

Translated from Doklady Akademii Nauk SSSR, Vol. 248, No. 1, pp. 230-234, Sept., 1979.

UDC 57.4

Genetics

Geodakian V.A.

EXISTENCE OF THE "PATERNAL EFFECT" IN THE INHERITANCE OF EVOLVING CHARACTERS

N.K. Kolt'sov Institute of Developmental Biology, Academy of Sciences of the USSR,
Moscow. (Presented by Academician D.K. Belyaev, March 5, 1979.)

Dioecious reproduction includes two fundamental phenomena: crossing (fusion of genetic information of two parents) and differentiation of sexes (separation into males and females). The classical genetics considers the differentiation products, which are delivered chiefly to the population level as a consequence of specialization of sexes. Therefore, the phenomena associated with differentiation, with the type of reproduction (hermaphroditism, dioecism), with the scheme of crossing or the structure of the population (mono- or polygamy, panmixia, etc.) find no treatment within the framework of classical genetics. It is suggested that certain premises of classical genetics need substantial supplementation and development in this sense.

In 1965 we proposed a new concept, treating dioecism as specialization at the population level according to two main alternative aspects of evolution: conservation and variation [1]. Such an interpretation followed from the more general cybernetic idea, formulated later [2]. The idea is that the subdividing of any adaptive system of automatic regulation, evolving in a variable environment, into two coupled subsystems, one of which is specialized for conservative and the other for operative tendencies of evolution, increases the stability of the system as a whole. Such an approach proved extremely fruitful and subsequently allowed to find a number of new principles, relating the evolutionary characters of the population and the environment [3-6].

The central premise of the new theory is the conclusion of greater phenotypic diversity of males compared to females. The greater diversity implies that the first victims of any extreme environmental conditions are males (obtaining of ecological information). At the same time, the number of progeny that a male can leave in a panmictic or polygamous population is incomparably greater than the number of progeny a female can leave (transmission of ecological information to progeny). This means that ecological information on changes that have occurred in the environment is received and transmitted to the progeny by males more effectively than by females. On the other hand, in a panmictic population the participation of different males in reproduction is unequal: some leave no progeny at all; others leave many, whereas the participation of females is more

uniform: they almost all leave progeny, but a small number each. This means that the picture of genotypic distribution in the population is more representative, more fully rendered by females. Consequently, the flow of hereditary information (from many previous generations) is realized more effectively by females, and the flow of ecological information (from the environment) is realized more effectively by males.

The greater phenotypic dispersion of males may, in the first place, be a consequence of the higher level of mutations in males. In the second place, it may be a consequence of the fact that female progeny inherit parental characters more additive than males [7]. Finally, it may be a consequence of the broader reaction norm of females [5].

The broad reaction norm makes females more adaptive and plastic in ontogenesis, which imparts greater stability of female phenotype in phylogenesis. On the contrary, the narrow reaction norm of males makes them less plastic in ontogenesis, subjects it to greater elimination, and as a result of this, makes the male phenotype more plastic in phylogenesis. This implies that evolutionary transformations affect primarily the males. This means that males can be considered as an evolutionary “vanguard” of the population, while sexual dimorphism with respect to a character can be considered as a vector showing the direction of the evolution of this character. It is directed from the norm (mode) of females in the population with respect to the given character to the norm of males. Perhaps the characters that more often appear in females should be of an “atavistic” nature, while those appearing in the males should be of a “futuristic” (exploratory) nature [3, 4]. Sexual dimorphism, just like all the other basic characters of a dioecious population – dispersion and sex ratio – depends on the conditions of the environment and determines the evolutionary plasticity of a species. Under extreme conditions, when high evolutionary plasticity of the population is required, sexual dimorphism becomes more distinct [6]. Consequently, in the ranges of species, sexual dimorphism should be more pronounced at the boundaries of the range and less pronounced at its center. The hypothesis of “sexual dimorphism” has been successfully tested on a large group (173 species) of lower crustaceans [3], as well as on extensive material (31,000 verified diagnoses) on the distribution of congenital defects of the heart and large vessels in males and females [4].

It should be noted that up to now sexual dimorphism has been considered only as a mutual adaptation of the sexes, which sometimes is significant for sexual selection, but it has never been associated with evolution of characters, i.e., sexual dimorphism has not carried any evolutionary meaning. Such a treatment could not explain many phenomena: for example, the existence of sexual dimorphism in plants, in which sexual preference and selection are excluded, and, on the contrary, the absence of appreciable sexual dimorphism in monogamous animals, in which sexual dimorphism (such as bright plumage or large size) could unquestionably give certain advantages in sexual selection (at least in the case of a shortage of females), or the presence of reciprocal effects in the

homogametic sex, etc.

The proposed treatment permits the detection of the evolutionary significance of sexual dimorphism. The genetic information that has already entered the male subsystem as a result of specialization of the sexes at the population level, but has not yet entered the female subsystem, is manifested as sexual dimorphism. Consequently, sexual dimorphism is associated primarily with the structure of the population: in strict monogamy it should be minimal, since monogamists use specialization of the sexes only at the level of the organism, and do not use it at the population level. Furthermore, as we have seen, sexual dimorphism is closely associated with the evolution of characters: it is minimal for invariant (stable) characters and is maximal for appearing, disappearing, or variable characters. This means that it might be expected that sexual dimorphism should have been more pronounced for phylogenetically recent (evolving) characters. Consequently, although in respect to the "old" characters, the genetic contribution of the father to the progeny is less than the contribution of the mother on account of the "maternal effect," due to cytoplasm inheritance and uterine development, in respect to the "new" characters the contribution of the father should increase somewhat. This may lead to compensation of the "maternal effect" or even to the appearance of a "paternal effect." In other words, in the case of transmission of genetic information with respect to "new" characters, there should be some dominance of the paternal characters over the maternal characters. Hence, considering the phenomenon of heterosis as a summation of the evolutionary achievements acquired divergently, it might be expected that the contribution of the father to heterosis should also exceed the contribution of the mother. The possibility emerges for a more complete explanation of the reciprocal effects, which are essentially nothing other than the sum of the "maternal" and "paternal" effects. We can also explain the different correlation of the progeny of one sex or the other with the mother and father. The predictions of the theory are easy to verify. For this it is necessary to select clearly "new" characters and to compare their inheritability among reciprocal hybrids in the crossing of different forms.

What characters can be considered as "new" characters or as characters "on the evolutionary path"? In agricultural animals and plants, evidently all the economically valuable characters, for which they were artificially selected in the requisite direction, are such characteristics. In animals such characters are: early maturity, productivity of meat, milk, eggs, wool, etc. Consequently, it might be expected that for all economically valuable characters there should be a "paternal effect"—some dominance of characters of the paternal line over that of the maternal line.

Such are the conclusions that can be drawn from the theory. Now let us turn to the observable facts.

Table 1 presents the results obtained by different authors on the inheritance of "new"

characters in chickens, pigs, and cattle.

In connection with the industrial (incubator) separation and selection on egg laying capacity, the white leghorn breed practically entirely lost its brooding instinct and acquired a greater early ripening and egg laying capacity with a lower live weight. In other breeds the brooding instinct is present. As can be seen from Table 1, for all the investigated characters, reciprocal hybrids “diverge” from one another toward the paternal breeds, i.e., there is a distinct paternal effect.

There have been attempts to explain the greater influence of the father on the egg laying capacity of the daughters by the fact that in birds the chickens of heterogametic sex are female, while the chickens of homogametic sex are male [9]. In maintaining such logic, it should be expected that in mammals everything should be vice versa, since the males are heterogametic in them, i.e., a greater influence of the mother than of the father should be observed, regardless of whether the “old” or the “new” character is being inherited, whereas according to our theory, regardless of the gametic content of the sexes, in all cases there should be a “paternal effect” with respect to the evolving (selected) characters.

We studied the inheritance of the number of vertebrae and certain characters of the digestive system in two contrasting breeds of pigs – the Swedish Landras and the large white [14, 15]. The Swedish Landras is a meat and bacon breed. In half a century of selection of this breed, the body size has been appreciably enlarged, and the effectiveness of the utilization of feed has been increased. The large white is a general meat-tallow breed.

Table 1 Inheritance of New Characters by the Reciprocal Hybrids.

Trait	Initial breeds		Direct cross		Back cross		Initial breeds		r	Author
	father - mother	inheri- tance of	father - mother	inheri- tance of	father - mother	inheri- tance of	father - mother	inheritanc e of the		
C h i c k e n s										
Brooding instinct, %	L - l	~0	L - c	37	C - l	88	C - c	~100	0.45	Roberts, Card,
	L - l	~0	L - a	17	A - l	55	A - a	~100	0.38	Morley, Smith,
	L - l	~0	L - n	37	N - l	85	N - n	~100	0.50	Saeki e.a., 1956
Early maturity of daughters, days	L _e - l _e	—	L - a	181	A - l	191	A ₁ - a ₁	—		Morley, Smith,
	L _e - l _e	—	L - n	189.5	N - l	231.4	N ₁ - n ₁	—		Saeki e.a., 1956
	R _e - r _e	222.7	R _e - r ₁	217.9	R ₁ - r _e	244.8	R ₁ - r ₁	269.0	0.59	Warren, 1934
Egg laying,	L - l	185	L - r	258	R - l	233	R - r	163	1.14	Dubinina, 1967
	L - l	167.6	L - m	202.1	M - l	160.1	M - m	152.1	2.71	Dobrinina, 1958
Weight at 12	M - m	2433	M - l	2277	L - m	2085	L - l	1805	0.30	Dobrinina, 1958
P i g s										
No. of vertebrae	S - s	28.35	S - w	28.11	W - s	27.26	W - w	27.18	0.72	Aslanian, 1962
	S - s	28.93	S - w	28.86	W - s	27.97	W - w	27.74	0.74	Aleksandrov,
C a t t l										
Milk yield per year, kg	H - h	6417	H - j	5808	J - h	5588	J - j	3582	0.0	Dubinina, 1967
	H - h	6417	H - k	6725	K - h	6352	K - k	5481	0.39	
	K - k	5481	K - j	5659	J - k	5223	J - j	3582	0.23	
Amt. of fat per year, kg	H - h	224.6	H - j	282.6	J - h	254.6	J - j	198.8	1.08	Dubinina, 1967
	H - h	224.6	H - k	264.4	K - h	249.0	K - k	216.0	1.79	
	K - k	216.0	K - j	271.3	J - k	265.4	J - j	198.8	0.34	

ORIGINAL ARTICLES

Note. Breeds of chickens: **L**—Leghorn; **C**—Cornish; **A**—Australorp; **N**—Nagoya; **M**—Moskovskaya; **R**—Rhode Island; **W**—New Hampshire; **P**—Plimutrock; **L_e**, **R_e**—early maturing; **A_l**, **N_l**, **R_l**—late maturing. Breeds of pigs: **S**—Swedish Landras, **W**—large white. Breeds of cattle: **H**—Holstein; **J**—Jersey; **K**—red Datch. The father is denoted by a capital letter, the mother by a small letter. Breeds and hybrids with a more significant useful character are printed in bold-faced type. A dash means no data are cited.

Table 1 presents data on the inheritance of the number of vertebrae in baby rats, determined according to X-ray photographs. As can be seen from the table, in inheritance of the number of vertebrae among reciprocal hybrids of pigs, a distinct “paternal effect” can also be noted. The inheritance of various characters of the digestive system reveals a “paternal effect” only with respect to the average length of the small intestine and esophagus, against a background of a maternal effect for other characteristics (for average weight of the embryos, digestive system and various parts of it, along the length of the large intestine). The “paternal effect” is also observed according to the dynamics of the growth of reciprocal hybrids. Thus, the “paternal effect” is due precisely to the characters for which the Landrases were selected: to the number of vertebrae (selection for a long body), to the length of the small intestine (selection for the best return on feed), and to dynamics of growth (selection for early maturity); it should be noted that the effect is “maternal” for the weight of newborn piglets. Table 1 also presents data on the production of milk and butter fat in three breeds of cattle and their reciprocal hybrids [12]. As can be seen, in cows, as well as in chickens and pigs, for such economically valuable (and, consequently, “new”) characters as milk yield and butterfat production, the “paternal effect” predicted by the theory is observed.

It is surprising that the characters exhibited only by females (brooding instinct, early maturation and egg laying in hens, or milk yield and amount of butterfat in cows), which, it might seem, should have been transmitted by the mother, nonetheless are more transmitted by the father.

The pattern revealed casts light on the nature of heretofore uncomprehended reciprocal differences and permits the use of the vector of the “paternal effect” as a “compass,” showing the direction of evolution of a character. Moreover, in contrast to sexual dimorphism, the “paternal effect” permits a judgment of the evolution of all characters, including those that are manifested in only one sex, including primary and secondary sex characters. It becomes understandable why heterosis in agricultural animals and plants is always directed toward an increase in characters useful for man. In addition to its theoretical significance, this pattern is also of practical importance, since it permits a qualitative prediction of the results of hybridization and a correct selection of parental pairs in crosses.

Original article submitted March 19, 1979.

Literature:

1. V.A. Geodakian, *Probl. Peredachi Inf.*, 1, No. 1, 105 (1965).
2. V.A. Geodakian, *Problems of Cybernetics* [in Russian], No. 25, Nauka, Moscow (1972), p. 81.
3. V.A. Geodakian and N.N. Smirnov, *Problems of Evolution* [in Russian], Vol. 1, Nauka, Novosibirsk (1968), p. 30.
4. V.A. Geodakian and A.L. Sherman, *Zh. Obsh. Biol.*, 32, No. 4, 417 (1971).

ORIGINAL ARTICLES

5. V.A. Geodakian, Zh. Obsh. Biol., 35, No. 3, 376 (1974).
6. V.A. Geodakian, Zh. Obsh. Biol., 39, No. 5, 743 (1978).
7. L. Shyuler, P.M. Borodin, and D.K. Belyaev, Genetika, 12, 72 (1976).
8. E. Roberts and L. Card, V World Poultry Congr., 2, 353 (1933).
9. F. Morley and J. Smith; Agric. Gaz. N. S. Wales, 65, No. 1, 17 (1954).
10. J. Saeki, K. Kondo, et al., Jpn. J. Breed., 6, No. 1, 65 (1956).
11. D. Warren, Genetics, 19, 600 (1934).
12. N.P. Dubinin and Ya.L. Glembotskii, Population Genetics and Selection [in Russian], Nauka, Moscow (1967).
13. A.Ya. Dobrynina, Transactions of the Institute of Genetics, Academy of Sciences of USSR [in Russian], No. 24 (1958).
14. M.M. Aslanyan, Nauchn. Dokl. Vyssh. Shkoly, No. 4, 179 (1962).
15. B.V. Aleksandrov, Genetika, 2, No. 7, 52 (1966).