression), in which the level of inheritance of the sign is determined by intraallelic and interallelic interaction of genes [2–5]. As O. I. Babenko [8] informed, the frequency of inheritance forms breeding value of milk yield of domestic dairy breeds is depend from the part of blood Holstein breed. A number of authors found that the phenotypic manifestation of additive forms of inheritance of dairy productivity of cows and breeding value of domestic dairy bulls was combined with the manifestation of non-additive forms of inheritance [6–11, 14].

The studies on the peculiarities of inheriting the breeding value of Holstein bulls on the basis of milk productivity, particularly non-additive form inheritance, under conditions of intra-breed breeding are necessary.

The aim of the research was to identify additive and non-additive forms of inheritance of the breeding value of Holstein bulls by milk yield of daughters and their relative variability with the level of breeding value of parents in the condition of intrabreeding.

**Materials and methods.** The nature of the inheritance of breeding value by milk yield was studied in 406 bulls-breeders of the Holstein breed in the United States, selected after their evaluation for reproduction [13].

Forms of inheritance of the breeding value of bulls were determined by the method of N. S. Kolyshkina and others [2], which is based on the value of the deviation of the breeding value (standard deviation – σ) from the half of sum of the indicators of the parent’s breeding value, namely:

– intermediate inheritance – the value of the deviation of the breeding value of the son is equal to or deviates by 0.5σ (±0–250 kg) both in positively and negatively site from the half-sum of the indicators of the breeding value of the parents (BV father + BV mather) / 2 ± 0.5σ;

– domination of the father or mother – the breeding value of the son deviates from the intermediate inheritance in the positive direction of the father (f) or mother (m) at a distance of up to 0.5σ (up to 250 kg);

– overdominance – the breeding value of the son exceeds the ancestor, which dominates by more than 1.0 σ (≥500 kg);

– regression – the breeding value of the son is lower than the worst of the parents by 1σ and more (≤-500 kg).

**Results.** It was found that in the group of bulls with inheritance of breeding value in a positive case, the phenotypic manifestation of the additive form of inheritance of breeding value by milk yield (intermediate and parental dominance) was in 334 (82.2%) bulls, and non-additive form (overdominance and regression) – in 72 (17.8%) including: dominance in 55 (13.5%) and regression – in 17 bulls (4.2%), (Table 1).

In the group of bulls with breeding value of parents in the negative version, the inheritance of the BV by milking by additive form was found in 16 sons (61.5%), including the intermediate form – in 9 heads (34.6%) and mother's dominance – in 7 heads (26.9%), and non-additive – in 10 heads 38.5%).

The ratio of these forms of inheritance depends on the level of breeding value of the parents and the intensity of selection. Under the conditions of high breeding value of the father (Manfred 2183007, whose BV is +922 kg and Formation 2163822 – BV +715 kg), their sons are significantly dominated by additive inheritance (intermediate form) (90%). The frequency of this form of inheritance decreases with decreasing breeding value of the fathers. With the reduction of the breeding value of parents to +461–+476 kg, the frequency of inheritance of breeding value by milk yield by intermediate type in their sons decreases to 62.5–66.6%.
Given the negative breeding value of milk from parents (Starbuck 352790 was -847 kg, Roterte 2040726 -33.7 kg, Radier 390409 -441.0 kg, Ambition 2026916 -148.0 kg and Prelude 392457 – 64.0 kg) the share of manifestation of breeding value by intermediate type of inheritance in their sons decreases to 50.3 and 19.2%.

### 1. Breeding value of bulls for milk yield in various forms of its inheritance

| Forms of inheritance | Frequency of forms of inheritance | Breeding value per milking, kg |
|----------------------|-----------------------------------|--------------------------------|
|                      | head %                            | fathers M ± m | cv, % | mothers M ± m | cv, % | sons M ± m | cv, % |
| **breeding value of both parents in a positive case** |
| Father dominance (FD) | 23 5.7                            | 661.3 ± 35.3 | 25.7 | 402.8 ± 39.0 | 46.9 | 857.3 ± 33.1 | 18.5 |
| Mother dominance (MD) | 20 4.9                            | 497.6 ± 45.8 | 41.2 | 756.0 ± 55.5 | 32.8 | 928.0 ± 48.3 | 23.2 |
| Father super-dominance (FSD) | 24 5.9 | 580.1 ± 30.4 | 25.5 | 446.4 ± 35.6 | 38.4 | 886.6 ± 33.5 | 18.2 |
| Mother super-dominance (MSD) | 31 7.6 | 465.4 ± 33.5 | 40.0 | 617.2 ± 34.5 | 31.2 | 953.4 ± 36.3 | 21.1 |
| Intermediate (I) | 291 71.7                           | 513.1 ± 13.2 | 42.6 | 578.8 ± 21.6 | 32.5 | 606.4 ± 11.6 | 14.7 |
| Regression (R) | 17 4.9                             | 514.8 ± 43.3 | 34.6 | 531.6 ± 43.2 | 33.5 | 226.7 ± 33.6 | 61.4 |
| **On average, the group in a positive case** | 406 100.0 | 534.0 ± 11.7 | 45.6 | 570.7 ± 14.3 | 47.5 | 681.4 ± 12.4 | 36.8 |

**breeding value of the father in the negative case**

|                      | head %                            | M ± m | cv, % | M ± m | cv, % | M ± m | cv, % |
|----------------------|-----------------------------------|-------|-------|-------|-------|-------|-------|
| Mother dominance (MD) | 7 26.9                           | -30.0 ± 7.14 | 63.0 | 422.7 ± 70.40 | 44.0 | 535.2 ± 82.3 | 40.6 |
| Mother superdominance (MSD) | 10 38.5 | -28.9 ± 8.22 | 28.5 | 353.4 ± 17.21 | 37.8 | 583.3 ± 35.9 | 19.8 |
| Intermediate (I) | 9 34.6                            | -147.4 ± 45.37 | 97.3 | 698.4 ± 91.90 | 39.5 | 296.6 ± 51.5 | 52.1 |
| **On average, the group in the negative version** | 26 100.0 | -70.0 ± 20.32 | 52.8 | 491.5 ± 40.60 | 42.6 | 471.1 ± 29.8 | 32.6 |

**Note:** D – dominance; FD – domination of the father; MD – mother’s dominance; FSD – father super-dominance; MSD – mother super-dominance; I – intermediate form; R – regression; \( \hat{L} \) – \( p < 0.05 \); \( \hat{L} \) – \( p < 0.01 \); \( \hat{L} \) – \( p < 0.001 \)

In the population assessment, for all forms of inheritance, there was a clear quantitative shift of the breeding value of sons after milking to positive (+) values, compared with the breeding value of their parents. This confirms that sons are selected after their evaluation and recognized as milk yield improvers.

The variability of the breeding value of sons by milk yield depending on the forms of its inheritance has been established. On average, at the population level of assessment, on the all forms of inheritance, 406 sons with an average breeding value of +681 kg were selected for a group of bulls with breeding value in a positive variant, with an average value of half the sum of breeding value of parents +534 kg F and +570 kg M / 2 = +552 kg milk, which exceeds the average size of the parents by +129 kg (0.5σ) and is 123%.

According to the same group of bulls, 291 (71.7%) sons, whose breeding value was 606.4 ± 11.6 kg and was higher than the half-sum of both parents (554 kg), which deviates from the action intermediate inheritance on 52 kg (109%). After all, the recognition of the intermediate nature of inheritance involves obtaining in the offspring of animals with the same set of chromosomes as their parents, and hence with the same phenotype. Therefore, from a theoretical point of view, genetic progress in the population should be not expected from this group of animals. However, in this case, the increase in breeding value was 9%, which is statistically significant (\( P > 0.99 \)).

A much larger increase in the breeding value of sons compared to fathers was found in the additive form of inheritance, namely: dominance of the mother – +302 kg (148.2%); parental dominance – +326 kg (161.4%). The highest pedigree value for milking was in sons with non-additive
inheritance and was: in the form of super-dominance of the fathers – +373 kg (172.7%) and super-dominance of the mothers – +412 kg (176.2%).

A rather high variability of the breeding value of sons from its level in their parents with an intermediate form of inheritance has been established. Thus, of the 159 bull-breeders in which the breeding value was inherited by intermediate form, only 30 sons (7.3% of the total population) of the bull Duster 2147488 (BV +579 kg and mothers with an average BV +632 kg, half the amount of the BV of both parents was +605 kg), was +605.5 ± 30.8 kg and was equal to the half-sum of the BV of both parents, and 9 (2.2%) sons of the bull Manfred 2183007, whose breeding value was, on average, at the population level +856.3 ± 37.6 kg and was equated to the half-sum of the parents' BV (+851 kg), (Table 2).

2. The variability of the breeding value of bulls-sons from its level in the parents in the intermediate form of inheritance

| Father's name and number | Number of sons with an intermediate form of inheritance | Breeding value per milk yield, kg |
|--------------------------|--------------------------------------------------------|----------------------------------|
|                          |                                                         | father | mothers | sons |
|                          |                                                         | M ± m  | Cv, %   | M ± m  | Cv, % |
| breeding value of both parents in a positive case |
| Manfred 2183007          | 9                                                      | +922   | +780.0 ± 52.61 | 19.1 | +856.3 ± 37.64 | 21.2 |
| Tesk Terry 2195662       | 8                                                      | +805   | +766.67 ± 90.26 | 26.5 | +574.5 ± 84.36 | 32.9 |
| Belwood 2103297          | 13                                                     | +814   | +409.0 ± 42.18 | 34.1 | +711.6 ± 46.72 | 44.3 |
| Formation 2163822        | 18                                                     | +715   | +613.0 ± 62.60 | 43.6 | +656.3 ± 38.32 | 24.7 |
| Rudolf 5470579           | 23                                                     | +703   | +620.0 ± 46.72 | 36.2 | +669.5 ± 34.02 | 24.4 |
| Mendel 2119526           | 5                                                      | +634   | +515.2 ± 108.80 | 47.4 | +547.9 ± 109.31 | 44.7 |
| Duster 2147488           | 30                                                     | +579   | +632.6 ± 53.84 | 45.8 | +605.5 ± 30.84 | 27.5 |
| Blackstar 2114601        | 10                                                     | +545   | +511.6 ± 75.29 | 46.4 | +618.2 ± 36.24 | 18.5 |
| Aerostar 383622          | 5                                                      | +476   | +361.5 ± 77.11 | 47.8 | +401.4 ± 66.67 | 37.3 |
| Cartridge 2160458        | 15                                                     | +461   | +639.1 ± 42.27 | 25.0 | +652.3 ± 33.11 | 19.7 |
| Bell Elton 1912270       | 11                                                     | +417   | +521.6 ± 43.54 | 36.0 | +492.1 ± 52.16 | 44.1 |
| Prelude 392457           | 6                                                      | +361   | +353.8 ± 95.70 | 75.8 | +404.6 ± 57.60 | 40.5 |
| Aero Wade 2182318        | 6                                                      | +271   | +694.4 ± 68.49 | 24.1 | +610.0 ± 47.94 | 19.2 |
| By group                 | 159                                                    | +496.1 | +580.1 ± 14.28 | 31.5 | +650.9 ± 12.42 | 36.8 |
| breeding value of parents in the negative case |
| Radiator 390409          | 9                                                      | -147.4 | +698.4 ± 50.72 | 439.5 | +296.6 ± 51.50 | 52.1 |
| Rote 2040726             | 3                                                      | -17.2  | -65.8 ± 22.94 | 60.3 | +101.4 ± 95.70 | 162 |

The total number of bulls in which the level of heredity of the BV for milk yield corresponded to the sum of these indicators in the parents (intermediate type) was 39 heads, or 9.6%. I. P. Petrenko – the author of the theory of dynamics of genetic-population processes in the breed, population at the chromosomal level and determination of the structure of the gene pool of the breed by individual variability of additive genetic potential of activity in certain individuals points to such a share of animals (10.26%) inheritance of breeding value by milk yield [15]. According to the author’s information, chromosomes in gametes are combined by additive genetic potential of activity (AGPA) with different frequency of corresponding gametes in the population. Based on these data, we assume that the breeding value of bulls for milk yield father's daughters is inherited at the individual level of analysis of offspring (sons) not only by intermediate type, as is typical for population analysis, but also by intermediate-binomial, which provides the basis for selection in the breed. With this type of inheritance in the offspring is formed a certain proportion of individuals whose genotype is higher than the breeding value of their parents.

The breeding value, which was formed by the intermediate form of inheritance adopted in selection, deviates from the absolutely intermediate inheritance in both positive and negative directions.
by +10 +128 and -8 -211 kg, or by 1.6–21% (0.1–1.0σ), which is doubtful to refer to the intermediate form of inheritance.

The relative variability of breeding value by milking along the line "father – son" and "mother – son" depends on the form of its inheritance. The coefficient of phenotypic correlation between the breeding value of parents and sons in the intermediate form of inheritance is +0.524–+0.560 and increases with parental dominance to +0.907 ± 0.040 and +0.985 ± 0.006, and overdominance to +0.887 ± 0.044 and +0.905 ± 0.033, at high statistical probability (Table 3).

Thus, the analysis of the obtained data confirms the opinion of some scientists that even in highly consolidated herds on quantitative features of milk productivity, in intra-breeding, selection progress in the breed is provided by combining the phenotypic manifestation of additive (intermediate inheritance, dominance of one parent) and non-additive (super-dominance) forms of inheritance. The frequency of manifestation of these forms of inheritance is determined by the number and quality of chromosome pairs in the karyotype of animals on a purely probable basis of their manifestation in the population [15]. In our studies, inheritance by non-additive form (over-dominance of parents) is more effectively associated with an increase in breeding value by milk yield their sons $F +29$ kg (3.4%) and $M +25$ kg (2.7%) than inheritance by additive form parental dominance. Therefore, the bull with the inheritance of quantitative signs in the form of over-dominance of parents is the basis of genetic progress in the breed.

**Conclusions.** 1. Under conditions of intra-breed breeding of highly consolidated breeds in terms of milk productivity, inheritance of breeding value in bulls on quantitative signs of milk productivity is carried out by a combination of additive (intermediate inheritance and parental dominance) and non-additive (over-dominance) form of inheritance, which is most associated with milk yield and is found in 13.5% of bulls-improvers.

2. Among bulls-improvers, whose breeding value was inherited by intermediate type, the half-sum of the breeding value of their parents was equal to only 9.6% of the heads, in other bulls its value deviated from the half-sum of the parent’s BV as in positive by +10 +128 kg, so in the negative (-8 – -211 kg), or 1.6–21.0% side.

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