EMBRYONIC MORTALITY IN FOXES WITH DIFFERENT GENOTYPES UNDER THE INFLUENCE OF PHOTOPERIODIC CONDITIONS

La mortalité embryonnaire chez les renards avec différents genotypes sous l'influence des conditions de photoperiodicité

La mortalidad embrionaria del zorro con diferentes genotipos bajo la influencia de las condiciones de fotoperiodicidad

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Silver foxes are farm-bred for more than seventy years. At present, several coat-colour variations are observed among populations of silver foxes: platinum, white face with lighter colour and distinctive piebald pattern and Georgian white, characterized by white coat and blac spots on the body, feet and face, a mutation which has first appeared in a farm of the Georgian Republic (USSR) in 1943.

It has been shown that coat-colour in platinum and white face foxes is under the control of dominant mutations which form an allelic series. The viability of individuals heterozygous for these mutations conforms to normal viability and homozygotes die at days 30-33 of embryonic development (L. COLE, R. SHACKELFORD, 1943; I. JOHNSSON, 1947; K. KOLSTAD, 1954). Basing on fragmentary genetical evidence, there was some reason to suggest that Georgian white coat colour is controlled by a single dominant gene and that homozygotes die at the embryonic period. This explain why the ratio of mutant offsprings to standard silver offsprings was 2:1 in all the so far reported crosses between Georgian white foxes. Thus, of 76 pups, 43 had Georgian white and 24 had solver coat-colour.

It is known that embryonic development is influenced by the activity of *corpora lutea* and by its product of progesterone (B. FRANKLIN, 1958; H. C. BYCMAH, 1960). It has also been established that the functional activity of *corpora lutea*, in turn, is under the control of photoperiodic conditions. Taking this into consideration, the investigation of the influence of different conditions of illumination on the embryonic survival of foxes belonging to different genetic classes appeared to be a well-grounded interesting problem.

The results of 16 crosses between Georgian white foxes are presented in Table 1. As the table shows, 6 females, along with typical (heterozygous) pups and standard

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TABLE 1

SEGREGATION RATIOS OF OFFSPRING IN CONTROL GEORGIAN WHITE ♀ × GEORGIAN WHITE ♂

Groups of females	No. females	Total No. pups	Homozygotes	Heterozygotes	Silver-black	Average No. *corpora lutea*
Females without homozygous pups in litters.	10	54	—	33	21	7.1
Females woth homozygous pups in litters ...	6	33	9	18	6	8.2
TOTAL	16	87	9	51	27	7.6

silver pups, had also white pups, with small coloured spots only on the feet and ears, which have never been described before (Fig. 1). The segregation pattern in these litters indicates that these pups are homozygotes. That they are homozygotes is also supported by the fact that they all died before the age of two months. The ofter 10 Georgian females mated to the same males gave no white pups.

Thus, our data evidence that the Georgian white mutation does possesses

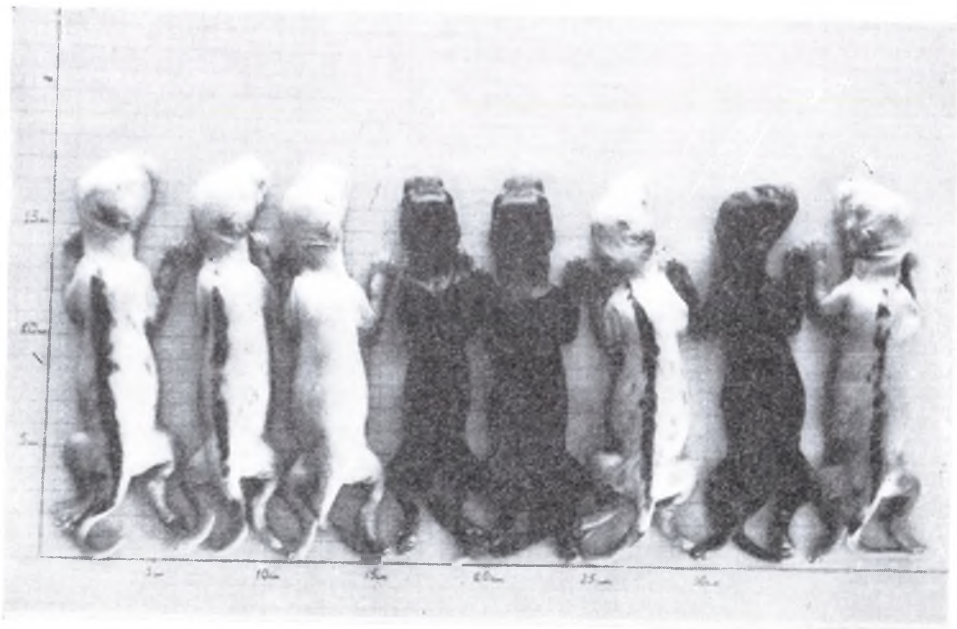

FIG. 1. Segregation pattern in offspring form from Georgian white female mated to Georgian white male and maintained under natural photoperiodic conditions during pregnancy (sacrificed on day 48 of pregnancy).

TABLE 2

SEGREGATION RATIOS OF OFFSPRINGS AND AVERAGE LITTER SIZE AT BIRTH IN GEORGIAN WHITE, WHITE-FACE AND PLATINUM FOXES MAINTAINED UNDER ADDITIONAL ILLUMINATION DURING PREGNANCY

Crosses	No. crosses	Total No. born	Homozygotes white	Heterozygotes	Silver-black	Average litter size at birth	Average No. *corpora lutea*
Georgian white×Georgian white homozygous offspring	15	93	29	39	25	6.2	6.6
Georgian white×Georgian white (no homozygous offspring) ..	3	11	—	6	5	3.7	6.5
Total Georgian white×Georgian white	18	104	29	45	30	5.7	—
White-face×White-face...	9	37	—	23	14	4.1	—
Platinum×Platinum...	16	62	—	44	18	3.9	6.25

a recessive lethal effect. Autopsy of pregnant females has shown that the mutation exerts its lethal effect prior to the preimplantation stage because not one of the females sacrificed on day 48 of pregnancy had a dead or underdeveloped embryo.

In order to study the effect of illumination conditions on the embryonic viability of individuals with different genetic constitution, we carried out an experiment in which mutant females were mated to mutant males and subsequently maintained through the whole period of pregnancy (March-April) under artificial illumination prolonging day-light by 5-6 hours.

Breeding data for the mutant females, which were exposed to additional illumination, are shown in Table II. 15 of the 18 Georgian white females, which were illuminated additionally, gave birth to white pups. Their total number is 29. Offspring ratio in these females is close to 1:2:1. However, most white pups had low viability. Only one reached the age of sexual maturity. In backcrosses with silver males during two mating seasons she gave birth to eleven pups typically heterozygous for the Georgian mutation. It was thus confirmed that this female and the other white pups with the same phenotype are homozygotes for the white Georgian gene.

From the data of Table II it is also evident that additional illumination in our experiments had no effect on the embryonic viability of homozygotes for white-face and platinum mutations. There was not a single pup with modified phenotype and the ratio of pups heterozygous for this mutation to standard silver pups was close to 2:1. The different influence exerted by light on the viability of homozygotes for platinum, whiteface and Georgian white mutations is tentatively explained by the different time of embryonic death of homozygotes for this mutation. We have shown that homozygotes for the Georgian white mutation die before the preimplantation stage. At this stage, embryo viability and the processes of implantation are under the strong influence of progesterone. The activity of *corpora lutea* producing this hormone depends on the light regime to which the pregnant female was exposed. On the contrary, homozygotes for the whiteface and platinum mutations die on about day 30 of pregnancy, when the

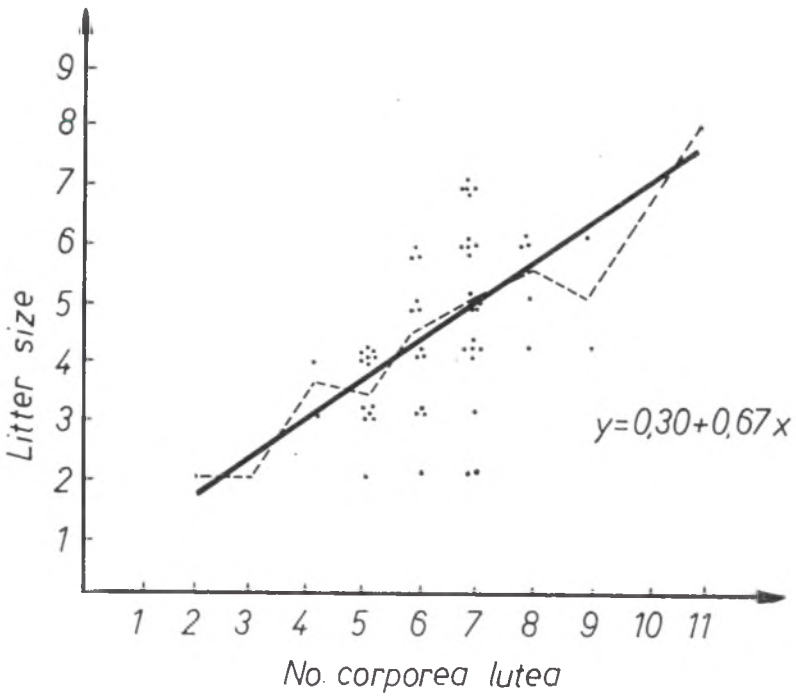

FIG. 2. Regression lines of actual fox fertility on potential fertility: empirical line and line abjusted by the method of least squares (solid).

activity of *corpora lutea* does not exert such a strong effect on the development of embryos.

Two questions arise when estimating the influence of light regime on the embryonic survival of homozygotes for the Georgian white mutation. The first question is why homozygotes are born to some females maintained under natural photoperiodic conditions during pregnancy. In the first years after the appearance of the Georgian white coat-colour breeders made many attempts to obtain homozygotes for this mutation, but they all failed. No doubt that actual fertility (litter size) all these years increased. It is reasonable to suggest that actual fertility in animals, in genetical, depends on potential fertility (number of *corpora lutea*) and the level of embryonic mortality. The studies we have carried out have shown that foxes are no exception in this respect. The level of embryonic mortality in females which have more than 4 pups in their litters, was much lower (17.9 %) than in females with 2-4 pups per pitter whose embryonic mortality attains 41.3 %.

The correlation coefficient between potential and actual fertility is $+ 0.60 \pm 0.08$ ($P = 0.999$) (Fig. 2). Quite obviously increase of potential fertility has led to the increase of the total functional activity of *corpora lutea* and presumably to higher probability of birth of homozygotes for the Georgian mutation in conditions of natural photoperiod.

It a should also be noted that the levels of embryonic mortality, which we

have estimated in Georgian white females under natural photoperiodic conditions and additional illumination, are almost the same (20-25 %), although the segregation pattern in these conditions differ: under natural photoperiodic conditions almost all the homozygotes die, whereas under additional allumination almost all homozygotes are born.

This difference in mortality indicates that embryos of different genotypes compete for survival as early as the stage of preimplantation. Illumination conditions probably modify these competitive relations. In conditions of natural photoperiod the majority of mutant homozygotes die, while under additional illumination heterozygous pups fail to survive (see Table II).

Thus, this work has shown that the influence of such an ecological factor as light on the survival of embryos with different genotypes may have broad genetical implications. It is known that many mutant forms are eliminated at the preimplantation stage. However, if they have some chances to survive in conditions of modified photoperiod, it may then be suggested that light can accelerate the processes underlying the emergence of new forms.

SUMMARY

The Georgian white mutation of coat colour in foxes (GWM) has a lethal effect manifested at the preimplantation stage of embronic development. It was found that additional illumination of pregnant females suppresses completely this effect. A homozygote for the GWM was produced for the first time which gave only heterozygous offsprings in backcrosses. Although no homozygote for the GWM died, actual fertility and embryonic mortality under additional illumination remained at levels observed under natural photoperiodic conditions. It is suggested that embryos with different genotypes compete as early as at the perimplantation stage.

RESUME

La mutation blanche de couleur de fourrure chez les renards georgiens (GWM) a un effet mortal manifeste au stage pré-implantation du développement embryonaire. On a découvert qu'une illumination additionnelle de femelles enceintes supprime completement cet effet. Un homozygote pour le GWM fut produit pour la première fois qui donna seulement des nouveaux nés heterozygotes dans des croisements précédents. Bien qu'aucun homozygote pour GWM mourut, la fertilité actuelle et mortalité embrionique sous illumination additionnelle demeurerent à des niveaux observés sous des conditions photoperiodiques naturelles. On suggère que des embryons de differents génotypes rivalisent dés le stage de pré-implantation.

RESUMEN

La mutación blanca georgiana en la capa de los zorros (GWM) tiene un manifiesto efecto letal en el período de preimplantación del desarrollo embrionario. Se descubrió que la iluminación adicional a hembras gestantes suprime por completo

este efecto. Se produjo por vez primera un homozigote para la GWM, que dio únicamente heterozigotes en retrocruzamientos. Aunque ningún homozigote para la GWM falleció, la fertilidad y la mortalidad embrionaria bajo iluminación adicional permanecieron al nivel observado en condiciones fotoperiódicas naturales. Se sugiere que embriones con diferentes genotipos compiten ya en el período de preimplantación.

LITERATURE

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