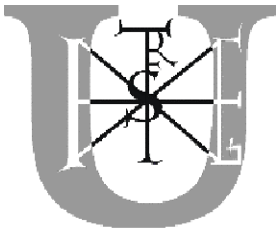

SZENT ISTVÁN UNIVERSITY

INVESTIGATION OF THE GENETIC BACKGROUND OF EARLY EMBRYONIC MORTALITY IN GOOSE

Ph.D. Thesis

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1. SCIENTIFIC BACKGROUND AND RESEACH OBJECTIVES

Goose is a poultry species with a relatively poor reproductive performance. Hatchability - being one of the most important traits in the poultry breeding - is about 60% of goose eggs compared to 80-90% in chicken. The hatchability is a very complex trait, because it is influenced by a lot of factors as genetical background, the inbreeding, the age of the pedigree birds, the qualitative parameters of the eggs (weight, form, shell-stability, contamination, etc.), climate, season, frequency of the egg-collection, the duration and circumstances of the egg storage, the hatching-technology, the feeding of stockers and their health (Bogenfürst 1992). The reproductiveness is very important in the goose. Its heritability value is low, h^2=0.1-0.2, even so during the selection it must not be eliminated. My experiments turned to the investigation of the early embryonic death among the countless factors, which influenced the hatchability. Namely, the examination of genetic background of embryonic death is reasonable when the breeding and hatching technological parameters are optimal.

Early embryonic death occurred on the first six days of incubation often due to genetic abnormalities, autosomal or sex linked recessive lethal genes and chromosome aberrations, originated from genetically predisposed abnormal meiosis, fertilization or early cleavage (Zartman and Smith 1975, Somes and Smyth 1967, Savage et al. 1988, Savage et al. 1992). The ability to produce chromosome abnormalities and embryonic anomalies is known to be inheritable in poultry (Zartman and Smith 1975, Telloni et al. 1976, Blazak and Fechheimer 1979) and they can accumulate in the population (Hidas et al. 1996, Liptói and Hidas 1998). Beaumont et al. (1997) have found that the heritability of the early embryonic mortality higher than mortalities occurred in the farther stages.

In the "pedigree" reproduction process of geese parents of each embryo are known and therefore ganders and layers producing abnormal embryos and/or chromosome abnormalities in higher proportion can be selected (Szalay 1989), as the ability to produce these anomalies is known to be inheritable in poultry (Zartman and Smith 1975, Telloni et al. 1976, Blazak and Fechheimer 1979). Parents selected for that trait generally have normal phenotype and karyotype.

The objective of this work was to determine the occurrence and variability of the early embryonic mortality and the chromosome abnormalities in the first five days of the incubation in three goose lines to select animals produced these trait in high proportion and to reveal the role of selected ganders and layers in the formation and inheritance of the types of abnormalities occurring. To enrich the phenotype categories of early embryonic mortality with more detailed types and to document them by photos.

The application of cytogenetic methods and embryonic studies is an important tool in determining the inheritance of embryonic and chromosome abnormalities in geese. Explanation of the genetic background of those abnormalities in a species having very limited data in this respect may be promising in the improvement of its reproduction traits.

2. MATERIAL AND METHODS

Three goose breeds were investigated in this study. Grey Landes (line 7), which were formed from several Landes lines and selected for reproduction and liver production. White Polish (line 4) meat type breed as well as the liver type line 9, which is a synthetic line of line 4 and line 7. The experiments were implemented in Artiguères (INRA - Station Expérimentale des Palmipèdes à Foie Gras, Benquet, France).

In the first experiment in line 4, five layers and one gander, in line 7 and 9, four layers and one gander were placed in each pedigree pen in open air and natural photoperiod, the reproduction being by natural mating. The eggs were collected by trapnest at the beginning (February), in the middle (April) and at the end (June) of the laying period and were recorded with line number, pen number and layer identity. Egg fertility was determined by candling at 5th day after egg set. Apparent clear eggs and eggs with abnormal embryos were opened and examined: 913, 822 and 1112 eggs from 95, 131 and 94 layers respectively in the lines 4, 7 and 9. The layers, which did not produce any fertile eggs, were excluded from the analysis. The numbers of studied layers were 70, 119 and 89 respectively in the lines 4, 7 and 9. Animals with high embryonic mortality (ratio of dead embryos to fertile eggs higher than 12%) were selected for mating in the following year to assess the repeatability and inheritance of the studied characteristics. These animals were presumed to be "carrier" in the following studies and marked with cP.

In the second experiment, matings were formed with selected individuals from line 7 supposed to be carrier parents (cP) of high EM (more than 12%) and with their progeny (F1). One male and four females were kept in each pen. Natural mating and trapnest were used throughout this study. Matings were performed as follows:

-original pairs (cPxcP),

-fathers with their daughters (cPxrF1)

-cP ganders with non-related one-year-old layers (cPxnrF1),

-F1 ganders with their sisters (F1xrF1)

-F1 ganders with non-related one-year-old layers (F1xnrF1). The F1 males were not related to each other.

In line 4, selected animals were mated on the same way like in the year before (cPxcP).

In the third experiment those ganders and layers were mated, which were studied in the previous two experiments independently they originated from line 4 or line 7. Eggs layed from the middle of February to May were studied. The objective was to examine whether ganders and layers equally contribute the high embryonic mortality ratio, as well as to test more ganders from carrier parents for repeatability of high embryonic mortality and low fertility. Avoiding the inbreeding the following matings were performed:

-carrier ganders and layers (cPxcP), with the same matings as in the previous years, so they originated from line 7 and they were in their 4^{th} laying period,

-carrier ganders with non-related, same aged non-carrier (nc) layers (cPxncP), where cP individuals originated from line 7 and were in their 4^{th} laying period, ncP individuals from line 4 and they were in their 3^{rd} laying period,

-carrier ganders with non-related, carrier layers from the offspring generation (cPxcF1), where cP individuals were in their 4^{th} laying period and cF1 individuals were in their 2^{nd} laying period, both from line 7,

-non-carrier ganders from parent generation with non-related carrier layers from the offspring generation (ncPxcF1), where ncP individuals were from line 4 in their 3^{rd} laying period, cF1 individuals from line 7 in their 2^{nd} laying period. Four layers and one gander were placed in each pen in open air and natural photoperiod.

Verifying or rejecting the hypothesis that progeny of carrier parents produce high ratio embryonic mortality with low fertility the following matings were performed using artificial insemination:

-Carrier ganders from offspring generation with carrier layers from parent generation (cF1xcP),

-carrier ganders and layers from offspring generation (cF1xcF1),

-carrier ganders from parent generation with carrier layers from offspring generation (cPxcF1).

The cP animals originated from line 4 and they were in their 3rd laying cycle, the cF1 individuals from line 4 in their 2nd laying period.

Males and females were kept in one air-space in 60x80 cm individual cages and in natural lighting. Three layers were inseminated per gander, except one gander, which was with four layers. Ganders were trained for semen collection during two weeks before the beginning of the experiments. Among the quality parameters of semen the motility, the quantity of the semen and the erection of the ganders were observed.

Verifying or rejecting the hypothesis that the reason of the high infertility of progeny of carrier ganders can be very early embryonic mortality (occurred in the oviductus) 9 ganders and 19 layers were tested using artificial insemination avoiding the inbreeding in the fourth experiment. Eggs were investigated from the middle of February to May. Four ganders were studied in the previous experiment with the same layers (cF1xcF1). Five ganders and nine layers originated from those parents from the third experiment, where the embryonic mortality was high (F2xF2). One, two or three layers were mated with every gander.

The early dead embryos as well as embryonic tissues were cut out and put into 0.9% NaCl solution for phenotypic classification using dissecting microscope (Olympus). The following categories were used according to Abbot and Yee, 1975 and Szalay, 1989:

- Positive development - (*pd*): The sheets of membranes consist of ectodermal and endodermal tissue only. Blood vessels are not developed.
- Blastoderm without embryo - (*bwe*): Ectodermal, endodermal and also mesodermal tissue can be observed. Blood islets are formed.
- Dead embryo - (*d1-5*): The embryos died at various stages of development during the 5-day incubation period.
- Abnormal embryo - (*ae*): Living embryos showing any malformations or retarded growth.

The very early embryonic death (occurred in the oviductus) was identified according to Eyal-Giladi and Kochav (1975) using dissecting microscope.

For cytogenetic studies, embryonic tissues were transferred into 0.56% KCl solution containing a few drops of 0.1% colchicine for mitotic arrest and they were incubated for 20 minutes in 37.5°C. Finally they were fixed with several changes of fixative (acetic acid: absolute ethanol - 1:3). Slides were prepared from fixed tissues suspended in 50% acetic acid. Karyotypes were analysed after 2.4% Giemsa staining. At least 10 metaphases were investigated on every slides using Zeiss microscope (1000x).

In the fifth experiment 132 unincubated eggs of Hungarian wild coloured and white ducks of the Institute of Small Animal Research (ISR) breeding stocks were used. After cracking the eggs, yolks were separated from the albumen and placed into 0.9% NaCl solution. Their fertility was assessed first by visual examination of the germinal disc. When germinal disc seemed to be infertile or uncertain fertile it was removed from the membrane vitellina, put into 0.9% NaCl solution, and stained on slide with 5 µl 0.005mg/ml propidium iodide (PI), which is a DNA specific, red colour fluorescent dye. 50 certain fertile eggs were stained also. If the egg is fertile, the propidium iodide stains the nucleus. When the egg is infertile, there is no nucleus, the staining shows dark-red background without lighting points.

To determine the presence of cell nuclei that is sign of fertility, fluorescence microscope was used (Leitz-Diaplan, magnification 500x). Then 160 incubated eggs of the intergeneric crossbred of Cairina moschata and Anas platyrhynchos were used. Eggs showing no normal embryonic development (infertile, dead) at candling on the 7^{th} day of incubation were cracked. Samples were compared with the categories of Eyal-Giladi and Kochav (1976). Germinal discs, which seemed to be infertile, were stained with PI.

3. RESULTS

The three lines differed greatly for the fertility rate and the embryonic mortality (EM) rate and not for chromosomal abnormality (CA) rate. The fertlility was the highest in line 7 (78.3%), the lowest in lines 4 (56.4%) and 9 (57.3%). The average incidence of EM was moderate. It was the greatest in line 4 (9.4%), the lowest in line 7 (5.2%) and intermediary for line 9 (7.3%). The detected incidence of CA was low, the mean values being 8.0%, 14.8% and 13.1%, respectively for line 4, 7 and 9. All the chromosomal abnormalities were numerical alterations: haploid, triploid and mosaic or chimeric haploid/diploid, diploid/triploid, diploid/polyploid karyotypes were identified. The diploid/polyploid mixed karyotype was the most frequent. In all the three lines some layers produced outstanding high EM. In line 4, 23.4% of all embryonic mortalities were produced by three layers. In line 7, two layers produced embryonic mortality over 30% (5 malformed embryos, which means 31.25% EM and 3 dead embryos, 37.5%). In line 9, two females showed outstanding EM of 37.5% and 38.46%. The BWE was the most frequent among the four phenotypes of embryonic mortalities in all three lines. Differences occurred mainly in the proportion of abnormal developed lived embryos (AE). The ratio of chromosomal abnormalities was the most frequent in the PD phenotype and almost the same in the BWE. The haploid karyotype was the most frequent in both cases (more than 10% and almost 6%). The triploid and the polyploid abnormalities were the most frequent in the AE phenotype.

In the second experiment 6 pairs selected from line 4 in the second laying period the high value of embryonic mortality (12.65%) occurred again but not the high value of chromosomal abnormalities. One-year-old individuals selected from line 7 originated from parents with high embryonic mortality showed low fertility and high EM mated non-related (F1xnrF1) and related (F1xrF1) ganders and layers. The presumed carrier parents and progeny produced again embryonic mortality over the population average. High EM was found at the mating of relatives too. The average of the chromosome abnormalities in 5 pair-types was 9.5%. Chromosome abnormalities occurred in some pairs of animals but the occurrence was not repeated. Repeatability coefficient of EM was 0.54 in line 7 calculated for 8 pairs of layers (average egg number per layer was 24 in the first year and 25 in the second) and it was 0.47 in line 4 calculated for 6 pairs (average egg number per layer was 17 in the first year and 21 in the second). The heritability value of embryonic mortality was 0.7 but this value was not significant.

In the third experiment the ratio of embryonic mortality was high (over 12%) in all pairs where presumed carrier animals were mated. In that case when non-carrier ganders were mated with carrier layers (ncPxcF1) the ratio of embryonic mortality was only 7.46%, which is significantly lower than in the other mating types, except the cPxcP type. In that pairs where the gander was presumable carrier but the layer was non-carrier (cPxncP) the EM did not differ significantly from those pairs where the layer was also presumable carrier (cPxcP, cF1xcP, cF1xcF1, cPxcF1). Using artificial insemination the pairs from presumed carrier individuals originated from carrier parents (cF1xcF1) showed significantly different EM from the other matings, except pairs from carrier ganders originated from offspring generation with carrier layers from parent generation (cF1xcP). Among the different type of embryonic mortalities the PD phenotype was the most frequent both in the artificial insemination and in the natural mating. The BWE phenotype did not occurred at all. Using artificial insemination the erection of ganders were “very good”, the motility of the sperm was between 1 and 3 as well as the volume of the semen was 0.3 on an average per ejaculation.

In the fourth experiment the presumed carrier pairs from the offspring generation (cF1xcF1) and their progeny (F2xF2) showed high EM. Individuals of cF1xcF1 pairs of the third experiment were the same in the fourth experiment. The EM was significantly higher in

this experiment, the fertility was similar. The three-year-old ganders gave less sperm than the one-year-old animals. The fecundity capacity was better of the previous ones, although the fertility of layers of each gander showed differences. The average motility was 2.4 (from 1 to 4) the erection was "very good" at each case. The individual and generation differences between the quality parameters had not any influences on the fertility and on the ratio of embryonic mortality.

Because the investigation of unstained germinal discs are uncertain even using dissecting microscope, it seems expedient to stain them. Big vacuoles can be seen in the unfertile germinal discs, which is not usual in the fertile ones. If the germinal discs were fertile the nuclei brightly lit. Fertile was the 72% of the 132 unincubated duck eggs. Unfertile was 1/3 of the remain 28% and 2/3 of it was visually uncertain. Using propidium iodide dye 41% (9/22) was fertile of the uncertain eggs. 50 visually fertile eggs proved fertile with propidium iodide staining too. Those 160 germinal discs, which seemed unfertile after 7 days incubation and after braking visually too, proved fertile in 25% using staining.

In these studies two recurrent, characteristic malformations were found. One of them was a blood-ring mutation, which cause embryonic death on the 2^{nd} or 3^{rd} day of the incubation and Savage et al. (1988) described as a recessive lethal trait. The other one was a degenerated blastoderm with a diameter of about 0.5 cm surrounded by white and bloody rings, which contained a dead embryo on the 2^{nd} or 3^{rd} day of incubation. Only one layer showed this abnormality in more than 25% (14/4) of her fertile eggs.

The categories according to Abbot and Yee (1975) as well as Szalay (1989) are useful to describe the phenotype of the embryo but in the practice variations in each main category occur frequently.

3.1. New scientific results

1. The ratio of early embryonic mortality among the fertile eggs showed significant difference between the meat type (9.4%), the reproduction-selected (5.2%) and the liver type line formed from the two previous (7.3%) goose lines.
2. The ratio of chromosome abnormalities among dead embryos were 8.0% in the meat type line, 14.8% in the reproduction-selected line and 13.1% in the liver type line formed from the two previous goose lines. All the chromosomal abnormalities were numerical alterations: haploid, triploid and mixed (mosaic or chimeric) haploid/diploid, diploid/triploid, diploid/polyploid karyotypes were identified.
3. In all lines there were found families, individuals, which produced dead embryos in higher ratio than the population average. Embryonic mortality in higher proportion recurs at the predisposed individuals in the following reproduction periods too. It refers to the high embryonic mortality can be carried in goose breeding stocks.
4. Both ganders and layers are involved in the formation of early embryonic mortality, however the role of the ganders seems to be predominant.
5. First description of application of propidium iodide staining for identification of the very early embryonic death, which occurred in the oviductus, was given.
6. First description of an overview with coloured illustrations on the phenotypes of early embryonic mortalities and abnormalities in goose was given. The system according to Abbot and Yee (1975) and Szalay (1989) was greatly developed, because beside the 4 main types 18 variations were described. Similar works have not published yet in the literature.
7. At the first time the ring degeneration of blastoderm was described in goose, which causes embryonic death on the second – third day of the incubation.

4. CONCLUSIONS AND SUGGESTIONS

4.1. Conclusions

All the five related experiments were carried out to investigate the occurrence of embryonic mortality and chromosomal abnormalities and their distribution in the different lines as well as to study the inheritance and recurrence of these traits. Goose has limited data in this respect. Special sexual behaviour, low fertility, seasonality, less eggs than other poultry species in the reproduction period cause particular difficulties in goose (Rouvier 1990, Bogenfürst 1992).

The population average of EM was 5.2% in line 7 and 17.7% in the selected animals from this line in the second reproduction period in the first experiment. The effect was provable of layers, ganders, father of layers and mother of layers for the forming of embryonic mortality, which refer to genetic effect. The presumed carrier animals mating in the same pairs showed on an average 13% embryonic morality in the following two years. Using artificial insemination this ratio was 31.8% in the fourth laying cycle. The presumed carrier ganders mated to their own daughters produced high embryonic mortality in all cases. This result referred to female progeny of carrier parents may carry the ability to produce embryonic mortalities. In that case when male progeny of carrier parents were mated with their sisters as well as non-related layers in their first laying cycle the fertility was very low and the early embryonic mortality was high in any case. The question was raised whether male and female equally contribute the high embryonic mortality ratio. The ranked carrier ganders (cP) mated with non-carrier layers (ncP) the embryonic mortality was 26.23% while non-carrier ganders (ncP) mated with carrier layers originated from offspring generation (cF1) the ratio of embryonic mortality was 7.46%, which is almost the same like the population average in the first year of the experiments. It may mean that the contribution of males in the formation of EM is larger. The low fertility of male progeny of carrier parents did not related to the increasing of occurrence of very early embryonic death.

Detailed description the phenotypes of the early embryonic death lets the determination of abnormalities and mutations easier. It may help in the identification of the true fertility of individuals and in the selection of the economically desirable characteristics. According to these results it seems that, when the animals age, the ratio of PD (positive development) increases in the population, while the D1-5 (embryonic death on the first 5 days of incubation) decreases. It means that, at the hatchery level, that the quantity of “clear” eggs will increase and the number of “bloody” eggs, which contain dead embryos will decrease at candling, because all eggs with PD, some eggs with BWE (blastoderm without embryo) and all eggs with dead embryos on the first 2 days of incubation will appear “clear” with candling. In this case, the true rate of the embryonic mortality, which is a characteristic of each layer and family will not be measured accurately. It may cause that the ability for the formation of abnormalities can persist and inherited in the population.

Some publications were written on the degenerated development of blastoderm and ring lethal mutations (Savage et al. 1988, Savage and Harper 1985, Thomas et al. 1992, Savage et al. 1992). They caused embryonic mortality on some of the first days of the incubation. In goose, there are no published references about any phenotypically visible mutations over the first few days of the incubation. Our finding was the first, characteristic malformation, which may refer to expression of a mutation in these early stages. It was a degenerated blastoderm with a diameter of about 0.5 cm surrounded by white and bloody rings, which contained a dead embryo on the 2^{nd} or 3^{rd} day of incubation. Only one layer showed this abnormality in more than 25% of her fertile eggs. In the previous year, that layer did not produce this abnormality when it was paired with another gander. It may mean that

this presumed mutation could be caused by a recessive gene being present in the gander as well. Further studies would be necessary to confirm this hypothesis.

Brah et al. (1991) investigated two White Leghorn lines. The early embryonic death was found inheritable and they suggested regarding this fact at the selection. According to these results it seems that both ganders and layers are involved in the formation of abnormalities in their progeny. However, the role of the ganders seems to be predominant. It means that the examination of each parent pair and culling of the layers and ganders, which produce dead embryos, could improve hatchability in goose lines.

4.2. Suggestions

- Excluding from the breeding of those ganders and layers, which produced embryonic mortality among their fertile eggs in higher proportion than the population average at the setting of goose breeding stocks, because probable the genetic origin and the heritability of these anomalies.

- In existing goose breeding stocks, in the event there are not technological, animal health problems and at the first candling the ratio of the "bloody" eggs is permanently over 10% in the studied line, it is suggested the control of the stock and excluding from the breeding those ganders and layers, which show the early embryonic mortality in high proportion.

- Examination of "clear" eggs at candling is reasonable, because all dead embryos with PD, some embryos with BWE category and dead embryos from the first 2 days of the incubation can be hid.

- Controlling the "true" fertility at poultry sperm deep freezing experiments after artificial insemination with thawed sperm, as well as controlling the effectiveness of the insemination in the practice it is suggested the application of propidium iodide staining of the germinal discs.

5. PUBLICATIONS RELATED TO THE SUBJECT OF DISSERTATION

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