Gene pools

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CHANGES OF VECTORS OF SELECTION FOR PIGLET'S NEWBORN WEIGHT DURING POPULATION FORMATION IN NEW ENVIRONMENT CONDITIONS

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Abstract

Studying changes of gene pools of populations of the domestic animals caused by selection and reflecting micro evolutionary processes, represents both practical and theoretical interest. As a rule, in such works the qualitative traits controlled by the principle «one genotype — one phenotype» are used that significantly simplifies the analysis. We investigated dynamic processes in Landrace population of domestic pigs (*Sus scrofa domestica*), having estimated a variation of one of continuous quantitative traits, the newborn piglet weight, for which similar relationship is not unambiguous. Statistical analysis of the zootechnical register data was carried out on more than 26 thousand pigs that were born within 23 years at an experimental farm (Novosibirsk Province), being the regional authorized Landrace breed nucleus. Ancestors of the formed population were delivered from Latvia in the early 1960s. They were the elite young animals estimated on a standard complex of selection traits. The entire period of existence of population the formation of its breeding nuclear was carried out on a complex of traits according to existing Instruction for estimation of breeding value of pigs. As the Instruction didn't contain standards on a large newborn weight, the selection on the specified trait wasn't made. The changes of statistical parameters of the newborn weight in piglets were estimated for each year of the observation, because the analyzed livestock was not a model laboratory population, but a typical breeding commercial herd in which continuous variability of a trait is interfaced to continuous «sliding» alternations of generations and the variability of age structure. During long-time analysis of the dynamics of this unselected trait, the directional (moving) selection on genotypes for the loci controlling growth rate of pigs in ontogenesis (in pre- and post-natal periods) is revealed. In the populations where such selection works, the newborn weight of piglets can be used for forecasting pig weight during the postnatal period. Application of «parent—descendant» regression on the newborn weight allowed to estimate the duration of a population gene pool adaptation to new environment. It appeared that process of adaptation lasted nearly two decades that made five full changes of the generations. In the same population at the same time the stabilizing selection optimized an individual animal weight at birth, cutting both minimum and maximum values. The described mechanism includes cyclic vector changes towards driving selection against the stabilizing selection vectors and thus maintains the population polymorphism on loci which control pre-natal growth and large weight in the newborns. An observed unevenness of wavy change of these cycles should be also noted.

Keywords: pigs, *Sus scrofa domestica*, Landrace, population, adaptation, piglet's newborn weight, regression, the vector of selection, directional (moving) selection, stabilizing selection, microevolution processes.

Changes in gene pools of population caused by selection or occurred due to a random gene drift are constantly attracting attention of the researchers (1-3), and in many works the domestic pigs were studied in this connection (4-12). However, the qualitative traits are mostly estimated as more simple because of a strong concordance of each specific genotype to a single phenotype according to the «one genotype—one phenotype» principle. For long time of our studying variations of qualitative traits the results of both practical and theoretical interest have been obtained (13-17). Importantly, once the quantitative trait changes were first statistically analyzed, a number of genetic determinations peculiar spe-

cifically to domestic animals were found out (18). Besides, the traits used in pig breeding were shown to reflect trends related to artificial selection rather than to natural. So we tried to find the trait convenient for estimation of the natural selection vectors. The number of nipples was first used, but it was good to indicate random factors affecting quantitative traits (19) and poor reflected the intrapopulation changes because of discreteness and a narrow variation range (18, 19). A newborn piglet weight was next tested. This is a continual quantitative trait with indefinite relationship of a genotype to the phenotype, meaning the same phenotype appeared in different genotypes and multiple trait values are observed in the same genotype (20). As far as a piglet weight at birth is a perinatal growth trait its variation in heterozygotes contains the ranges of variations in homozygotes on each allele (21). Reasonably, a piglet birth weight, being a continuous quantitative trait with rather wide variation range and known genetic control, was used as a quantitative trait (22-26).

In this research our goal was to find out whether a piglets' weight at birth is influenced by artificial or by natural selection whereas the population of domestic pigs are being newly formed due to adaptation to unusual environmental conditions.

Technique. Landrace domestic pigs (*Sus scrofa domesticus*) born from 1964 to 1965 and from 1967 to 1986 at an experimental farm (Novosibirsk Province) were analyzed. Ancestors of the formed population were delivered from Latvia in the early 1960s. They were the elite young animals with an estimated standard complex of selection traits (27). During the observation the rearing technologies and feeding were as described (28, 29). Twice a day the animals were fed with standard SK compound feeds (Russia) according to the recommended rations (30).

The entire period of existence of the population the breeding for a complex of traits was carried out according to the Instruction for estimation of pigs' breeding value which didn't contain standards of a large animal weight (9) or a newborn weight. At a breed herd formation the piglets were twice selected, particularly in 2 month of age when weaned and in 5 months of age when a remount group of 25 % of breed nucleus was formed.

To evaluate the trait dynamics, the statistical parameters were annually compared. An average piglets' birth weight in each year was compared to those of their parents, exactly 21461 piglets from 312 paternal boars and 1181 sows were estimated. Additionally, to evaluate the upper limit of the trait values a total of 26086 newborn piglets from 2587 litters were weighed.

The data were processed by common statistical methods (31).

Results. The experimental piggery was the regional authorized Landrace breed nucleus. In the population adapted to Siberian environment no targeted selection for an above standard animal weight was used. In created population its value was increasing for 23 years, mostly in the parent animals from the reproductive herd nucleus and in much less extent in their offspring.

A year was the least period for comparison since the analyzed livestock was not a model laboratory population, but a typical breeding commercial herd. In such a herd the reproductive nucleus consists of animals of different ages and is constantly renewing due to some new boars and sows included while the others discarded because of age or other reasons. Thus, a change of generations in the herd is a continuous process extended in time. At that an annual variability of the trait is linked to a continued change of generations and the age structure of breeding stock. As the latter was almost the same among years, being subject only to random variations, a calendar year as a time unit was reasonably used in a

comparative study of the trait dynamics.

A birth (kg) variation in piglets and their parents in a Landras pig population during long adaptation to unusual environmental conditions (experimental farm, Novosibirsk Province)

Year	Descendants		Boars		Sows		Regression coefficient (b_{xy})	
	<i>n</i>	$M \pm m$	<i>n</i>	$M \pm m$	<i>n</i>	$M \pm m$	boar— descendant	saw— descendant
1964	524	0.98±0.007	9 ^p	1.40±0.116	40 ^p	1.24±0.040	-0.006	0.091
1965	405	1.14±0.012	14	1.08±0.074	31	1.13±0.032	-0.140	-0.403
1967	262	1.16±0.013	10	1.19±0.038	28	1.15±0.041	-0.670	-0.163
1968	355	1.20±0.007	6	1.18±0.048	30	1.14±0.046	-0.111	-0.123
1969	592	1.29±0.019	10	1.38±0.092	56	1.36±0.046	0.212	0.098
1970	1027	1.26±0.004	22	1.48±0.063	100	1.35±0.030	-0.007	0.032
1971	1116	1.38±0.009	17	1.37±0.051	94	1.45±0.032	-0.189	0.231
1972	1506	1.47±0.007	24	1.38±0.074	106	1.46±0.030	-0.063	0.034
1973	1652	1.33±0.012	14	1.39±0.075	122	1.46±0.025	-0.067	0.018
1974	1255	1.42±0.005	15	1.37±0.064	98	1.43±0.025	-0.030	0.037
1975	1066	1.35±0.009	15	1.39±0.070	73	1.44±0.025	-0.070	-0.042
1976	748	1.42±0.010	16	1.44±0.055	74	1.51±0.025	-0.056	0.029
1977	1329	1.18±0.008	22	1.56±0.056	92	1.49±0.017	0.038	0.024
1978	1451	1.28±0.007	26	1.18±0.076	109	1.24±0.026	0.052	-0.028
1979	1720	1.35±0.007	30	1.47±0.040	115	1.35±0.023	0.007	0.029
1980	1187	1.31±0.008	32	1.48±0.047	101	1.36±0.023	-0.045	-0.141
1981	1663	1.34±0.007	33	1.56±0.063	128	1.34±0.024	-0.009	0.085
1982	1114	1.34±0.010	29	1.51±0.039	79	1.44±0.033	0.224	-0.059
1983	724	1.45±0.012	24	1.59±0.062	67	1.47±0.037	0.046	0.134
1984	562	1.30±0.014	15	1.55±0.061	53	1.49±0.046	0.110	0.191
1985	853	1.24±0.010	23	1.55±0.058	74	1.47±0.034	0.203	0.171
1986	350	1.12±0.009	10	1.32±0.053	31	1.37±0.038	-0.150	-0.022
Total	21461	1.32±0.002	312	1.44±0.017	1181	1.38±0.008		
<i>r</i>	0.33; unreliable		0.61; P < 0.01		0.57; P < 0.01			

Comments. 1964, 1969, 1973, 1977, 1981 and 1985 are the years of complete change of the parental animals in the breed nucleus; p in upper index marks offspring of the animals delivered from Latvia; $M \pm m$ is an average value and the error; *r* is a correlation coefficient between year and the birth weight.

Fig. 1. Birth weight trends in Landras pig population and its reproductive nucleus during long adaptation to unusual environmental conditions: ♦ — descendant, □ — boars, ○ — sows (experimental farm, Novosibirsk Province).

In the basic experiment only piglets individually weighed as well as both their parents were considered (Table) that allow to indicate a correct trends in the trait changes regarding random variation and annual succession of the breed nucleus.

For the trait a positive trend was found reliable ($P < 0.01$) in parents and unreliable in the population as a whole, being probably observed due to expression in the parent animal groups (Fig. 1).

Thus, the animals from reproductive nucleus were selected for an increased birth weight while its influence on the population was insufficient. Herewith, the changes resulted from three factors, namely natural selection for the early postnatal viability, a positive correlation between the weights at birth and at weaning, as demonstrated by the curves (Fig. 2) constructed according to published data (29), and a standardizing selection for total weight specific to domestic animals (18). The first two factors significantly increased probability of more large animals inclusion into effective nucleus of the population. Providing both prenatal and postnatal growth is genetically controlled by the same loci, a standardizing selection for total weight could influence a newborn weight despite the fact that artificial selection for weigh at remount herd formation first occurred in 2 month

old animals, as thereat required (27).

Fig. 2. Viability of suckling piglets (1) and their weight at weaning in 8 weeks of age (2) as related to birth weight (consorted according to published data) (29).

weight increase, but to the high rate of prenatal and postnatal growth. Therefore, in the effective part of the population there are the individuals not just large at birth but also fast growing during postnatal period.

Fig. 3. Birth weight regression coefficient in Landras pig population during long adaptation to unusual environmental conditions: 1 — boar—descendant, 2 — sow—descendant, 3 — trend of boar on descendant regression coefficient, 4 — trend of sow on descendant regression coefficient (experimental farm, Novosibirsk Province).

The Landras pigs delivered from Baltic region to West Siberia for introduction had to adapt to unusual conditions. As a result, a gene pool has changed during formation of a new population. According to the analyzed trait, these changes were estimated by a linear regression trends for both boars' and sows' phenotypes on that of their offspring (see Table, Fig. 3).

On the curves the longest initial segments of the negative regression coefficient should be noted (see Fig. 3). Suggestible, under unusual feeding and housing conditions the piglets born larger were more viable during sucking period and also gaining greater weight by weaning (see Fig. 2) (29). As a result, the population was subjected to selection for the high rate of prenatal and postnatal growth. Obviously, initially in the population the analyzed phenotype was poor related to genotype. Therefore, in the offspring the birth weight did not exceed an average value in the population even if the parents were larger at birth, resulting in negative regression coefficients. Selection for high growth rate during ontogenesis gradually decreased indetermination of the relationship between genotype and phenotype to a positive parent—descendant regression level occurred 15 years after the adaptation started (see Fig. 3). It probably means that the animals

The observed trends on the birth weight in parental groups and reliable differences between the breeding males and females ($t_a = 3.06$, $P < 0.01$) resulted from the standardizing selection. More clear positive trend (see Fig. 1) and higher birth weight (see Table) in boars resulted from much more strong selection compared to sows. A summarizing vector of the discussed three factors obviously was directed not to the birth

Piglet's birth weight is polygenically controlled (20, 21) with an expressed indefinite relationship between genotype and phenotype, meaning not only effects of randomness but also probable adequate response to external impact. The influence of both these factors may be described by the regression of a parental phenotype on the descendant phenotype. Thus, the both ambiguities, i.e. for the genotype-phenotype relationships in a parent and its offspring, could be considered.

with relatively stable and locally adapted relationship of the genotype to phenotype exceeded in rate, if compared to those with unstable relationship.

Hereby, a selection for increased birth weight was really found in the studied population. Nevertheless, the weight of newborns remained relatively unchanged due to genetic and physiological mechanisms acting towards stabilization within the limits of sows' and offspring viability. In other words, birth weight can vary in different population as well as in the same population among the years (see Table) but within definite range, so that the selection for the trait can not be effective in the essence. The lowest values are obviously limited by the high death rate in small piglets. Optimization of the birth weight in the population should correlate with some other traits. Particularly in pig as a prolific animal there is a collision between birth weight of a piglet and the number of piglets in the litter resulting in negative correlation of these traits (32). Similar correlation was also observed in the population studied ($r = -0.82$; $P < 0.001$).

Fig. 4. Litter weight (A) and averages birth weight (B) depending on number of piglets in a litter in Landras pig population during long adaptation to unusual environmental conditions: 1 — actual distribution, 2 — trend line (experimental farm, Novosibirsk Province).

and horizontal segments corresponded to the numbers from 1 to 13 and from 14 to 19, respectively. For the first and second segments the correlation coefficients between size of the litter and weight of the litter at birth were $+0.995$ ($P < 0.001$) and $+0.039$ (unreliable), in the other words, the curve quite well described a relationship between the litter weight at birth and the number of piglets per litter (see Fig. 4, A). The litter weight at birth is related both to the number of piglets per litter and the piglet's weight at birth, in turn, both being physiologically limited by the maternal physiological capabilities. As a result, a negative correlation occurs between fetus number and weight. Thus the second curve of relationship between birth weight and number of piglets in the litter should obviously be

A probable factor limiting birth weight is a total offspring weight. Abstractly, a curve of its dependence on piglets' number must contain two segments, of which the first tended to a population maximum, looking as an upward sloping line, and the second fluctuated around the horizontal line somewhat below the maximum level. The piglets with no data on their parents' weight, a total of 26086 newborns including those stillborn from 2587 litters, were additionally analyzed to verify this suggestion. The highest weight in the sample was 28.8 kg (Fig. 4, A). We compared a reliability of approximation R^2 (Microsoft Excel) for the most frequent numbers of piglets in the litter to find the end of the first segment. In case of 12, 13 and 14 piglets R^2 was 0.9880, 0.9905 and 0.9823, respectively. So the ascending

similar in character but reversed, so that the horizontal segment was followed by inclined line (see Fig. 4, B). Correlation coefficients (r) between the number and an average birth weight of piglets in the litter were -0.467 (unreliable) and -0.856 ($P < 0.05$) for two segments, respectively, being in line with our suggestion. Consequently, it can be asserted that the vector reducing birth weight is a factor of stabilizing natural selection towards optimization of the correlation between piglet weight and number.

Fig. 5. Changes in birth weight in Landras pig population during 23 year adaptation to unusual environmental conditions: 1 — actual, 2 — trend line (experimental farm, Novosibirsk Province).

provides higher viability of sucking piglets should be resumed and continued until the piglet number fall. Then the next cycle should begin, and so it goes on all time during the population existence. Because of a collision between selection for higher birth weight and its upper limitation, the curve should show wavy fluctuations around optimum value for rather long time that exactly was observed in the studied population (Fig. 5). During 23 years there were two waves, when an average birth weight increased from 1.01 to 1.46 in 1964 to 1972, then decreased to 1.18 kg in 1977, and again increased to 1.45 kg in 1983 and dropped to 1.13 kg in 1986. Generally, the birth weight as a quantitative trait seems to be influenced by the limitations resulting in elimination of the largest individuals (see Fig. 4) rather than by selection towards higher weight parameters, probable due to some other factors reducing piglet's weight at birth to an optimal value.

It should be noted that at long-term adaptation the classical population research based on annual dynamics estimation (33) is more effective compared to constructing series based on the limited data (see Table) for the years of complete change of generations in the reproductive herd nucleus. In fact, exactly classical approach is appropriate to studying real but not model populations. Our findings contribute to current knowledge about genetic and breeding aspects of newborn's weight in pigs (20, 34).

Thus, in Landras pig population formed in the course of adaptation to unusual conditions the directional (moving) selection for the loci controlling growth rate of pigs in ontogenesis, i.e. in prenatal and postnatal periods, is revealed. In the populations where such selection works, the newborn weight of piglets can be used for forecasting pig weight during the postnatal period. A regression of parent—descendant birth weight in the population allows to estimate the time of gene pool adaptation to new environment. Adaptation in the studied population took nearly two decades that made five full changes of generations, and there were two key events observed. First, a predominance of the individuals with reduced ambiguity in genotype—phenotype relationship has been reached

As far as the litter size negatively correlates with birth weight per piglet, and standardizing selection for higher litter size as an important economic trait is constantly occurring in the commercial pig populations, its intensification presumably intensifies the natural selection for lower weight of the newborns. After fixation of the alleles encoding optimal number of piglets in the population the selection for an increased birth weight which

after 15-year adaptation, and secondly, optimization admittedly considered the final adaptation of the population has been achieved 5 years later. In the same population at the same time the stabilizing selection optimizes an individual animal weight at birth, cutting both minimum and maximum values. The described cyclic changes of driving and stabilizing selection vectors seem to provide the population polymorphism on loci which control prenatal growth and large weight in the newborns. An observed unevenness of wavy changes in these cycles should also be noted.

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