DOCTORAL (PhD) DISSERTATION

NGUYEN ANH THI

Kaposvár

2025

HUNGARIAN UNIVERSITY OF AGRICULTURE AND LIFE SCIENCES
KAPOSVÁR CAMPUS

DOCTORAL SCHOOL OF AGRICULTURAL AND FOOD SCIENCES

Head of Doctoral School:

PROF. DR. MELINDA KOVÁCS, DSc.

Supervisor:

PROF. DR. ISTVÁN NAGY, DSc.
Professor

Co-supervisor:

DR. GYÖRGY KÖVÉR, PhD.
Associate Professor

ANALYSIS OF THE INBREEDING EFFECTS ON THE POPULATION STRUCTURE AND GENETIC DIVERSITY OF THE MANGALICA PIG BREEDS

Written by:

NGUYEN ANH THI

Kaposvár
2025

Appendix 1.

The PhD School

Name: Doctoral School of Agricultural and Food Sciences

Discipline: Animal Sciences

Head of the Doctoral School:
Prof. Dr. Melinda Kovács
University Professor, Full Member of the Hungarian Academy of Sciences

Supervisor(s):
Dr. István Nagy
Head of Department, Professor, DSc.
Hungarian University of Agriculture and Life Sciences,
Institute of Animal Sciences, Department of Animal Breeding

Dr. György Kövér
Associate Professor, PhD.
Hungarian University of Agriculture and Life Sciences,
Institute of Animal Sciences, Department of Animal Breeding

....

Approval of the Head of Doctoral School Approval of the Supervisor(s)

List of abbreviations

AI	Artificial insemination
AR	Average relatedness
A_{HC}	Ancestral history coefficient
F	Inbreeding coefficient
fa	Effective number of ancestors
F_{Bal}	Ballou's inbreeding coefficient
fe	Effective number of founders
fg	Effective number of founders genome
F_{Kal}	Kalinowski's inbreeding coefficient
F_{New}	New inbreeding coefficient
F_{OLD}	Ancestral inbreeding coefficient
F_{PED}	Pedigree-based inbreeding coefficient
F_{ROH}	Genomic inbreeding coefficient (estimated from Runs of Homozygosity)
F_W	Wright's inbreeding coefficient
GD	Genetic diversity
GI	Generation interval
GWAS	Genome-Wide Association Study
HNAMB	Hungarian National Association Mangalica Breeders
LE	Lethal equivalent
ll	Likelihood of genetic death
NBA	Number born alive
Ne	Effective population size
PBW	Piglet birth weight
TNB	Total number born
QTL	Quantitative trait loci

List of tables

Tables in the main text

Tables in the appendices

List of figures

Figures in the main text

Figures in the appendices

TABLE OF CONTENTS

1. INTRODUCTION

Maintaining genetic variability of a certain population is one of the crucial strategies for an effective genetic conservation program as it ensures the adaptation of the population to environmental change and genetic selection. Genetic variability is basically measured by the expected heterozygosity Nei (1973) known as the probability that two randomly chosen alleles from the population are different. The heterozygosity and homozygosity are two opposing states involved in genetic diversity (GD) in the process by which alleles frequency is passed down from a certain generation to subsequent generations. The reduction of heterozygosity is due to various reasons from which inbreeding is probably the most substantial because inbreeding is recognized to increase homozygosity (Curik et al., 2017). According to Woolliams (2007) inbreeding even causes higher rate loss of alleles in a closed and small population, since the contribution of founders to the gene pool is not equal. Therefore, studying genetic variability and structure of a population provides valuable information for a conservation program to approach dual targets: inbreeding reduction and high genetic variation maintenance.

The inbreeding levels are traditionally estimated according to the method proposed by Wright (1922) where inbreeding coefficient is defined as the probability that the two alleles at any locus in an individual are identical by descent. In recent decades, some improved and extended methods for inbreeding coefficient estimation have been published such as ancestral inbreeding coefficient (e.g. Ballou, 1997). This method approached the inbreeding with consideration of whether any allele in an individual has been autozygous at least once in previous generations. It is assumed that an inbred progeny of non-inbred ancestors is more vulnerable to negative effect of inbreeding than the inbred progeny of inbred ancestors (Suwanlee et al., 2007).

Genetic variability and inbreeding have been studied for centureries (Darwin and Tangley, 1984), but in recent years, numerous studies have focused on various livestock species for both commercial and conservation purposes (Carolino et al., 2020; García-Atance et al., 2023; González-Cano et al., 2022; Gvozdanović et al., 2020; Mandal et al., 2020; Nyman et al., 2022; Rodríguez-Ramilo et al., 2019; Wang et al., 2022). Among the conservation programs in Hungary probably the most characterizing is that of the Mangalica pigs, which is an autochthon Hungarian pig breed group preserved for its biological diversity after having held a significant role in the commercial lard supply chain (Egerszegi et al., 2003, Rátky et al., 2007).

The Mangalica breed originated in the 1830s when Serbian Sumadia pig breed was crossed with local Hungarian stock, producing a rustic, curly pig called Blonde Mangalica (Egerszegi et al., 2003, Botha et al.,2014) through intensive selection. The Swallow-Belly Mangalica was later developed by crossing Mangalica with Szerémségi pigs (Black Mangalica), while the Red Mangalica emerged in the early 19th century from crosses with Szalontai and Újszalontai pigs (Egerszegi et al., 2003). Mangalica pigs are characterised by excellent fat production, strong maternal tendencies and a good adaptability to extensive husbandry conditions, but their reproductive capacity is low Botha et al. (2014).

The Mangalica pig was the most important Hungarian pig breed until the 1950s. After World War II, Mangalica lost its former popularity due to changing consumer dietary habits and its less competitive reproductive and growth performance compared to modern breeds (Egerszegi et al., 2003). The populations were at the risk of extinction when in 1975, only 34 breeding sows were recorded in the herdbook (Egerszegi et al., 2003). Fortunately, the National Association of

Mangalica Breeders, originally established in 1927 but suspended during World War II (Egerszegi et al., 2003), was re-established in 1994 to preserve the genetic and phenotypic appearance of the Mangalica pig in an unaltered form (Egerszegi et al., 2003). Thanks to their efficient activity, the number of registered sows and boars (of the three breeds combined) in 2019 was 6,723 and 354, respectively (Novozánszky et al., 2019).

Currently, the Mangalica pig exists in three well-known breeds - Blonde, Red, Swallow-Belly which molecular genetic analysis by Zsolnai et al. (2006) confirmed as distinct breeds. Posta et al. (2016) studied the population structure and GD based on the data of the pedigree up to 2011 of the Mangalica populations in Hungary. However, during the last decade, the population of these pig breeds has changed significantly in numbers and an internal change in genetic variation was highly probable. A comprehensive analysis of updated data from the herdbook up to 2021 is important to elucidate these changes in population structure, refine our understanding of the genetic parameters related to these native breeds, and serve as an information basis for further study. In addition, in terms of breed loss, it is necessary to study the population substructure and migration in order to make an appropriate assessment of the management and conservation of genetic variability (Cervantes et al., 2008b) as all breeds are kept in several herds, these herds can be interpreted as subpopulations.

1.1. Research objectives

1. To assess the genetic variability in Mangalica pig breeds using pedigree data, key metrics such as inbreeding coefficients, effective population size will be calculated. This evaluation will help identify levels of genetic diversity, detect bottlenecks and uncover historical breeding patterns that support preservation of genetic diversity and control of inbreeding rates.

2. To calculate the probability of gene origin, pedigree information will be used to trace the ancestral contributions within a population. The distribution of gene origins can be estimated, providing valuable insights into the genetic structure and the influence of different founders on the current gene pool.

3. To calculate the inbreeding coefficients, different approaches will be employed, allowing for a comparison of the results and an assessment of a new-inbreeding coefficient, which is expected to have more negative effects. In addition, the correlation between these various inbreeding coefficients will be evaluated.

4. To monitor the potential population subdivision among different herds of Mangalica pigs, pedigree data will be analysed to assess the potential for genetic differentiation between the herds. This will involve calculating genetic distances using Wright's F_{ST}. The results will provide valuable insights into population dynamics and potential isolation.

5. To analyze migration patterns between herds of Mangalica pigs, the birth identified herds and current identified herds recorded in the pedigree will be used to track movements among different herds. This approach provides insights into how these movements affect genetic diversity and population structure across various herds.

2. LITERATURE REVIEW

2.1. Characterizing and eliminating the inbreeding load

Inbreeding is defined as the identity by descent probability at any given autosomal locus and results from the mating of related individuals (Casellas et al., 2008). According to Sonesson et al. (2005) , truncation selection (picking a portion of breeders with the best calculated value) based on BLUP (Best Linear Unbiased Prediction) breeding values (Henderson,1975) has become a standard method in breeding. Unlike phenotypic truncation selection, this approach not only improves the selection response but also increases the rate of inbreeding. Inbreeding decreases the frequency of heterozygous individuals relative to a defined base population, and therefore, if directional dominance is present, a reduction in mean performance for the trait under consideration occurs (Sewalem et al., 1999). The increase in homozygosity has negative effects on heterozygosity, which is known as an individual's genetic diversity (Schäler et al., 2020). As a result, higher levels of inbreeding lead to lower genetic diversity and inbreeding depression (Haig et al., 1990; Zhang et al., 2015), which are two out of seven main genetic issues in the field of conservation biology (Frankham, 1995). It rises the importance of measurement in individual inbreeding because with such information, breeding programs can be well-designed to control the unfavourable effects on individual fitness and population dynamics due to inbreeding (Koenig and Simianer, 2006; Zhang et al., 2015). The level of inbreeding is measured by the inbreeding coefficient, which is the probability that the two genes at any locus in an individual are identical by descent (Falconer and Mackay, 1996). In the conventional approach, the inbreeding coefficients and other diversity-related parameters are pedigree – based statistics (Galla et al., 2022). Although, in recent years, the advance of technology in generating genome-wide sequencing and genotyping data has allowed for more accurate estimation levels of homozygosity in the population (Kardos et al., 2015), the pedigree-based analysis is contended to keep its vital role in conservation management (Galla et al., 2022).

Inbreeding depression considerably affects the survival of the inbred population Frankham et al. (2001) and population size. Eventually, species extinction may happen, especially for populations that are already small in size and have a closed structure. However, inbreeding depression is not limited to fitness traits, and it may affect any trait of interest in the wild, zoos and in domesticated animal populations (e.g. Crnokrak and Roff, 1999; Doekes et al., 2021; Gutiérrez-Reinoso et al., 2022; Kardos et al., 2016; Keller and Waller, 2002; Leroy, 2014; Vega-Trejo et al., 2022). In order to minimize the unfavourable effects of inbreeding, standard procedures (Gebregiwergis et al., 2020; Sonesson and Meuwissen, 2000, 2001; Weigel, 2001) can be applied to maintain long-term sustainable livestock production in the future (Kristensen and Sørensen, 2005).

However, under various circumstances inbreeding avoidance is simply impossible. Zoological gardens often encounter with the issue of having a captive population originated by a small number of animals, and obtaining additional animals is not possible. A well-known example is the Speke's Gazelle (*Gazella spekei*) population in the St. Louis Zoo, which was founded in 1969 by one male and two females from wild. In 1972, another female was imported but since then, no other animals had been introduced (Templeton and Read, 1983). The details of the management and breeding of this population can be found in the paper by Read and Frueh (1980). Because of the small population size, the population experienced a severe inbreeding depression.

However, an unorthodox breeding program was developed based on the following steps: rapidly increasing the population size, choosing inbred animals with genes from as many different ancestors as possible to be parents, and producing inbred offspring with diverse genetic ancestry (Templeton and Read (1983, 1984). Templeton and Read demonstrated that after applying this breeding program, the inbreeding load was halved in just a three-year long period, so they concluded that inbreeding depression did not cause an unsolvable problem in the context of long-term maintenance of a population in which inbreeding cannot be avoided. Although this conclusion was debated by others and it generated an inspiring back-and-forth debate (Kalinowski et al., 2000; Templeton, 2002; Templeton and Read, 1998; Willis and Wiese, 1997), the breeding program of Templeton and Read (1983, 1984) was probably the first example in which the authors deliberately used the interaction between inbreeding and selection in order to eliminate inbreeding depression (i.e. decreasing the inbreeding load). This phenomenon is called purging (Hedrick and Garcia-Dorado, 2016) which has mostly been described in laboratory conditions so far (e.g. Bijlsma et al., 1999; Miller and Hedrick, 2001; Pérez-Pereira et al., 2021). However, the number of available studies is much lower in zoo biology (e.g. Moreno et al., 2015) and very low in domesticated animals (e.g. Hinrichs et al., 2015; Mc Parland et al., 2009).

2.1.1. Parameters characterizing inbreeding load and purging

According to Hedrick and García-Dorado (2016) the inbreeding load is the genetic damage that is concealed in heterozygosis and would be expressed in a complete homozygote form. Under some simplified assumptions (fitness multiplicative across unlinked non-epistatic loci), inbreeding load equals the rate at which fitness declines with increasing inbreeding in the absence of selection (roughly, the percentage of reduction in fitness expected from each 0.01 increase in F), depression while purging is the increased purifying selection facilitated by inbreeding that can reduce both the inbreeding load and the actual of fitness. The related parameters are listed in **Table 1**. The characteristics of conventional inbreeding coefficient (F) (Wright, 1922) are considered to be known. The likelihood of genetic death (ll) is also an inbreeding coefficient, but it is only slightly related to F. When one is zero, the other must also be zero. If a given ancestor is assumed to have one lethal gene (l) and leads through a separate and uncomplicated line of descent to each of the parents of a particular animal, the value of (ll) will be half of the F value due to this same ancestor, since F measures homozygosity for L and for l, but (ll) measures homozygosity for the latter only. However, if the lines of descent are not separate or if one or more of the intermediate ancestors is also inbred with respect of the given ancestor, then the value of (ll) will be less than half that of F (Slatis, 1960) **Table 1**.

Table 1. Inbreeding load related parameters

Studies	Concept	Sign	Definition	Formula	Software
Wright (1922) Boichard (2002) Gutiérrez and Goyache (2005) Suwanlee et al. (2007) Coster (2022)	Inbreeding coefficient	F	The probability that the two alleles at any locus in an individual are identical by descent	$F_x = \sum \left(\frac{1}{2}\right)^{n+n'+1} (1 + f_{a(c)})$	PEDIG ENDOG Package "pedigree" in R
Morton et al. (1956) Hoeck et al. (2015)	The number of lethal equivalents	B	The number of deleterious genes per gamete that, when combined in a homozygous state, would result in the death of an individual	$S_F = e^{-A-BF}$	R script
Slatis (1960) Kennedy et al. (2014)	Likelihood of genetic death	ll	The likelihood of genetic death (ie. all founders carry a recessive lethal gene)	Equation was not given	R script
Ballou (1997) Baumung et al. (2015) Doekes et al. (2020)	Ancestral inbreeding coefficient	F_{Bal}	The cumulative proportion of an individual's genome that has been previously exposed to inbreeding in its ancestors.	$F_{Bal(x)} = \frac{\begin{bmatrix} F_{Bal(s)} + (1 - F_{Bal(s)}) * F_{W(s)} + \\ F_{Bal(d)} + (1 - F_{Bal(d)}) * F_{W(d)} \end{bmatrix}}{2}$	GRAIN
Kalinowski et al. (2000) Baumung et al. (2015) Doekes et al. (2020)	Ancestral inbreeding coefficient	F_{Kal}	The probability that any allele in an individual is currently autozygous and has been autozygous in previous generations at least once.	Equation was not given	GRAIN

Kalinowski et al. (2000) Baumung et al. (2015) Doekes et al. (2020)	Kalinowski "new" inbreeding coefficient	F_{New}	The probability that any allele in an individual is autozygous for the first time.	$F_{New(x)} = F_{W(x)} - F_{Kal(x)}$	GRAIN
Baumung et al. (2015) Doekes et al. (2020)	Ancestral inbreeding coefficient (Ancestral history coefficient)	A_{HC}	The number that tells how many times during pedigree segregation (gene dropping) a randomly taken allele has been in IBD status	Equation was not given	GRAIN
Hinrichs et al. (2007)	Ancestral inbreeding coefficient	F_{OLD}	The inbreeding occurring further back in the population history ("Old" inbreeding)	$F_{i,old}\,(t,u) = \frac{F_i\,(0,u) - F_i\,(t,u)}{1 - F_i(t,u)}$	PEDIG
Hinrichs et al. (2007)	New inbreeding coefficient	F_{NEW_H}	The inbreeding occurring in recent generations ("New" inbreeding)	$F_{i,new}\,(t,u) = F_i\,(0,u) - F_{i,old}\,(t,u)$	PEDIG
Gulisija and Crow (2007)	Expressed opportunity for purging	O_E	The expressed opportunity for purging is the potential for reduction in expressed load in the present generation as a consequence of having inbred ancestors	$O_{Ei} = \sum 2F_{i(j)}F_j$	PurgeR
Kardos et al. (2015)	Genomic inbreeding coefficient	F_{ROH}	The proportion of the autosomal genome, in which autozygosity is derived from the assumption that very long stretches of homozygosity (ROH) can only result from inbreeding	$F_{ROH} = \Sigma L_{ROH}/L_{AUTOSOME}$	PLINK version 1.07

García-Dorado et al. (2016) López-Cortegano et al. (2021)	Purging coefficient	d	The part of deleterious effect that is exposed to genetic purging due to inbreeding	d = s(1/2–h)	PURGd
López-Cortegano et al. (2021) López-Cortegano (2022)	Purged inbreeding coefficient	g	The inbreeding coefficient (F) adjusted by the deleterious frequency that is expected by considering purging	$\hat{g} = \frac{1-2d}{1+2d\ (2N-1)}$	PurgeR

- F_x is the conventional inbreeding coefficient of the individual x, $f_{a(c)}$ is the inbreeding coefficient of the common ancestors, n and n' are the number of generations from sire and dam respectively to the ancestor of individual x.

- $FBal_{(x)}$ is the ancestral inbreeding coefficient for an individual *(x)* with the subscripts (s) and (d) representing for the sire and dam, respectively.

- $F_{i,old}\ (t,u)$ is the old inbreeding coefficient of individual i in generation u with respect to a base generation at generation t.

- $F_{i,new}\ (t,u)$ is the new inbreeding coefficient of individual i in generation u with respect to a base generation at generation t.

- s is the selection coefficient against the homozygote and h is the dominance coefficient

- $\hat{g}$ is the predicted purged inbreeding coefficient based on the purging coefficient d and effective population size N

- ΣL_{ROH} is the total length of all ROH according to a priory specified threshold of succeeding number of homozygotes SNP obtained from the chip arrays, and $L_{AUTOSOME}$ is the specified length of the autosomal genome covered by SNP in chip

- O_{Ei}, is the probability that an allele, autozygous in *I*, $F_{i(j)}$ is the probability of an allele in *I* being derived from an allele in *j* and being autozygous in *i* ;

- S_F is the probability of survival of individuals with an inbreeding coefficient of $\boldsymbol{F}$, e^{-A} is the survival in a non-inbred random mating population (F = 0) and B is haploid lethal equivalents.

- $F_{New(x)}$ is Kalinowski "new" inbreeding coefficient of individual x

- $F_{W(x)}$ is Wright's inbreeding coefficient of individual x, this is sometime called conventional inbreeding coefficient of individual x (F_x)

- $F_{Kal(x)}$ is Kalinowski inbreeding coefficient of individual x

The inbreeding load of the population can be characterized by the number of lethal equivalents (LE) (Hoeck, 2015), **Table 1**, where if it decreases over time in a given population then it signals the possibility of purging (Templeton and Read, 1984).

Alternatively, based on the inbreeding coefficients of (F), (F_{Bal}), (F_{Kal}), (A_{HC}) and (F_{OLD}), the possibility of purging is indicated either by the positive interaction between (F) and (F_{Bal}) (Ballou, 1997) or by the significantly positive effect any of the following inbreeding coefficient: (F F_{Bal}), (F_{Kal}), (A_{HC}) and (F_{OLD}) on the examined trait (i.e., the possibility of purging is indicated by means of ancestral inbreeding of any type (Ballou, 1997; Baumung et al., 2015; Hinrichs et al., 2007; Kalinowski et al., 2000) **Table 1**.

The purging coefficient signals the possibility of purging when it is significantly different from zero. In that case, the purged inbreeding coefficient is significantly lower compared to the Wright inbreeding coefficient (i.e., purging is indicated by the so-called inbreeding-purging model (López-Cortegano et al., 2021) **Table 1**.

The expressed opportunity for purging (O_E) is the potential for reduction in expressed load in the present generation as a consequence of having inbred ancestors. The procedure wants to express the reduction of expressed load because of purging as a fraction of expressed load when purging is absent (Gulisija and Crow, 2007) **Table 1**.

2.1.2. Softwares estimating inbreeding load related parameters

There are several softwares calculating the conventional inbreeding coefficient (F) (Baumung et al., 2015; Boichard, 2002; Coster, 2022; Gutiérrez and Goyache, 2005) based on the algorithm of Meuwissen and Luo (1992). On the contrary the other inbreeding coefficients (F_{Bal}), (F_{Kal}), (F_{New}) and (A_{HC}) can be estimated using the GRAIN software developed by Baumung et al. (2015) which was recently updated by Doekes et al. (2020). The software is based on the stochastic method of "gene dropping" (MacCluer et al., 1986; Suwanlee et al., 2007) where the number of the used iteration is generally 1.000.000. Gene dropping is a simulation procedure approaching by first assigning two unique hypothetical alleles to each founder. Then, a random number generator is used to determine which one of each founder's genes is transmitted to each offspring. At the end of a single gene drop, every animal in the pedigree has a genotype (MacCluer et al., 1986; Suwanlee et al., 2007, Baumung et al., 2015).

Likelihood of genetic death (ll) can be calculated using the R script developed by Kennedy et al. (2014).

The purging coefficient (d) and the purged inbreeding coefficient (g) can be calculated using the PURGd (García-Dorado et al., 2016) and PurgeR (López-Cortegano, 2022).

The lethal equivalent (LE) can be calculated using the R script developed by Hoeck et al. (2015).

After the parameters listed in the previous section are calculated they must be evaluated where the method depends on the characteristic of the evaluated trait. If the trait has a normal distribution, then the effect of inbreeding (F, F_{Bal}, F_{Kal}, A_{HC} and F_{OLD}) is determined by running a breeding value estimation procedure (animal model) (Henderson, 1975) where the inbreeding coefficients are treated as covariates. A widely used software for performing breeding value

prediction is ASREML (Gilmour et al., 2009). On the contrary if the trait of interest is binomial then generalized linear mixed models (GLMM), has to be fitted using the lme4 or pedigreemm package in R (Bates et al., 2015; Bates and Vazquez, 2023). If the purging coefficient and the purged inbreeding coefficients are used then the non-linear regression method was used to find the more accurate values of these coefficients (nls function, stats package of R).

2.1.3. Correlation among inbreeding coefficients

There are only few available studies (Curik et al., 2020; Justinski et al., 2023; Piles et al., 2023; Posta et al., 2020) estimating correlation coefficients among the various inbreeding coefficients. Based on Spanish and Hungarian rabbit populations Curik et al. (2020) and Piles et al. (2023) both reported very high (0.97 – 1.00) correlation coefficients between (F_{Bal}) and (F_{Kal}). Piles et al. (2023) also reported the possible maximum correlation coefficients (1.0) between (A_{HC}) and (F_{Bal}) and (A_{HC}) and (F_{Kal}), while Posta et al. (2020) reported a lower correlation especially between (A_{HC}) and (F_{Kal}) (0.77)**.** The conventional inbreeding coefficient (F) showed high (0.88 – 0.90) correlation coefficients in both studies with all of the different ancestral inbreeding coefficients ((A_{HC}), (F_{Bal}) and (F_{Kal})). On the contrary, Piles et al. (2023) reported only medium correlation coefficients between the old inbreeding (F_{OLD}) and the conventional (F) and the other ancestral type ((A_{HC}), (F_{Bal}) and (F_{Kal})) inbreeding coefficients, where the reported values ranged between 0.60 and 0.70, respectively. The estimates in German sheep breeds ranged between 0.55 and 0.73 between the conventional and ancestral inbreeding coefficients (Justinski et al., 2023). The lowest correlations (0.00 – 0.57) were found among the new and ancestral inbreeding coefficients (Curik et al., 2020; Piles et al., 2023; Posta et al., 2020), but it has to be emphasized that the calculation of the new inbreeding coefficient was different based on either (Kalinowski et al., 2000) or (Hinrichs et al., 2007) and consequently the estimated correlations were different in the various studies where Piles et al. (2023) reported very low (0.00 – 0.20) values while Curik et al. (2020) and Posta et al., (2020) observed low to moderate (0.17 – 0.57) values. Similarly, the new and the conventional inbreeding coefficients showed different correlation coefficients in the two studies due to the same reason mentioned before. Again, the reported values of Piles et al. (2023) was low (0.20) compared the other studies (Curik et al., 2020; Posta et al., 2020) where much higher values were reported (0.67 – 0.90). Altogether, the results indicated that the conventional, new, and ancestral inbreeding coefficients are measuring distinct population parameters. These findings are important because not all inbreeding is expected to be equally harmful. As demonstrated by Doekes et al. (2019), inbreeding in recent generations was more harmful than inbreeding on distant generations for yield, fertility and udder health traits in Dutch Friesian cattle. Therefore, inbreeding depression can be best characterized by using (F_{Kal}) rather than the conventional Wright inbreeding coefficient. In addition, according to Schäler et al. (2020), due to the identification of ancestral inbreeding, it is possible to select individuals with simultaneously high classical and ancestral inbreeding coefficients and mate them with unrelated animals in order to achieve purging effects.

2.1.4. Studies signalling purging based on ancestral inbreeding or inbreeding-purging model

The studies which are likely to observe purging are summarized in **TableS 1**. The first comprehensive studies analysing the effect of ancestral inbreeding were performed on zoo populations (Ballou, 1997; Boakes et al., 2007). In these studies, many captive populations were evaluated but only a small fraction of these showed the signs of purging (one out of 25 in Ballou,

1997) and 14 out of 119 in (Boakes et al., 2007). Interestingly, the studies by Ballou (1997) and Boakes et al. (2007) reported conflicting findings regarding purging in the Sumatran tiger population. Ballou's 1997 study detected signs of purging, while Boakes et al. (2007) found no evidence of it when reanalyzing the same population. The discrepancy may stem from differences in the models used. Ballou (1997) employed a model that included the inbreeding coefficient of the litter, the inbreeding coefficient of the dam, the interaction between the inbreeding coefficient and the ancestral inbreeding coefficient of the litter, and the year of birth. In contrast, Boakes et al. (2007) used a model based on Boakes and Wang (2005), which omitted the interaction term but included the inbreeding coefficient of the litter, the inbreeding coefficient of the dam, and the ancestral inbreeding coefficient of the litter as separate variables. Computer simulations demonstrated that the model proposed by Boakes and Wang (2005) is more advantageous in situations when inbreeding depression is caused by mildly deleterious alleles.

Computer simulations indicated that purging is more likely to occur when deleterious mutations are of a large effect and when inbreeding occurs slowly and over many generations (Hedrick, 1994). The rabbit studies of Curik et al. (2020) and Piles et al. (2023) were highly adequate from this aspect as they covered 25 – 40 generations where the inbreeding was only slowly accumulated. The studies show that in the Pannon white rabbit breed (Kövér et al., 2023), this slow increase in inbreeding level was mainly due to the applied circular mating system (Nagy et al., 2010). However, by 2017 the Pannon white rabbit showed that more than 65% of the rabbits' genome has already experienced inbreeding in previous generations making it less susceptible to inbreeding depression (Curik et al., 2020) (**Figure 1**). This value is substantially higher than any of examined zoo population (Boakes et al., 2007) where the populations with the highest (F_{Bal}) were Addax (*Addax nasomaculatus*) and Przewalskii's horse (*Equus ferus przewalskii*) having mean (F_{Bal}) values of 49.50 and 54.60%, respectively. However, it is important to note that the Pannon white rabbit population has a considerably lower inbreeding coefficient (**Figure 1a,b**) than these mentioned zoo populations where the mean (F) values were 18.40 and 21.00%, respectively. It must be emphasized that in the study of Curik et al. (2020) signs of purging were only detected between 1992 – 1997 where the litter inbreeding showed significant inbreeding depression on the survival of kits at birth while one of the ancestral inbreeding coefficients (F_{Kal}) had a significantly positive effect. However, (F_{Bal}) had no effect on the examined trait. Later, no signs of purging were detected but inbreeding depression was also absent between 1997 and 2017, so it was concluded that the effects of new inbreeding involving several genes with large harmful effects were already purged between 1992 – 1997 (Curik et al., 2020).

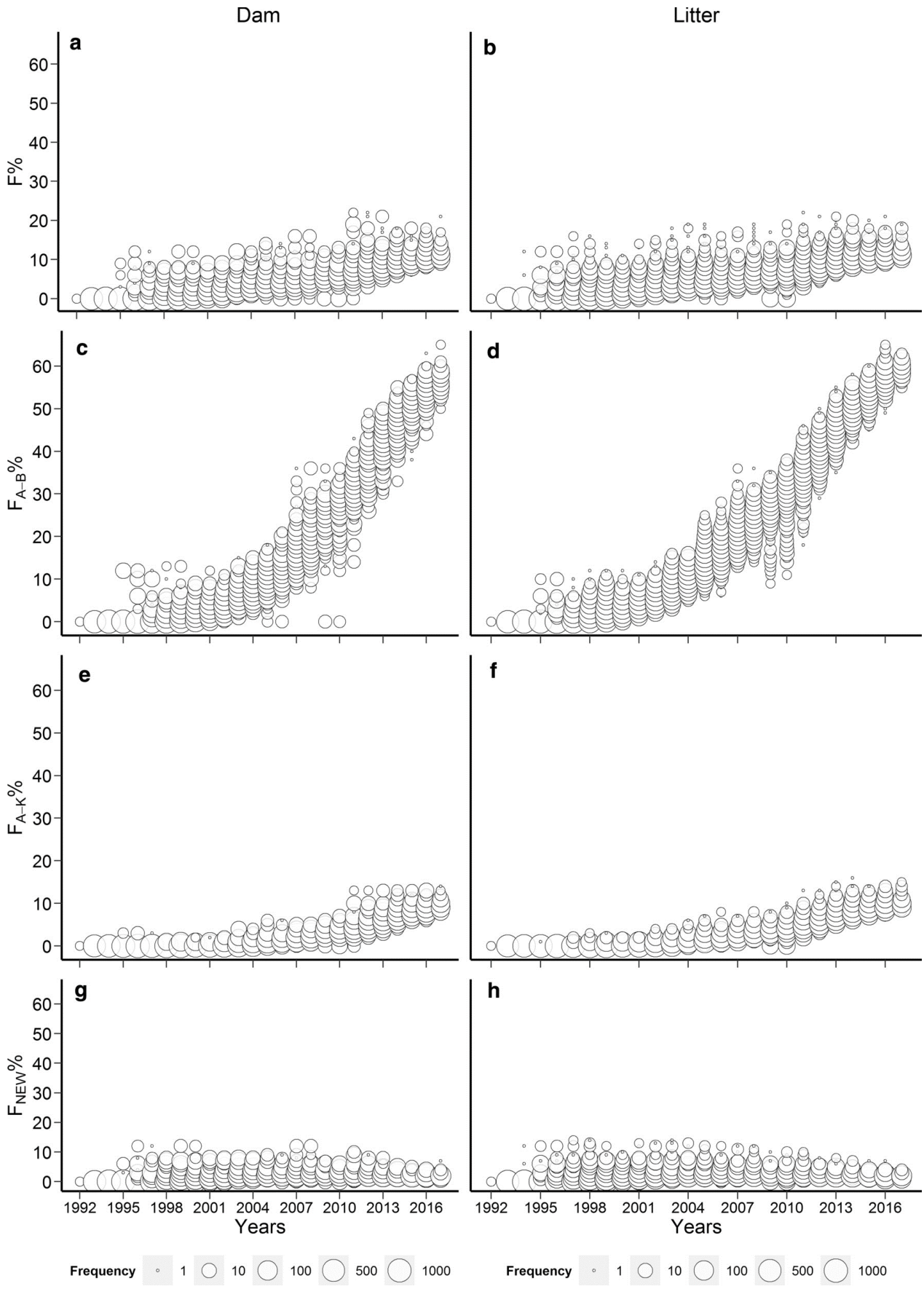


Figure 1. Evolution of the different dam and litter inbreeding coefficients of the Pannon white rabbits (Wright: a, b; Ballou: c, d; Kalonowski: e, f; Kalinowski new: g, h).

The other rabbit study Piles et al. (2023) was also not fully consistent from the aspect of purging indication since these authors found the positive effects of the old inbreeding only (F_{OLD}) on the slaughter and weaning weights respectively, while the other ancestral coefficients (F_{Bal}, F_{Kal} and A_{HC}) had no effect on either trait. In the cattle studies (Hinrichs et al., 2015; Mc Parland et al., 2009), Hinrichs et al. (2015) found significantly positive effect of (F_{Bal}) (but nonsignificant (F_{Kal}) on birthweight signalling purging, but this finding is still not favourable as the increasing birthweight may cause problems with calving. Besides, when Hinrichs et al. (2015) applied the original model of Ballou (1997) then a significant positive interaction was observed between (F) and (F_{Bal}) for birth weight and for stillbirth as well, showing the possibility of purging for both traits. No evidence of purging was detected for calving ease in any of the models. In the study by Mc Parland et al. (2009), the ancestral inbreeding coefficients (F_{Bal} and F_{Kal}) showed consistent positive effects on milk and protein yield of Irish Holstein-Friesian population. However, these coefficients did not influence other traits analyzed, such as fat yield, calving interval, age at first calving, or survival. Evidence of potential purging were reported in other studies, including Vostra-Vydrova et al. (2020) for White Shorthorn goats and Perdomo-González et al. (2020) for Pura Raza Espanola mares. In these studies, positive effects of ancestral inbreeding (F_{Kal}) were observed for milk production in White Shorthorn goats (Vostra-Vydrova et al., 2020) and for several reproductive traits in Pura Raza Espanola mares, including age at first foaling in months, the average interval between first and second foaling in months, and the average interval between foaling in months (Perdomo-Gonzaslez et al., 2020).

When evaluating the potential for purging base on genealogical data, the inbreeding-purging model represents an alternative methodology to ancestral inbreeding. The theoretical framework was developed by García-Dorado (2012) and subsequently tested through laboratory experiments using Drosophila melanogaster with effective population sizes ranging from 6 to 50 (Bersabé and García-Dorado, 2013; López-Cortegano et al., 2016). Both studies recorded purging coefficients greater than 0 (0.02 – 0.30) and they concluded that in order to show purging the product of the effective population size and purging coefficient has to exceed 1 that implies that purging should be efficient for population sizes of order of a few tens or larger but purging might be inefficient against nonlethal deleterious alleles in smaller populations (Bersabé and García-Dorado, 2013; López-Cortegano et al., 2016). In the case of captive mammals, López-Cortegano et al. (2021) evaluated the genealogy of different threatened ungulate species of the Family Bovidae with different demographic histories: barbary sheep (*Ammotragus lervia*), Cuvier's gazelle (*Gazella cuvieri*), dorcas gazelle (*G. dorcas*), and dama gazelle (*Nanger dama*). These populations had different sizes ranging between 4 (barbary sheep) and 39 (Dorcas gazelle). The study estimated purging coefficients larger than zero for all species (ranging from 0.08 to 0.48), but these estimates were only significant for the Cuvier's gazelle and dama gazelle. Consequently, the conventional and the purged inbreeding coefficients (g – **Table 1**) were clearly separated for these species (**Figure 2**).

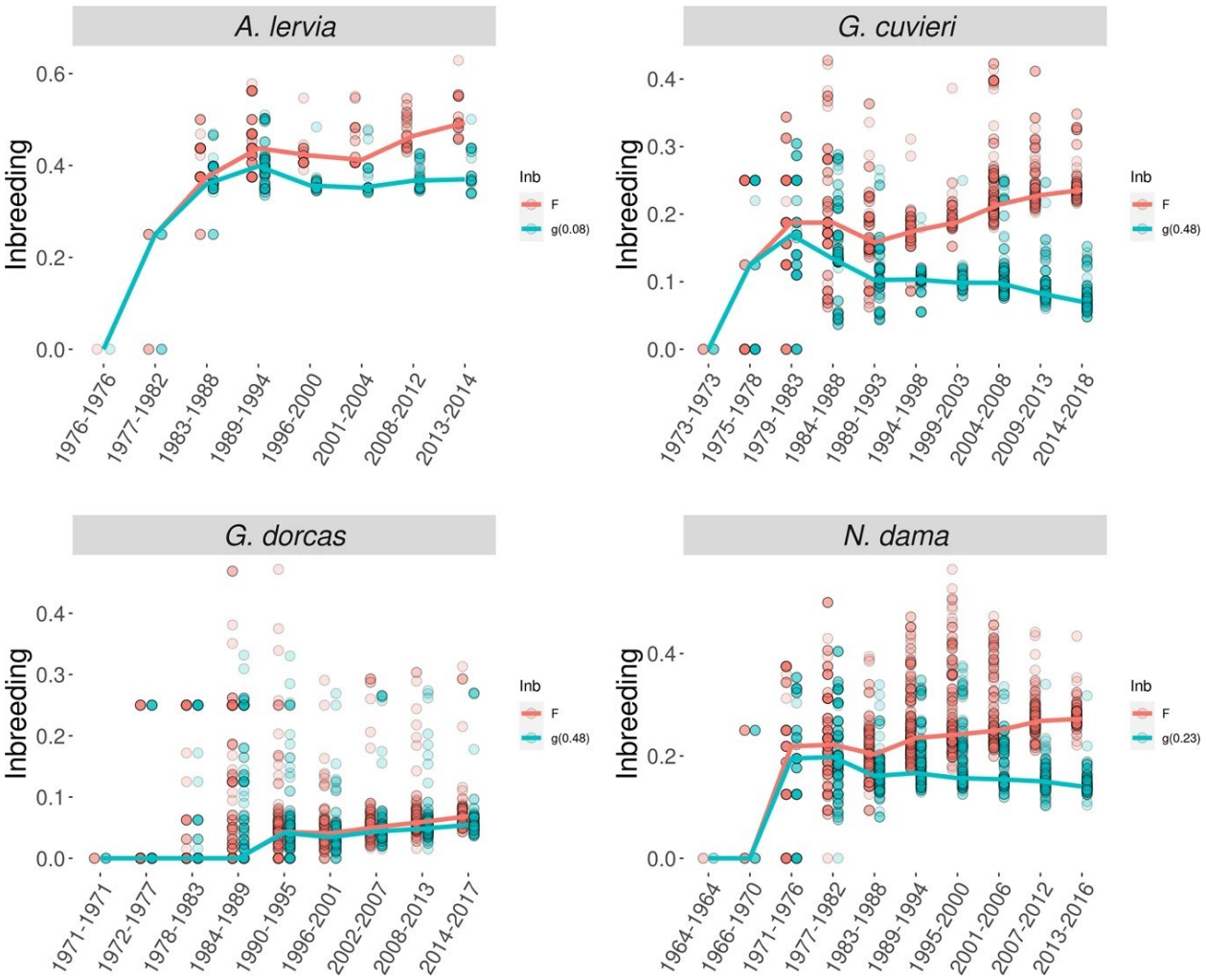


Figure 2. Evolution of the standard (F, red) and purged (g, green) inbreeding coefficients through time.

Purging leads to a fitness rebound, characterized by an initial decline in fitness due to inbreeding depression followed by a subsequent increase in population fitness, as illustrated in (**Figure 3**). The effect is most pronounced in the dama gazelle population. Interestingly, of the four evaluated populations, neither the smallest (barbary sheep) nor the largest (Dorcas gazelle) exhibited signs of purging. In the barbary sheep population, genetic drift likely overwhelmed purging due to its small size, while detecting purging in the Dorcas gazelle population probably requires additional generations López-Cortegano et al. (2021).

In the domesticated animals according to our best understanding the only available study is that of Kövér et al. (2023) where the authors re-analysed the Pannon white rabbit data of Curik et al. (2020). The only other study where the ancestral inbreeding and Inbreeding-Purging model were applied for the same dataset was López-Cortegano et al. (2018) claiming that Inbreeding-Purging Model had superior predictive characteristics compared to ancestral inbreeding predicting the future fitness of the evaluated population. The results of Kövér et al. (2023) were very similar to that of Curik et al. (2020) finding purging signs only between 1992 – 1997 but not afterwards.

Concerning the predicted fitness, it showed partial purging (Figure 4) which means that after a certain period the fitness stabilized and did not show further decrease. It also confirms the

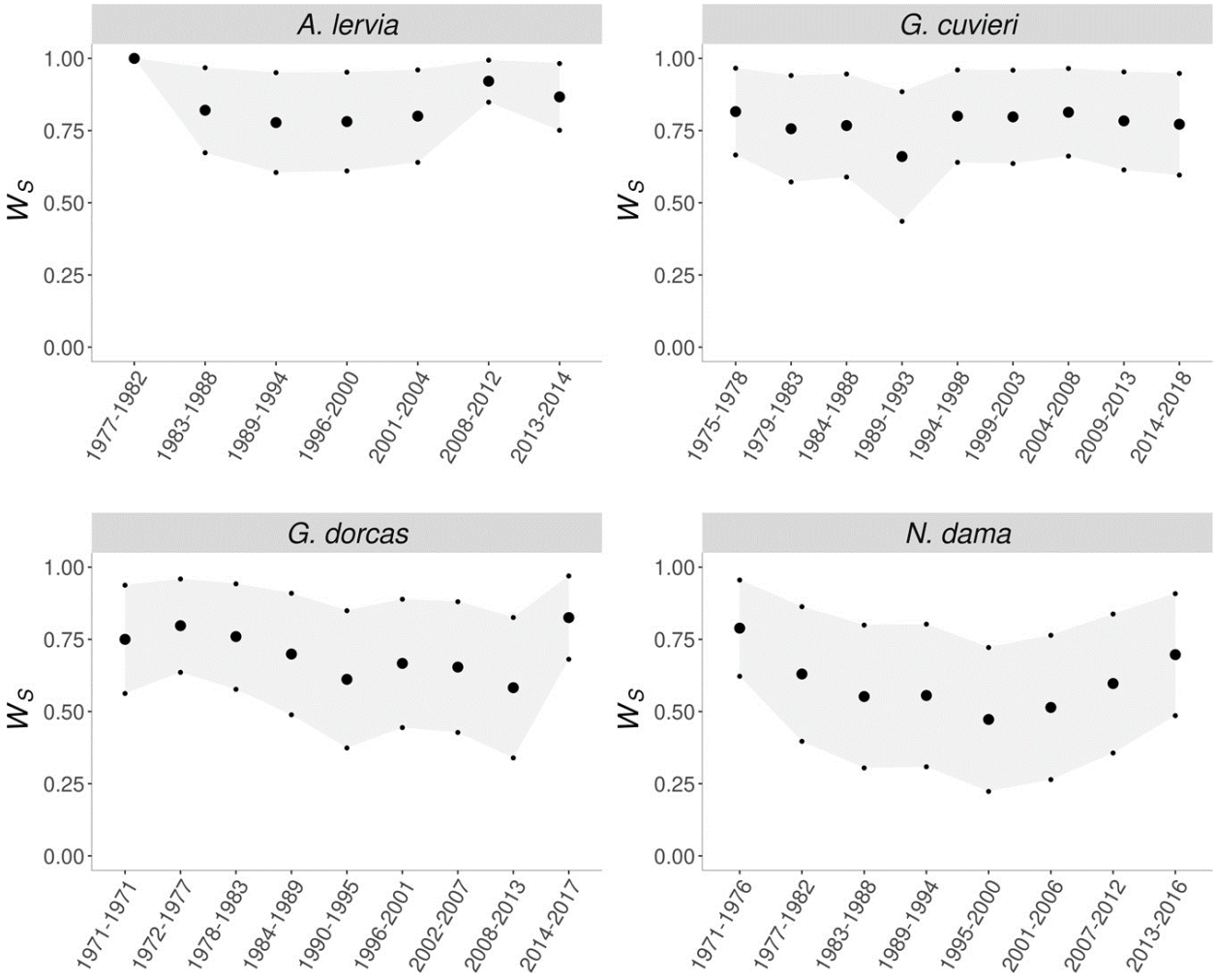


Figure 3. Evolution of the early survival (Ws). Large dots represent mean W_S, while small dots correspond to the mean value plus or minus one standard error.

conclusions of Curik et al. (2020) that in the first period genes with large affects were purged contrary to that of the genes with mild effects.

Advancements in genomic methods have enabled the detection of purging in the absence of pedigree data through whole-genome analysis (Dussex et al., 2021; Khan et al., 2021; Kleinman-Ruiz et al., 2022). These studies typically compare different populations of the same species (i.e. small–isolated and large–connected Bengal tiger (*P. tigris tigris*) populations (Khan et al., 2021); island vs. mainland Kākāpō (*Strigops habroptila*) populations (Dussex et al., 2021) and Iberian (*Lynx pardinus*) vs. Eurasian (*Lynx lynx*) lynx populations (Kleinman-Ruiz et al., 2022) in order to evaluate the differences in the frequency and genomic distribution of potentially deleterious genotypes.

.

2.1.5. Application possibilities of purging and future perspective

Although the purging phenomenon was investigated very extensively, especially in zoo populations (Ballou, 1997; Boakes et al., 2007) only a small fraction of these population showed the signs of purging, and the observed amount of the purged inbreeding load was usually not too large. Since inbreeding can fix harmful mutations there is a general consensus in the field of animal breeding that intentional inbreeding should be avoided Kristensen and Sørensen (2005) when possible. However, in conservation genetics several studies suggested that based on different breeding designs (e.g. circular sib mating) inbreeding may be beneficial due to purging (De Cara et al., 2013; Pérez-Pereira et al., 2022; Theodorou and Couvet, 2015). However, the efficiency of inbred mating depends on the balance between the loss of diversity, the initial decrease of fitness and the reduction of the inbreeding load De Cara et al. (2013). Therefore, the so-called application of purging should be treated with caution (Caballero et al., 2017; Ralls et al., 2020).

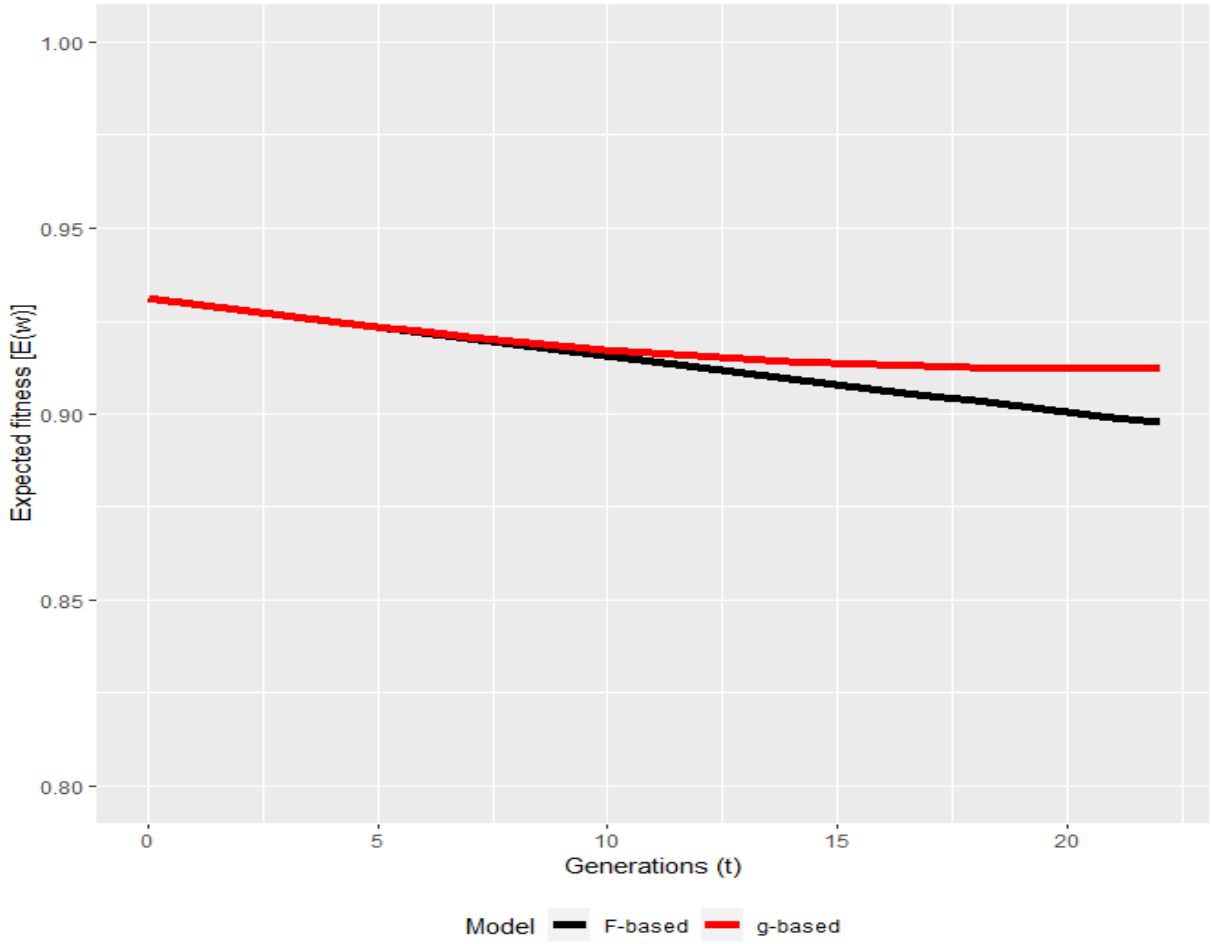


Figure 4. The predicted fitness based on the Wright (F_W) and on the purged (g) inbreeding coefficients.

2.2. Physiological and genetic aspects of some fitness traits' performance in pigs

2.2.1. Litter size

Throughout the research conducted, a consistent trend of increasing litter size (total number born – TNB or number born alive – NBA) has been observed. According to Lanferdini et al. (2018)

the litter size ranging from 9 to 16 piglets through the examined database. One year later, Feldpausch et al. (2019) reported the average litter size was 13.18 piglets when analysing two datasets from EU and US studies with emphasize that the EU studies averaged 2.12 more pigs per litter comparing to the U.S. studies. Danish pig production witnessing a significant increase from 11.80 total born piglets per litter in 1992 to 19.60 total born piglets per litter in 2020 (Riddersholm et al., 2021). The average TNB was 17.10 ± 3.40 (mean ± SD), with 16.10 ± 3.10 live born and 1.00 ± 1.40 stillborn (5.80%) piglets (Van den Bosch et al., 2022).

Litter size, as a complex and sex-limited trait, is influenced by a range of biological, nutritional, management, and environmental factors (Luković and Škorput, 2015; Vaishnav et al., 2023). The determination of physiological litter size in pigs involves several components that contribute to its complexity, such as ovulation rate, fertilization, embryonic development, uterus capacity, and fetal survival (Argente, 2016; Distl, 2007). Argente (2016) found out that the selection for ovulation rate or/and prenatal survival had been proposed to improve litter size indirectly. In pigs, it is common to observe high rates of fertilization, typically exceeding 90.00 to 95.00% that can provide the number of potential embryos needed to increase litter size (Geisert and Schmitt, 2002). Therefore, embryonic loss, especially during the 2nd to 3rd week of gestation is a significant hurdle to increasing litter size in pigs (Geisert and Schmitt, 2002). According to Langendijk (2021), the majority of prenatal losses in pigs occur during the embryonic phase (before day 35), with 20.00 to 30.00% of embryos lost by day 21, and an additional 10.00 to 15.00% lost by day 35. Variations in embryonic growth and elongation rates during the peri-attachment period (day 12 – 30 of pregnancy) can potentially modify the uterine environment, resulting in decreased survival rates for less-developed conceptuses (Tan et al., 2022). The success or failure of pregnancy in pigs is likely to be decided within the first 30 days of gestation (Almeida and Dias, 2022). In the period of mid-gestation (day 50 – 70 of pregnancy), accelerated fetal growth has the potential to surpass the uterine capacity, thereby causing the arrest of neighboring littermates due to overcrowding of conceptus attachment sites (Tan et al., 2022).

In addition, the maternal uterine condition during gestation is crucial for achieving good reproductive performance in pigs, which includes factors such as litter size, number of live or stillborn piglets, and growth (Argente, 2016). If the interaction between the embryos and the uterus is insufficient, the pregnancy may be lost, or there may be a compromise in embryo survival (Langendijk, 2021). Moreover, a litter with many mummified fetuses found at farrowing can be caused by various stressors experienced by the sow or developing offspring during the earlier stages of gestation, such as rough handling, poor nutrition, environmental stressors, or disease stress (Hines, 2021). Maternal nutrition during pregnancy, whether it is undernutrition or overnutrition, can alter organ structure, impair prenatal and neonatal growth and development, and reduce feed efficiency for lean tissue gains in pigs (Ji et al., 2017).

Numerous studies have found reductions in litter size with increasing levels of inbreeding (Köck et al., 2009; Saura et al., 2015; Zhang et al., 2022; Farkas et al., 2007; Rodrigáñez et al., 1998; Rodríguez et al., 2013; Silió et al. 2016; Rodríguez et al., 2013; Vitezica et al., 2016; Shi et al., 2021). The estimation suggests that, on average, there was a reduction of 0.14 percent in the mean of a trait in domestic animals including pigs for every 1 percent increase in inbreeding, indicating the presence of inbreeding depression (Leroy, 2014). In a separate study conducted on Austrian Large White and Landrace pigs, it was observed that both litter and dam inbreeding

negatively impacted all reproductive traits, specifically by 10.00% inbreeding coefficient increase of litter and dam, the weaned litter size decrease 0.16 – 0.29 piglets (Köck et al., 2009). However, in the case of Large White pigs, sire inbreeding did not have a significant effect, while in Landrace pigs, it surprisingly showed a significant increase of total number piglets born (0.45) and born alive (0.43) with 10.00% of sire inbreeding coefficient (Köck et al., 2009). In addition, this research also figured out the effects of both old and new inbreeding on reproductive traits in general. Rodrigáñez et al. (1998) found negative effects of litter inbreeding on TNB and NBA in Large White pigs, with 10.00% increase in litter inbreeding associated with significant mean reductions of 0.27 piglets born and 0.39 piglets born alive while the dam inbreeding also showed a similar negative trend, but not statistically significant. Similarly, Farkas et al. (2007) estimated negative regression coefficients per 10.00% increase in inbreeding for NBA in Hungarian Landrace (−0.16 to −0.05 by litter inbreeding and −0.20 to −0.04 by dam inbreeding) and Hungarian Large White (−0.231 to −0.10 by litter inbreeding and −0.28 to −0.11 by dam inbreeding) populations. Culbertson et al. (1997) likewise reported negative regression coefficients of −0.09 and −0.06 per 10.00% inbreeding for NBA in Hampshire and Duroc, respectively. According to Zhang et al. (2022) an increase of 10% in inbreeding coefficient contributed to a decrease of approximately 0.50 piglets both for TNB and NBA. Silió et al. (2016) reported that there were significant negative impacts of new and fast inbreeding on litter size of Torbiscal pigs. Specifically, a 10.00% increase in new inbreeding resulted in a decrease of 0.20 born piglets per litter, while 1.00% increases in total and new inbreeding rates led to reductions of 0.03 and 0.02 piglets, respectively. For Gamito pigs, the reduction of 0.91 piglets due to a 10.00% increase in old inbreeding and a decrease of 0.17 piglets associated with X-linked genes inbreeding were found. Rodríguez et al. (2013) observed a significant decrease of 0.21 (Posterior *Prob.* > 0 = 0.02) piglets per litter for every 10.00% increase in F_{New} whereas the effects of F_{Old} were non-significant. In Iberian pigs, Saura et al. (2015) found that a 10.00% rise in F_{HOM} on chromosome 13 reduced both TNB and NBA by approximately 0.12 piglets. When analysing the pedigree data using all available information, the estimates of inbreeding depression for NBA indicated a value of –0.197 ± 0.092, representing the negative impact on NBA per 10% increase in the inbreeding coefficient (Fped). Significant reductions were observed in the number of piglets per 10.00% increase in the inbreeding coefficients Fsnp (–0.12 ± 0.05), Froh (–0.23 ± 0.09), and Froh_long (–0.18 ± 0.07) for SSC13. Vitezica et al. (2016) reported inbreeding depression (based on average homozygosity) of 1.29 and 1.07 piglets born per 10.00% increase in inbreeding for pure line 1 and 2, respectively. Shi et al. (2021) illustrated reductions in TNB of 0.57, 0.34 and 0.82 piglets (Canadian line) per 10.00% increase in F_{ROH}, F_{GRM} (genomic relationship matrix derived from single nucleotide polymorphism), and F_{PED}, respectively. However, only F_{ROH} showed a significant effect in the French line, with 0.69 – piglet decline in TNB per 10.00% increase.

Traits such as ovulation rate, embryonic survival, uterine capacity and litter size were affected by genetic factor (Chen et al., 2022; Yu et al., 2022; Zak et al., 2017; Zhang et al., 2020). However, the heritability of the embryonic survival rate and ovulation rate was quite high, ranging from 0.14 – 0.42 (Zak et al., 2017) while the heritability of litter size was in lower range of 0.06 – 0.09 (Chen et al., 2022; Yu et al., 2022; Zhang et al., 2020). This can be inferred that the negative effects of inbreeding on litter size in pigs are likely mediated indirectly through the regulation of ovulation and embryonic survival. There is a complex genetic regulation of pigs' litter size, with the mapping of more than 50 quantitative trait loci (QTL) associated with litter size traits in pigs (Distl, 2007; Ernst and Steibel, 2013). Recent relevant research has indicated that in pigs, there are

multiple genes that have a significant impact on litter size and its component traits, both at allelic and genome-wide levels (Vaishnav et al., 2023). Litter size traits in pigs have been linked to over 12 candidate genes (Mo et al., 2022; Sell-Kubiak et al., 2022). In addition, Balogh et al. (2019) found that litter size (total number of piglets born) was associated with 3 SNPs markers located on chromosome 1, 6 and 13. Similarly, Shi et al. (2021) reported inbreeding depression for TNB in Canadian pig line linked to chromosome 6,7,8 and 13, with candidate genes *CUL7*, *MAPK14* and *PPARD* implicated in placental development, and *AREG* and *EREG* associated with oocyte maturation.

While there have been numerous studies documenting the increasing trend of litter size in commercial pigs, limited data exists regarding litter size in conservation pig. Litter size, a multifaceted trait that is influenced by various biological, nutritional, management, and environmental factors, exhibits complexity and sexual dimorphism. This trait has also been studied in terms of estimating the influence of inbreeding depression on it. Despite some studies identifying genes that affect litter size, this trait still exhibits low heritability, and the underlying physiological mechanisms of inbreeding depression on this trait remain unclear. Further research is needed to fully understand the genetic and physiological aspects of inbreeding depression and its impact on litter size.

2.2.2. Piglets born alive/dead.

The proportion of stillborn piglets can vary from 5.00% to 14.30% (Langendijk & Plush, 2019; Lanh & Nam, 2022). The number of piglets born alive was determined by subtracting any stillborn piglets from the total litter size (Threadgold et al., 2021). Modern breeding sows have undergone selection processes to enhance their litter sizes, resulting in increase the number of piglets weaned and ultimately sold. However, a correlation exists between increased litter sizes and reduced viability of piglets (Rutherford et al., 2013). To enhance the number of piglets born alive and subsequently improve the weaning count, achieving production targets might be more effectively accomplished by prioritizing the reduction of stillbirths rather than solely focusing on increasing the overall litter size (Threadgold et al., 2021).

Leenhouwers et al. (2003) classified stillbirth into four categories: non-fresh (characterized by partial brown skin colour resulting from tissue degradation and autolysis), prepartum (occurring before delivery), intrapartum (taking place during the farrowing), and postpartum (occurring shortly after birth). Non-fresh and prepartum stillbirths are primarily attributed to infectious agents, while intrapartum and postpartum piglet deaths are predominantly caused by non-infectious factors (Leenhouwers et al., 2003; Vanderhaeghe et al., 2013). Among all stillborn piglets, 10% experienced mortality shortly prior to farrowing, 75.00% died during the actual farrowing process, and the remaining 15.00% death immediately after farrowing (Leenhouwers et al., 1999). Therefore, studying physiological mechanism of stillborn piglets would focus on non-infectious factors.

Physiological mechanisms that affect piglets born alive or dead can be influenced by various factors including genetic factors, maternal factors (body condition, litter size, parity, gestation length, farrowing duration), piglet factors (birth interval, birth order, and birth weight) and environmental factors (Vanderhaeghe et al., 2013). According to Jatfa et al. (2018) approximately 70.00% of the risk factors associated with stillbirth can be attributed to non-

infectious factors, in which genotype, dystocia and hypoxia were emphasized. Therefore, in this review the component factors namely the genotype, litter size and birth weight were considered to clarify.

The heritability of stillborn piglets and NBA are relatively low ranging around 0.05 – 0.08 and 0.02 – 0.12, respectively (Hollema et al., 2020; Ogawa et al., 2019; Paixão et al., 2019), and they are influenced by a large number of genetic loci with effects that are low to moderate in magnitude (Bergfelder-Drüing et al., 2015). In addition, heritability based on the sire and dam components for stillborn piglets ranged between 0.08 to 0.24, respectively (Strange et al., 2013). This means that genetic factors have a limited influence on total number of piglets born dead.

According to Vanderhaeghe et al. (2013) the incidence of stillborn piglets was genetically affected by both sows and piglets themselves. Leenhouwers et al. (2003) clarified that the sow's genetic factors were found to affect the probability of mortality during the farrowing process while the piglets' genetic factors were found to influence mortality rates before and right after farrowing. Variations in the occurrence of stillbirth among different lines or breeds of pigs can be attributed to a complex interplay of genetic factors (Leenhouwers et al., 1999; Vanderhaeghe et al., 2010). Although Imaeda et al. (2021) found that the incidence of stillborn piglets was higher in Microminipigs compared to other pig breeds, this could be because of the too small body size of Microminipig. Canario et al. (2006) documented that stillborn piglets from Meishan sows were significantly lower than piglets born from Large White, Laconie male line and F1 Duroc x Large White sows. This difference was speculated by the ability to limit conceptus growth and crowing uterine based on the vascularity of the placenta and the homogeneity of placenta weight in a litter of Meishan pigs (Canario et al., 2006). Leenhouwers et al. (1999) similarly reported that purebred lines tend to have a higher number of stillborn piglets (+0.5 to 1 piglet) per litter compared to crossbred lines. However, the authors also noted that the differences in the number of stillborn piglets among different lines may vary depending on the litter size or parity under consideration (Leenhouwers et al., 1999). It seems that the incidence of stillborn piglets and total number of piglets born alive are some extents affected by the genetic factor, but the majority effects are indirectly through the interaction of litter size, birth weight, parities and other components.

The latest version of quantitative trait loci (QTL) mapping in the pig genome includes a total of 28,720 identified QTLs (Chen et al., 2019). Among these QTLs, a subset of 2,129 QTLs has been specifically identified for reproduction traits, including 163 QTLs associated with "Total number born alive", 97 QTLs associated with "Number of stillborn", and 95 QTLs associated with "Mummified pigs" (Chen et al., 2019). A study has identified specific regions on the pig genome (QTL SSC5, SSC13) that are linked to early lethality, contributing significantly to the occurrence of stillborn piglets (Cassady et al., 2001). Wu et al. (2019)reported some specific regions on the pig genome that affect the number of mummified and stillborn piglets, specifically being SSC3 (for Landrace at parity 3) and SSC9 (for Large White at parity 2), in which the effect genes ASTN1/BRINP2 on SSC9 was also identified.

The research findings indicated that the relationship between litter size and stillbirth was not linear (Vanderhaeghe et al., 2013). Both large and small litters showed an increased likelihood of stillbirth, suggesting that the probability of stillbirth was higher in both extremes of litter size (Vanderhaeghe et al., 2013). However, a recent research found that each additional piglet added to the litter resulted in a linear increase of 0.50% in the percentage of stillbirths (Van den Bosch

et al., 2022). Andersson et al. (2016) reported that larger litters can lead to a rise in the number of piglets born dead, a decline in the proportion of piglets successfully weaned, and greater variability in the overall quality of the piglets. In the presence of larger litter sizes, low-birth weight piglets face increased disadvantages when competing with their littermates, and this disadvantage is further intensified when the litters come from older sows (Cabrera et al., 2012). There was a high positive correlation (r = + 0.98) between increase number of newborn in the litter and stillborn piglets since the proportion of stillborn piglets increased significantly from 5.90% to 14.60% when the number of piglets in the litter increased from 7 – 11 to 17 – 21 piglets (Siraziev & Gruzdova, 2020).

An increase in litter size was connected with fetal crowding and the extended durations of farrowing (Rutherford et al., 2013; Van Rens and van der Lende, 2004), which subsequently increases the risk of hypoxia for the piglets (Herpin et al., 2001). Van den Bosch et al. (2023) also confirmed that prolonged farrowing can reduce piglet survival during birth or in the first day of life as successive uterine contractions may hinder oxygen supply from the mother to the fetus through the placenta and umbilical cord. According to Roongsitthichai and Olanratmanee (2021); Threadgold et al. (2021) asphyxia and dystocia during birth were significant factors leading to stillbirths and early mortality in live-born piglets. However, Van den Bosch et al. (2022) found no interaction between litter size and prolonged farrowing duration although both of these two factors were independently detrimental effect stillborn piglets. In addition, Van den Bosch et al. (2022) suggested that litter size has a greater influence on stillbirth percentages compared to the duration of farrowing.

In another aspect, a small litter size has a negative impact on the proportion of stillborn piglets (Canario et al., 2006; Knol et al., 2002a), as it is potentially associated with the presence of oversized piglets, resulting in difficulties during the farrowing process (Vanderhaeghe et al., 2013). Furthermore, small litters (less than 6 piglets) frequently indicate reproductive abnormalities, which in turn lead to diminished chances of piglet survival when compared to intermediate litters (6-11 piglets) (Cecchinato et al., 2008).

In relation to stillbirth rate, a low birth weight of the litter (<0.80 kg) was frequently cited as a commonly reported risk factor (Gourley et al., 2020; Le Cozler et al., 2002; Leenhouwers et al., 2003; Nam and Sukon, 2021; Udomchanya et al., 2019; Vanderhaeghe et al., 2013; Zaleski and Hacker, 1993). Gourley et al. (2020) reported that there was a significant association ($P < 0.01$) between an increased stillborn rate and larger litters with heavier litter weights and lighter piglet weight at birth. There was a significant difference in piglets birth weight of piglets born alive and piglets born dead (1,175 vs. 1,002 g, $P < 0.001$), respectively (Udomchanya et al., 2019). In the same research, the occurrence of stillborn piglets was higher among piglets with a birth body weight of ≤1,000 g compared to those with a birth body weight of 1,001 – 1,300 g or >1,300 g. According to the findings, piglets weighing between 0.10 – 0.60 kg more than the average birth weight of their litter exhibited the lowest risk of intrapartum stillbirth (Nam & Sukon, 2021). Conversely, piglets smaller than the average birth weight of their litter and those excessively heavy had a higher probability of being stillborn (Nam & Sukon, 2021). The presence of a low birth weight could indicate a diminished quality of uterine support, such as under or malnutrition of the sow, which in turn can lead to reduced overall vitality of the litter during the onset of parturition (Vanderhaeghe et al., 2013). In addition, lower body weight piglets may have relatively smaller

umbilical cords that are more susceptible to umbilical rupture (Vanderhaeghe et al., 2013). According to Mota-Rojas et al. (2006), Zaleski and Hacker (1993) piglets with lower body weight may exhibit reduced efficiency in utilizing oxygen due to their lower blood haemoglobin concentration that make them more susceptible to hypoxia during farrowing. In contrast, piglets with heavy birth weight (>2.10 kg) may experience dystocia, leading to prolong farrowing duration, resulting in hypoxia (Canario et al., 2006; Nam and Sukon, 2021; Vanderhaeghe et al., 2013). Several studies reported a higher incidence of stillbirths and lower individual birth weights in male piglets compared to their female counterparts, speculating that male piglets were more risky to be born dead (Canario et al., 2006; Knol et al., 2002b; Vanderhaeghe et al., 2013). Knol et al. (2002c) documented that selecting for a higher average birth weight had the potential to reduce postnatal mortality but concurrently lead to an increase in the proportion of stillborn piglets.

Both litter size and birth weight have effects on piglets born alive or dead in a way of optimum threshold, meaning that the detrimental effects happen to the two extreme values of those factors. In addition, these two factors exhibit a causal relationship that influences the piglets born alive or dead, and their interplay is also influenced by various other factors such as environmental conditions and dam-piglet interactions. It is important to note that their effects are not independent but rather interconnected within a complex system.

The proportion of stillborn piglets can range from 5.00% to 14.30%, and reducing stillbirths is important for improving production targets. Genetic factors have a limited influence on the number of stillborn piglets, with heritability estimates ranging from 0.05 to 0.08. The occurrence of stillbirths is affected by genetic factors in both sows and piglets. Litter size and birth weight also play significant roles in stillbirth rates. Both large and small litter sizes increase the probability of stillbirth, and low birth weight is associated with higher stillbirth rates.

2.2.3. Birth weight

It can be seen from **TableS 2** that the average birth weight of piglets is around 1.50 kg, ranging from 0.30 – 3.30 kg. Most of the published research is related to prolific pig breeds (Landrace, Yorkshire, Duroc or mixed), so they shared similar average birth weights, except for Piau pig breed which is Brazilian pure pig breed having lower average birth weight (0.997 kg). This could be because different genotype made the birth weight variations. According to Moreira et al. (2020) litters of high prolific sows comparing to low prolificacy had 43.00% higher average birth weight of total piglets born and total piglets born alive. This can be explained by the fact that high prolific sows, after many years of selection targeting for bigger litter size, have bigger litter birth weight.

Within commercial practice, birth weight is widely utilized as the predominant indicator to assess a piglet's vigour of survival until the weaning stage (Tucker et al., 2021). The threshold for defining low birth weight piglets was determined based on a raw value derived from analysing the relationship between birth weight and the statistical increase in the risk of mortality (Mugnier et al., 2023). Feldpausch et al. (2019) suggested that piglets with birth weight around 1.11 kg have more chance to survive until weaning than the others.

Research indicates that increased parity and larger litter sizes have detrimental effects on piglet birth weight, resulting in a decline in the average birth weight along with an increased level

of variability (Kitkha et al., 2017). Birth weight of the piglets is affected by large litter size as there is an association between larger litter sizes and reduced birth weights (Heuß et al., 2019). Peltoniemi et al. (2021) also agreed that increasing litter sizes concomitantly resulted in decreased piglet birth weight and increased within-litter birth weight variations. Each additional piglet born to a litter linearly decreased average piglet birth weight (17.60 g, $p < 0.01$), increased farrowing duration (11min, $p < 0.01$), and increased stillbirth (0.50%, $p = 0.04$) (Van den Bosch et al., 2022). In addition, according to Riddersholm et al. (2021) the impact of litter size on piglet birth weight (PBW) was found to be statistically significant; for each additional piglet within a litter, the average PBW decreased by 19.50 g for first-parity sows and 21.70 g for sows with 2nd to 9th parity. PBW of sows from parity 2 – 9 decreased by 25.80 g with increasing weaning to insemination interval ($p < 0.001$). Furthermore, birth weight of piglets and within-litter birth weight variations were also affected by the parity of the sows, with unfavourable affections came from older sows (Riddersholm et al., 2021).

The development of the litter is influenced by the quality of follicles, which is determined in the period before to insemination (Riddersholm et al., 2021). It was reported that the length of the previous lactation has an influence on litter size (Hoshino and Koketsu, 2009) and a weaning-to-insemination interval of less than eight days had a negative impact on the high within-litter variation in piglet birth weight compared to intervals above 21 days (Wientjes et al., 2013). After the insemination, intrauterine environment with nutritional status of the sow become important factors for placenta and litter development (Riddersholm et al., 2021). Inadequate placenta function posed a hindrance to the growth and development of foetus (Town et al., 2004) as well as the size and effectiveness of the placenta can impact PBW and its variation (Che et al., 2017). In sows, the crowded uterine affected the sex ratio of litter, the development of placenta and the expression of embryonic myogenin in early gestation (Tse et al., 2008) such that increased litter size had negative effects on piglet birth weight and birth weight variations.

Previous research has indicated that the heritability of birth weight was low, ranging from 0.02 to 0.21 (Kaufmann et al., 2000). According to Zaalberg et al. (2023), heritability estimates were high for mean litter weight at birth (0.33) but low for litter size traits (0.04 – 0.08) and individual piglet weight (0.06 – 0.07), with maternal heritability being significantly higher for individual piglet weight than direct heritability. However, applying a Bayesian multivariate threshold-linear model to a dataset of 22,483 piglets revealed significant estimates indicating maternal and direct heritability for birth weight ranging from 0.29 to 0.36, respectively (Nguyen et al., 2021). Another research using the similar model to a data of 21,835 individual piglets reported similar results with maternal and direct heritability for birth weight range from 0.28 to 0.36, respectively (Roehe et al., 2010). In relation to piglet birth weight, the heritability of birth weight variability was documented in previous studies, with estimates ranging from 0.08 to 0.12 (Damgaard et al., 2003; Wittenburg et al., 2008). These studies indicated that the heritability of birth weight was in the wide range from 0.02 to 0.36 and the variation in birth weight was influenced significantly by both foetal genetic factors and maternal genetic effects, making it valuable to identify the specific genes or variants responsible for this variability.

The examination of candidate genes such as MyoD (Te Pas et al., 1999) , MSTN (Jiang et al., 2002), and DBH (Tomás et al., 2006) has led to the identification of several markers associated with birth weight. A total of 17 genomic regions associated with birth weight were identified, with

12 of them overlapping with previously reported QTL regions for piglet birth weight, average birth weight, and litter birth weight (Zhang et al., 2014). A genome-wide association study (GWAS) on 82 sows with extreme birth weight variability identified 266 genome-wide significant SNPs ($p < 0.01$), enriched on chromosomes 7, 1, 13, 14, 15, and 18, and further analysis revealed genes related to plasma glucose homeostasis (GLP1R), lipid metabolism, and maternal-fetal lipid transport (AACS, APOB, OSBPL10, and LRP1B), suggesting their potential role in birth weight variability (Wang et al., 2016). Recently, some more genes associated with birth weight were reported based on genome-wide association study (GWAS), being SKOR2, SMAD2, VAV3, NTNG1 (Li et al., 2020), and ARAP2 and TSN (Lee et al., 2020).

The biological mechanism underlying piglet birth weight involves a combination of genetic, maternal, and uterine environmental factors. In which, the heritability of birth weight ranges from 0.02 to 0.36, indicating a significant contribution of both foetal and maternal genetic effects. Several candidate genes have been associated with birth weight, providing insights into the genetic basis of birth weight variability in pigs. Larger litter sizes have a negative effect on piglet birth weight, resulting in decreased average birth weight and increased variability. Factors such as the quality of follicles, weaning-to-insemination interval, and placenta function also influence piglet birth weight and birth weight variation within litters.

2.3. Genetic background of Mangalica pigs

According to Egerszegi et al. (2003) tracing the historical origins of ancient swine breeding in Hungary is challenging due to the scarcity of archaeological evidence. In the research of Egerszegi et al. (2003), Mangalica was described as progenies of crossing extinct Hungarian Alföldi, Szalonta and Bakony breeds and Serbian Sumadia pig breeds in the 19th century. In 1833, Serbian Prince Milos gifted the first Sumadia stock (9 sows and 2 boars) to Archduke József, and these animals were brought to Kisjenő in Hungary. Crossbreeding extinct Hungarian pig breeds with this stock led to the rapid spread of Sumadia bloodlines across Hungary's large breeding populations. While there were mentions of Mangalica existing prior to 1833, the widespread integration of Sumadia genetics standardized the fat-type swine in Hungary, which came to be known as Mangalica (Egerszegi et al., 2003).

Currently, three Mangalica breeds (Zsolnai et al., 2006) (**Figure 5**) are recognized in Hungary namely Blonde, Swallow-Belly, and Red, with the Blonde being the most dominating. In addition to these three recognized breeds, the Black Mangalica, previously documented as an extinct color variant in Hungary (Porter, 2020), has been the focus of recent resurgence efforts. The HNAMB has undertaken initiatives to recreate this variant by crossbreeding, involving a population of about 700 females and six male lines distributed across 12 herds (personal communication, 2025).

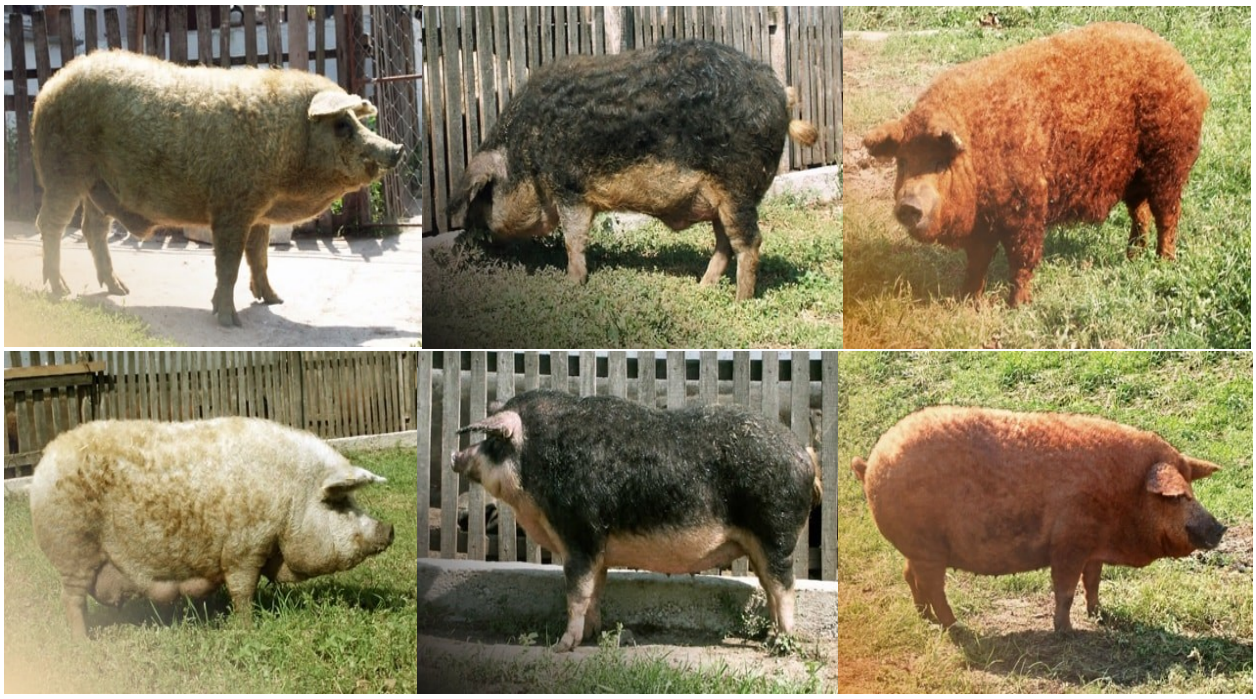


Figure 5. Male (upper row) and female (lower row) Mangalica pigs in Hungary: Blonde, Swallow-Belly, and Red breeds (left to right) (HNAMB, n.a.) (***https://moe.org.hu/en/breeding/breeds/***).

The development of the Mangalica breeds was documented in (Egerszegi et al., 2003, Botha et al., 2014) and further illustrated in **Figure 6** (Zsolnai et al., 2013). The Blonde Mangalica likely presented earlier than others and originated from crossing the small, extinct Alföldi pig with the Serbian Sumadia swine, followed by crossbreeding with Szalonta and Bakony pigs. The Swallow-Belly was derived from crosses between Blonde and Black Mangalica pigs. The Red Mangalica emerged in the late 19th century through mating Blonde sows with Szalonta boars, producing a type initially named New-Szalonta (NHAMB, n.a.). The Red Mangalica population shows characteristics closely resembling those of the Blonde Mangalica, with superior meat quality and enhanced growth performance (Hankó, 1940).

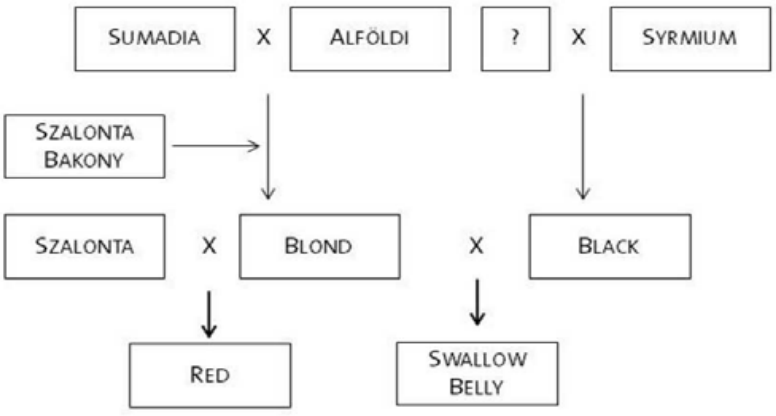


Figure 6. Breeding schemes for Mangalica breeds in accordance with herd books (Zsolnai et al. 2013).

The advances of genomic technology have facilitated investigations into the historical origins of the Mangalica population using mitochondrial DNA (mtDNA). Marincs et al., (2013) conducted a comprehensive comparative analysis of mtDNA D-loop sequences from Hungarian Mangalica and other European pig breeds to reveal their origins and relationships. The findings suggest that the existing Mangalica population in Hungary likely developed through two possible scenarios. These include either the admixture of other European breeds and wild board or independent evolution following the divergence of ancient European swine lineages. Further research by Frank et al., (2017), sequenced the mitogenome of one male from each Mangalica breed, revealing a close relationship between the mitogenome of some Mangalica individuals ant the Croatian Turopolje breed. This similarity indicates either a shared maternal lineage or historical admixture between these populations. However, the mitogenome origins of specific purebred Mangalicas preserved in the Hungarian Mangalica Gene Reserve remain undetermined.

3. MATERIALS AND METHODS

3.1. Genealogical data

Data for analyzing in this study were provided by the Hungarian National Association of Mangalica Breeders. The organization recorded the data of the registered Mangalica pigs in the Herdbook born between 1981 and 2023, respectively. Genealogy analysis was restricted to breeding animals.

From the examined Mangalica pig breeds the pedigree of the Blonde Mangalica was the largest containing 12,808 individuals (up to 2021). The Swallow Belly and the Red Mangalica pedigrees were smaller, and they consisted of 2,393 and 3,963 pigs, respectively. The pigs born in the period from 2016 to 2021 (REF2021) were determined as reference population which was used to assess the genetic variability. Besides, several reference populations were defined for pigs born between 1981-1985, 1986-1991, 1992-1997, 1998-2003, 2004-2009 and 2010-2015, respectively to characterize the evolution of pedigree-based parameters.

For population subdivision and mingration assessment, the genealogical data were extended up to 2023 as in **Table 2**.

Table 2. Number of herds and breeding animals in three Mangalica breeds from 1980 to 2023.

	Blonde	**Swallow-Belly**	**Red**
Total number of individuals	14,550	2,638	4,566
Total number of herds	258	94	145
Number of active herds	78	31	55
Total number of sires	748	237	305
Number of active sires	427	129	188
Total number of sows	6,393	1,094	1,779
Number of active sows	3,944	669	951

3.2. Pedigree completeness

The pedigree completeness was evaluated by: (1) the number of full generations traced which is defined as the number of generations separating the offspring from the furthest generation of which ancestors are known (Gutiérrez and Goyache, 2005), (2) the maximum number of generations traced is defined as the number of generations that separates the individual from its furthest ancestor (Gutiérrez and Goyache, 2005), (3) the complete generations equivalent (CGE) for each animal in the pedigree data that is computed as the sum over all known ancestors of the terms computed as the sum of $(1/2)^n$, where n is the number of generations separating the individual from each known ancestor (Maignel et al., 1996), (4) the pedigree completeness index which is the completeness of each ancestor in the pedigree to the 5th parental generation and MacCluer et al. 's (1983) index of completeness. Pedigree of depth d generations for paternal and maternal lines:

$$I_{dpat/mat} = \frac{1}{d}\sum_{i=1}^{d} a_i$$

Where a_i is the proportion of ancestors present in generation i. The overall completeness index for the pedigree of each animal was computed as the harmonic mean of the paternal and maternal indices MacCluer et al. 's (1983).

$$I_d = \frac{4\, I_{dpat}\, I_{dmat}}{I_{dpat} + I_{dmat}}$$

This I_d calculates the average proportion of known ancestors from generation 1 to d, using information on all d generations while weighting them unequally: each parent contributes twice the influence of each grandparent and so on. This is because inbreeding can only be identified when both the mother's and father's ancestral lines are known MacCluer et al. 's (1983).

3.3. Diversity parameters

3.3.1. Average relatedness coefficient (AR) and inbreeding coefficient

AR of each individual is defined as the probability that an allele randomly chosen from the whole population in the pedigree belongs to a given animal (Gutiérrez and Goyache, 2005)

Inbreeding coefficient was defined as the probability that the two alleles at any locus in an individual are identical by descent (Wright, 1922) and was computed following Suwanlee at al. (2007).

$$\mathrm{F}_{W(x)} = \sum \left(\frac{1}{2}\right)^{n+n'+1} \left(1 + f_{a(c)}\right)$$

In which x is the individual, n and n' are the number of generations from sire and dam respectively to the ancestor in question, and $f_{a(c)}$ is the inbreeding coefficient of the common ancestors.

Ballou (1997) defined inbreeding as the cumulative proportion of an individual's genome that has been previously exposed to inbreeding in its ancestors. The Ballou's inbreeding coefficient was calculated as the following formula.

$$F_{Bal(x)} = \frac{\left[F_{Bal(s)} + \left(1 - F_{Bal(s)}\right) * F_{W(s)} + F_{Bal(d)} + \left(1 - F_{Bal(d)}\right) * F_{W(d)}\right]}{2}$$

Where $F_{Bal(x)}$ is the ancestral inbreeding coefficient for an individual *(x)*, F_W is the Wright's inbreeding coefficient and the subscripts *(s)* and *(d)* represent for the sire and dam, respectively.

Kalinowski et al. (2000) defined inbreeding coefficient ($F_{Kal(x)}$) as the probability that any allele in an individual is currently autozygous and has been autozygous in previous generations at least once. The Kalinowski "new" inbreeding coefficient was defined as the probability that any alleles in an individual is autozygous for the first time and was calculated as the deduction of $F_{W(x)}$ and ($F_{Kal(x)}$) (Kalinowski et al., 2000; Schäler et al., 2020).

$$F_{New(x)} = F_{W(x)} - F_{Kal(x)}$$

3.3.2. Generation interval (GI)

The GI determined the average age of parents at the birth of their progeny that were subsequently kept for reproduction (Gutiérrez and Goyache, 2005), being computed for the 4 pathways (sire – son, sire – daughter, dam – son, and dam – daughter).

3.3.3. Effective population size (N_e)

N_e is defined as the number of breeding animals that would lead to the actual increase in inbreeding if they contributed equally to the next generation (Wright, 1931). In this study, the N_e was estimated from individual increase in inbreeding (ΔF_i) called as "realized effective population size - $\overline{N_e}$) (Cervantes et al., 2008a; Gutiérrez et al., 2009).

$\overline{N_e} = \frac{1}{2\overline{\Delta F}}$ in which $\overline{\Delta F}$ represents the average increase in inbreeding across individuals in a reference subpopulation, calculated from individual inbreeding increases (ΔF_i)

3.3.4. Predicting future inbreeding

The inbreeding coefficients in the next 25 years were predicted and the relevant populations were classified in the five categories of endangerment according to (Alderson, 2009). The predicted inbreeding coefficients were the sum of initial inbreeding coefficients (t = 0) of reference populations and the expected inbreeding increase in the next 25 years (t = 25). Using the annual inbreeding rate (ΔF_y) the inbreeding increase was calculated as $F_t = 1 - (1-\Delta F_y)^{t-1}$ (Falconer and Mackay, 1996; Gutiérrez et al., 2009).

3.3.5. Effective number of founders (f_e)

The effective number of founders (f_e) means the number of founders contributing equally that would be expected to produce the same amount of GD as in the studied population (Lacy, 1989). This parameter was calculated by the equation: $f_e = \frac{1}{\sum_{k=1}^{f} q_k^2}$ where q_k is the genetic contribution of the *k*th founder (the proportion of genes in the current living, descendant population that originated from founder k) reference population and *f* is the total number of founders. Total number of founders (*f*) was defined as ancestors with unknown parents. Under the selection, the contribution of reproductive individuals is usually unequal so that another parameter known as effective number of ancestors was calculated to complement for the loss of genetic variability.

3.3.6. Effective number of ancestors (f_a)

The effective number of ancestors (f_a) is the minimum number of ancestors (not necessarily founders), explaining the complete genetic diversity of the population (Boichard et al., 1997). This parameter is calculated as $f_a = \frac{1}{\sum_{j=1}^{a} q_j^2}$ where *qj* is the marginal contribution of an ancestor j, which is the genetic contribution made by an ancestor that is not explained by other ancestors chosen before. The ratio of the two values (f_a/f_e) indicates whether bottleneck effects occur in the studied population. The bottleneck happens when the ratio value is much lower than one.

3.3.7. Effective number of founder genomes (founder genome equivalents – f_g)

Founder genome equivalents (f_g) is the number of founders that would produce the same expected heterozygosity in the studied population if the founders equally contributed and were not lost of alleles (Ballou and Lacy, 1995). This parameter was calculated by the method of Caballero and Toro (2000).

3.3.8. Genetic diversity (GD)

The loss of GD was considered in two aspects: the unequal contribution of founders and the genetic drift. The bottleneck effect was characterized by the ratio f_a / f_e, occurring when the effective number of ancestors is much smaller than the effective number of founders or the ratio is much smaller than one.

Total GD of the reference population was estimated according to (Lacy, 1995) with GD = 1–1/(2f_g). The loss of genetic variation in both aspects was inferred as 1– GD. Similarly, the total amount of genetic diversity in the reference population possibly disappeared due to unequal founder contribution was calculated as GD* = 1–1/(2f_e) and the actual GD loss with this reason was measured as 1–GD*. Finally, the difference of GD* and GD was calculated to expose the genetic diversity loss because of genetic drift (Caballero and Toro, 2000; Honda et al., 2004).

3.4. Population subdivision

The genealogical data were used to analyse the structure of the subpopulations using the concept of Wright's F–statistics (Wright, 1978), calculated according to Caballero and Toro (2000) for each specified subpopulation. As described in Gutiérrez and Goyache (2005), we first calculated the average pairwise coancestry coefficient (f_{ij}) between individuals from two distinct subpopulations labelled i and j. The analysis includes all possible pairs of individuals within the entire metapopulation, considering the size of these subpopulations, so that the total of N_ixN_j pairs are considered. According to Caballero and Toro (2000), pedigree-based calculations assume that all coancestries are known through genealogical information back to the base population, in which all individuals are unrelated. Within a given subpopulation, labelled i, the following metrics can be calculated: the average coancestry, represented as f_{ii}, the average self-coancestry among the N_i individuals, represented as si, and the average inbreeding coefficient, represented as $F_i = 2s_i - 1$. The average distance between individuals of subpopulations *i* and *j* (or the kinship distance – D_k, for moleculary coancestry) is given by

$$D_{ij} = \left[\frac{(s_i + s_j)}{2}\right] - f_{ij}$$

From these parameters (s_i, s_j, f_{ij}) and the corresponding within subpopulation means (f_{ii}, f_{jj}), Caballero and Toro (2000, 2002) derived Nei's (1987) minimum genetic distance between two subpopulations (D_{ij}) as $D_{ij} = D_{ij} - [(D_{ii} + D_{jj})/2] = [(f_{ii} + f_{jj})/2] - f_{ij}$. Thus, the average minimum genetic distance over the entire metapopulation is $\overline{D} = \frac{\sum_{i,j=1}^{n} D_{ij} N_i N_j}{N_T^2}$.

Finally, Wright's F-statistics (Wright, 1978) (also called Wright's inbreeding coefficients) are calculated using the following formulae: where $F_{IS} = \frac{\tilde{F}-\overline{f}}{1-\overline{f}}$; $F_{ST} = \frac{\bar{f}-\tilde{f}}{1-\tilde{f}} = \frac{\bar{D}}{1-\tilde{f}}$ and $F_{IT} = \frac{\tilde{F}-\tilde{f}}{1-\tilde{f}}$, where F_{IS} is defined as the inbreeding coefficient of an individual with respect to the subpopulations, F_{ST} is defined as the mean inbreeding coefficient of the subpopulation with respect

to the entire metapopulation, F_{IT} is defined as the inbreeding coefficient of an individual in relation to the entire population and while $\tilde{f}$ and $\tilde{F}$ are the average coancestry coefficient and inbreeding coefficient for the entire metapopulation and $\overline{f}$ is the average coancestry coefficient for the subpopulation. Wright's inbreeding coefficients are not independent, as they are functionally interrelated since $(1 - F_{IT}) = (1 - F_{IS})\,(1 - F_{ST})$. The concept of population structure has more often been theorised as a deviation from the Hardy–Weinberg equilibrium, where F_{ST}, for example, was originally defined as the correlation between random gametes within subdivisions (subpopulations) relative to gametes in the entire population. For the link between the original concept and Wright's F coefficients estimated from pedigree, see Wright (1965). In population genetics theory, the F_{ST} is often regarded as a parameter that quantifies genetic drift and is therefore interpreted as a genetic distance ranging between zero and one (no difference in allele frequency if the F_{ST} is zero, or different alleles are fixed in each population if the F_{ST} is one). In this concept, the population structure can be represented by an F_{ST} matrix formed from the pairwise distances or the pairwise F_{ST} coefficients (distances) between all subpopulations. Here, the F_{ST} matrix was visualised using a heat map. The normality of the F_{ST} coefficients was evaluated by an Anderson–Darling normality test. We checked all F_{ST} values for every herd from which the largest value for each herd was taken. Then, we sorted these (maximum) F_{ST} values from lowest to highest and calculated the proportion of the total population they represent. Finally, the results were depicted as histograms and the cumulative population proportion according to the maximum F_{ST} values per each herd.

3.5. Migration assessment

The actual migration of pigs among herds derived from the stud book was visualised by the chord diagram. Every individual's herd ID was documented from birth to the most recent assessment. Those with incomplete ID information at either birth or the present assessment were excluded from the parameter analysis. Chord diagrams were employed to illustrate the transition of individuals from their birth herds to another current herd, with separate diagrams for males and females, as well as a combined one. However, to enhance clarity, only individual chord diagrams for male and female migrations were presented.

3.6. Programme used

ENDOG software programs version 4.8 (Gutiérrez and Goyache, 2005) was utilized to calculate all pedigree parameters and the F_{ST} matrix based on the differentiation between the herds (pairwise F_{ST} coefficients). The subpopulations submenu in the population menu was used to compute F_{ST} values. The outcomes were documented in the table *Fis_Fsts* of a Gener.mdb file. Based on the F_{ST} results from ENDOG's running, the F_{ST} diagonal full matrices were created in Ms Excel 365. The function heatmap.2 of the R package "gplots" was used to create a heatmap to visualise the pairwise F_{ST} matrix.

Different inbreeding coefficients were determined using the GRain software version 2.2 (Doekes et al., 2020, Baumung et al. 2015). Spearman correlations and the significance among the different inbreeding coefficients were tested by the Performance Analytics-package in R-studio. The chordDiagram function from the R package "circlize" (Gu, 2014) was used to create the chord diagram of migration intensity. The direction of arrows in the chord chart showed the direction of migration, and arrows sizes reflect the number of migrants.

4. RESULTS AND DISCUSSION

4.1. Characterization of the pedigree structures and completeness

The pedigree structures were briefly described in **Table 3**, in which the number of individuals was the largest for the Blonde-pig pedigree and the smallest for the Red one.

Table 3. The characterization of the pedigree structures and completeness

Breeds	**Blonde**	**Swallow-Belly**	**Red**
No. of animals in the whole pedigree	12,808	2,393	3,963
Complete generation equivalent (CGE)	**7.08**	**4.29**	**6.17**
No. of complete generations	6	5	6
Max no. of generations traced	22	18	18
No. of animals in the reference population (REF2021)	2,058	243	629
Complete generation equivalent in reference population	**9.73**	**6.87**	**9.03**

The number of animals in the reference population (REF2021) was accounted for less than 20.00% compared to the number of pigs in the whole pedigree, specifically the population Blonde and Red shared similar proportion of 16.06% and 15.87%, respectively, whereas that of the Swallow-Belly was lower with 10.15%. The longest and most complete pedigree was found in the Blonde Mangalica pig population both for the whole and in the reference populations. The Blonde pedigree could be traced maximum 22 generations, being 4 generations longer than other pedigrees.

Figure 7 explicitly presented the completeness of the pedigrees. The Blonde and Red shared similarity of more than 90.00% of pedigree completeness up to the sixth generation while that proportion of the Swallow-Belly was observed in the fifth generation.

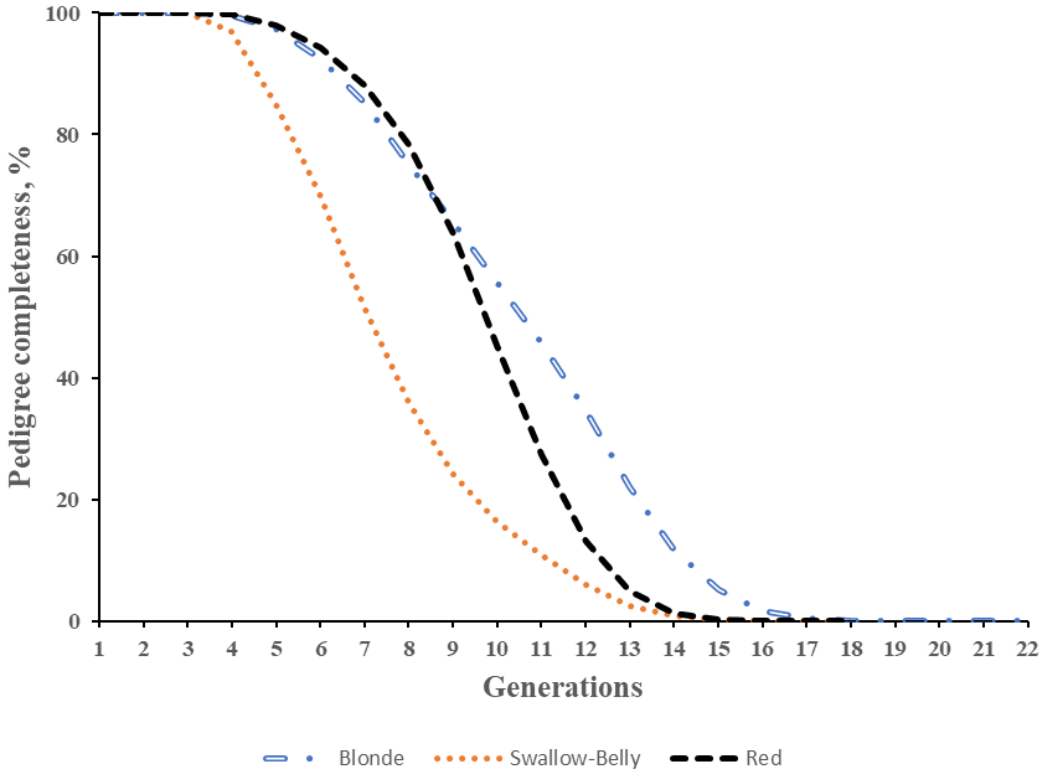


Figure 7. Average percentage of known ancestor per generation of each reference population (2016-2021).

According to Perdomo-González et al. (2022) pedigree analysis continues to be the most useful method for the reproduction management of populations even in the genomic era if the pedigree has sufficient depth and reliability. Being representative of the quality of the pedigree - to estimate the genetic diversity parameters - the CGE indicates the reliability of the results relying on pedigree data. The longer the CGE is the more reliable estimation parameters are but in order to avoid underestimated inbreeding measure, pedigree data should show CGE more than 4 (Michels and Distl, 2022). In the present study, the CGE values of the evaluated Mangalica populations ranged between 4.29 and 9.73 and between 6.78 and 9.73 in the whole period and in REF2021, respectively. These reported values of CGE were similar to that of Krupa et al. (2015) in five Czech Republic pig breeds with CGE in the range of 5.21 to 8.80 or to that of Wilmot et al. (2020) who analyzed the pedigree of Wallon Piétrain pig population and reported an average CGE of 5.78 generations. Among the various pig related studies Melka and Schenkel, (2010) reported exceptionally high CGE in four Canadian swine breeds with most CGE being higher than 10 generations. On the contrary in autochthon Brasilian and Croat pig breeds very low (1.32 and 2.05) CGE values were calculated (Carneiro et al., 2014; Gvozdanovic et al. 2020). The relatively large CGE in the current study indicates that all of the analyzed Mangalica pedigrees were sufficiently deep and complete making reliable genetic variability and population structure analyses possible.

4.2. Average relatedness coefficient (AR) and inbreeding coefficients

The evolutions of the various inbreeding and AR coefficients of the different Mangalica breeds were depicted in **Figure 8, 10, 12**. In general, most parameters increased continuously except for F_{New} which decreased in all breeds in the last decade. The rate of increase was the

highest for F_{Bal} which reached high values by the end of the examined period, especially for the Blonde and for the Red population where their mean values exceeded 20.00% and 25.00%.

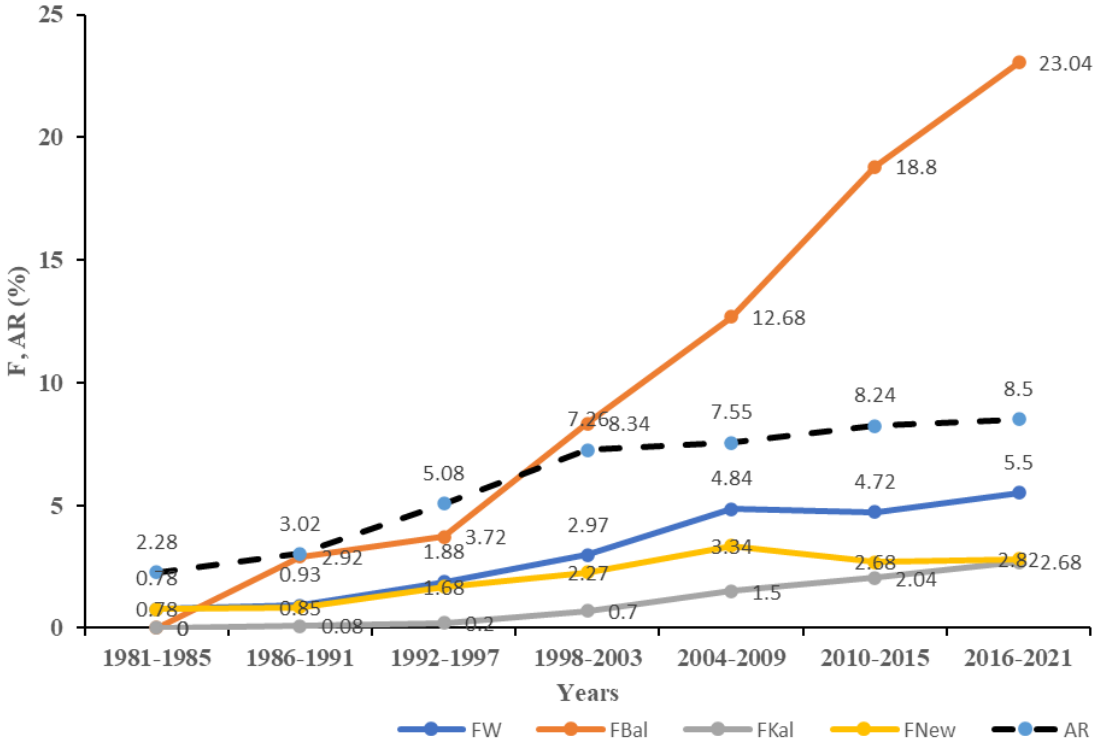


Figure 8. The evolution of different inbreeding coefficients and average relatedness in the Blonde pedigree. F: inbreeding coefficients, AR: average relatedness, F_w: Wright's inbreeding, F_{Bal}: Ballou's inbreeding, F_{Kal}: Kalinowski's inbreeding, F_{New}: Kalinowski's New inbreeding.

Compared to those breeds the Swallow-Belly Mangalica breed showed substantially lower mean F_{Bal} value. AR and F_W coefficients increased in parallel during the last two decades for all breeds and similarly to that of F_{Bal} the highest and lowest values were observed for the Red and for the Swallow Belly Mangalica breeds, respectively. Nevertheless, in the REF2021 68.00% of the F_W of the Swallow Belly Mangalica breed was composed of F_{New} while in the other two breeds (Blonde and Red) the proportion of ancestral inbreeding F_{Kal} exceeded (51.00% and 56.00%, respectively) that of the new inbreeding.

The estimated correlation coefficients among the different inbreeding coefficients of the Mangalica breeds can be found in (**Figure 9, 11, 13**). These values were all positive except for F_{New} and F_{Bal} which were significantly negative in all breeds, but the strength of correlation was negligible. In general F_W showed strong correlation with F_{New} and low correlation with F_{Bal} while the correlation coefficients among the two types of ancestral inbreeding coefficients (F_{Bal} and F_{Kal}) ranged between moderately strong and strong in every breed.

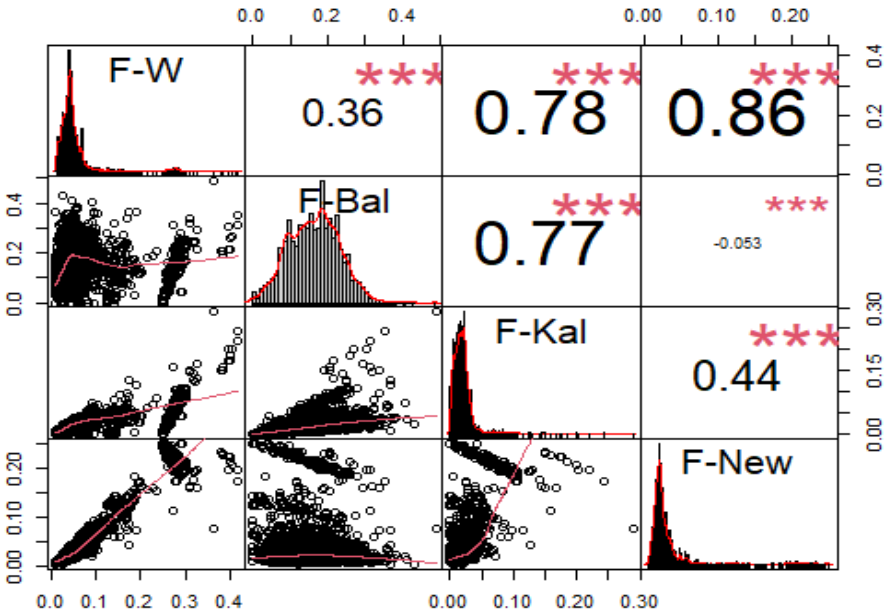


Figure 9. The correlations among inbreeding coefficients in the Blonde pedigree. F-W: Wright's inbreeding, F-Bal: Ballou's inbreeding, F-Kal: Kalinowski's inbreeding, F-New: Kalinowski's New inbreeding.

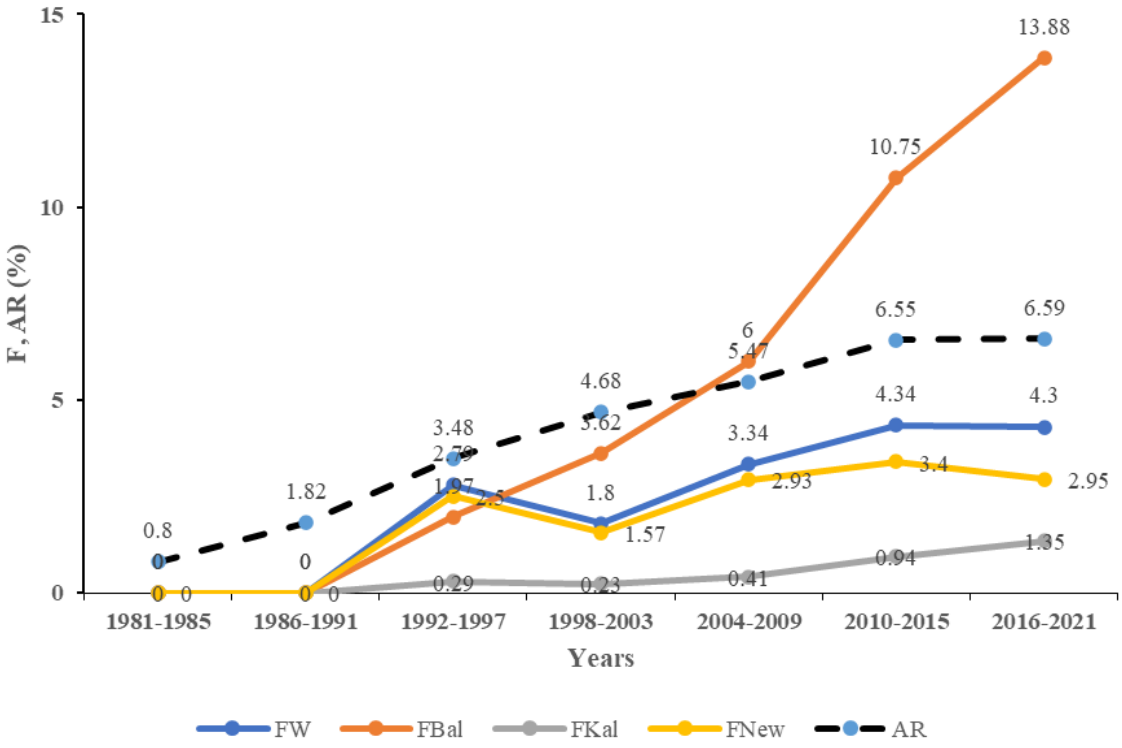


Figure 10. The evolution of different inbreeding coefficients and average relatedness in the Swallow-Belly pedigree. F: inbreeding coefficients, AR: average relatedness, F_w: Wright's inbreeding, F_{Bal}: Ballou's inbreeding, F_{Kal}: Kalinowski's inbreeding, F_{New}: Kalinowski's New inbreeding.

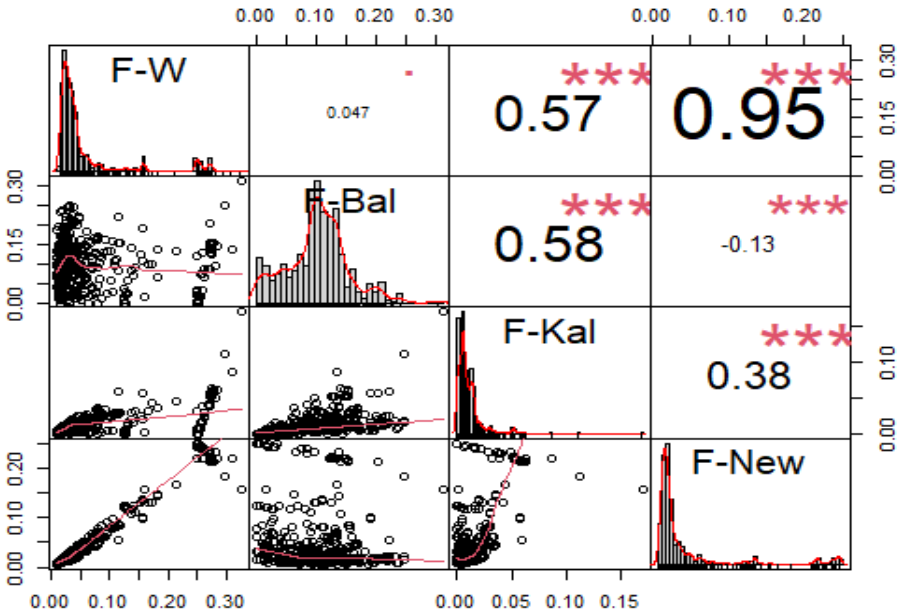


Figure 11. The correlations among inbreeding coefficients in the Swallow-Belly pedigree. F-W: Wright's inbreeding, F-Bal: Ballou's inbreeding, F-Kal: Kalinowski's inbreeding, F-New: Kalinowski's New inbreeding.

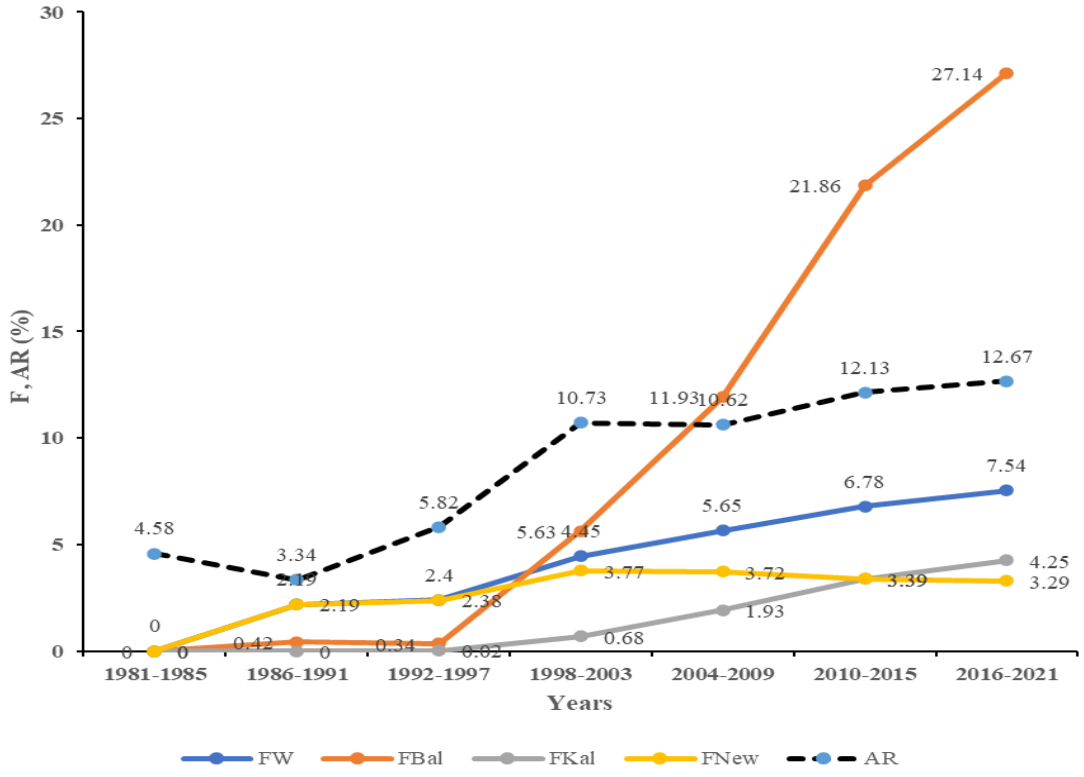


Figure 12. The evolution of different inbreeding coefficients and average relatedness in the Red pedigree. F: inbreeding coefficients, AR: average relatedness, F_w: Wright's inbreeding, F_{Bal}: Ballou's inbreeding, F_{Kal}: Kalinowski's inbreeding, F_{New}: Kalinowski's New inbreeding.

The average relatedness (AR) sharply increased in the Red population from 1991 to 2003, ranking first at the current end pedigree with 12.67% **Figure 12** comparing to 8.50% (**Figure 8**) and 6.59% (**Figure 10**) of the Blonde and Swallow-Belly populations, respectively. These parameters explain the highest and lowest inbreeding coefficients of the Red and the Swallow-Belly, respectively, because mating of closer relatives causes higher inbreeding levels. Inbreeding is known as the status heterozygosity decrease in an individual to the population, consequence lowering the genetic diversity (Schäler et al., 2020; Zhang et al., 2015). It was confirmed in this research that the highest inbred Mangalica population experienced the highest genetic diversity loss in the Red population.

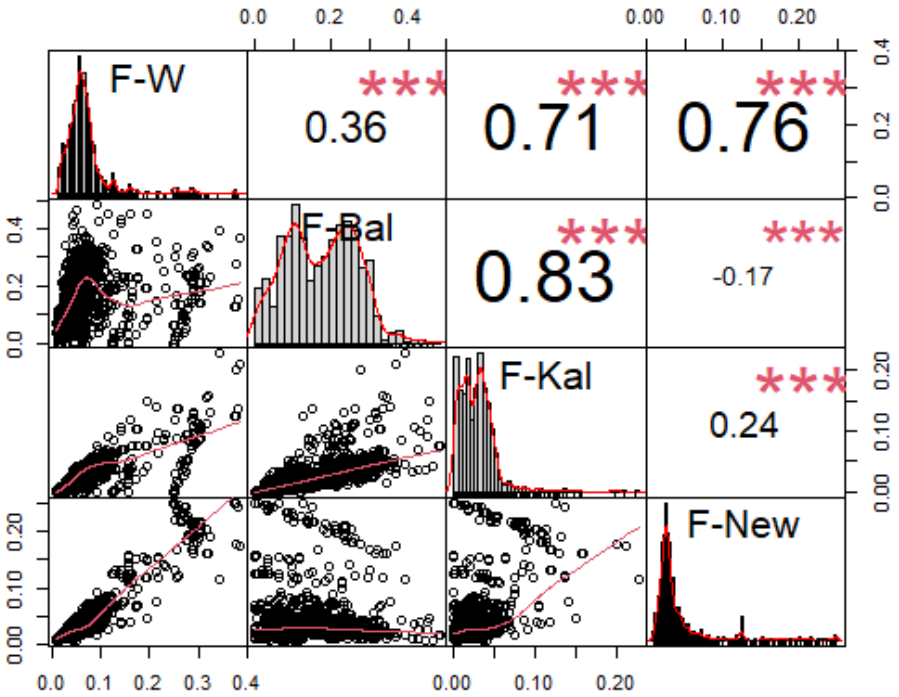


Figure 13. The correlations among inbreeding coefficients in the Red pedigree. F-W: Wright's inbreeding, F-Bal: Ballou's inbreeding, F-Kal: Kalinowski's inbreeding, F-New: Kalinowski's New inbreeding.

However, the consequence of inbreeding somewhat depends on the historical inbreeding, that first time inbred individuals expose to negative effects of inbreeding more severely than inbred individuals of inbred parents (Suwanlee et al., 2007). The inbreeding level calculated by different methods was generally the highest in the Red (**Figure 12**) and smallest in the Swallow-Belly (**Figure 10**). F_W ranging from 4.30 to 7.54 for the Swallow-Belly and Red population, respectively is similar to the research of (Posta et al., 2016), meaning that after a decade F_W in this Mangalica population is likely maintained. In contrast, Bâlteanu et al. (2019) found higher F_{ROH} in the Swallow-Belly and Red breeds (0.14) than in Blonde (0.10) using SNP data from the same populations. Comparing inbreeding levels of different breeds is only meaningful with similar CGE. Our results were comparable with that of Krupa et al. (2021) who reported CGE and F_W of 7.53 and 7.95%, respectively for a local Czech pig breed. Showing an exceptionally long and complete pedigree, the estimated inbreeding levels of the various Canadian pig breeds were also high (ranging between 5.00 and 18.00%) exceeding our values (Melka and Schenkel, 2010). On the

contrary F_W values of the Mangalica pig breeds were much higher than reported other conservation pig populations (0.06% and 3.26%) (Carneiro et al., 2014; Gvozdanović et al., 2020). However, as mentioned before the low CGE of these pigs breeds (1.32 and 2.05) made these inbreeding estimates unreliable.

The different approaches of inbreeding coefficient allow looking insight into the time scaling and potential effects of inbreeding. Besides the conventional F_W, F_{Bal} considers the autozygous alleles previously happened. The Kalinowski and Kalinowski "new" inbreeding coefficient splits the autozygous alleles to two parts the proportion that was autozygous already in the past and for the first time. Although recently the concept of old and new inbreeding is getting more and more recognition in animal science (e.g. Addo et al., 2017; Krupa et al., 2021) in pig related studies the two types of Kalinowski inbreeding coefficients (F_{Kal} and F_{New}) have not yet been applied, except for the study of Schäler et al. (2020) who examined only 76 pigs.

F_{Bal} accounted for the highest inbreeding values, being three to five times higher than F_W. According to Perdomo-González et al. (2022) the F_{Bal} and probability of harmful genes occurrence in the individuals and the populations are negatively correlated. Schäler et al. (2020) suggested that for the mating plan pigs with high F_{Bal}, F_W should be identified and mated but with low coancestry.

Among three Mangalica populations examined in this study the Red population has highest F_{New} value compared to the lowest one of the Blonde population (**Figure 12** and **Figure 8**, respectively). This finding for the Red population was confirmed by its higher genomic coverage (129.4Mb, 5.30% autosomal genome) of very long run of homozygosity (ROH, >30 Mb), indicating recent and strong inbreeding compared to Blonde and Swallow-Belly breeds (Bâlteanu et al., 2019). F_{New} showed a decreasing tendency in the final decade (2010-2021) with the corresponding increase of F_{Kal}, which is favourable for the conservation program of this Red population from the aspect of possible inbreeding depression (Doekes et al., 2019).

For the Swallow-Belly population, the inbreeding coefficient F_W was mainly composed of the F_{New}, meaning recent inbreeding events predominate, which likely exacerbates inbreeding depression. Besides, in this population the F_{New} showed a very strong correlation with F_W while these correlations were lower on the two other breeds (**Figure 11**). The correlation between F_{New} and F_W was only moderate (0.53) in the the study of Schäler et al. (2020) carried out on pigs, while in other species (horse and rabbit) the estimated correlations were strong (0.73 – 0.84) (Perdomo-Gonzales et al., 2022; Curik et al., 2020) but they were far from unity. Compared to the Swallow-Belly Mangalica pigs similar results were reported in German dogs (Michels and Distl, 2022) where 62.00% of the conventional inbreeding was F_{New}. Consequently, the authors suggested that the mating plan of this dog breed should focus on F_{New} instead of F_W. The weak correlation between F_{New}/F_W and F_{Bal} indicates that recent and ancestral inbreeding metrics provide distinct information, which could be useful for comprehensive assessment of inbreeding load in conservation or breeding programs. The slight negative correlation between F_{New} and F_{Bal} suggests a possible trade-off between recent and historical inbreeding, but its practical impact is small.

4.3. Generation interval (GI)

The four-pathway generation intervals were shown in **Table 4**. The average GI for Blonde population was the shortest of 3.06 years and the longest one belonged to Swallow-Belly population with 3.45 years. The difference in average GI between pathways was not significant. The sire – son and dam – son paths were longer than the sire – daughter and dam – daughter paths in all breeds.

Table 4. Average GI (years) for different pathways in the pedigrees

Color variation	Blonde	Swallow-Belly	Red	Mean	SD
	$\bar{X}$±SD	$\bar{X}$±SD	$\bar{X}$±SD		
GI for S-S	3.76 ± 3.444 *(n=647)*	4.11 ± 4.155 *(n=185)*	3.60 ± 2.654 *(n=262)*	3.82	0.261
GI for S-DT	2.93 ± 2.398 *(n=5536)*	3.40 ± 3.472 *(n=930)*	2.96 ± 2.177 *(n=1549)*	3.10	0.263
GI for D-S	3.32 ± 2.854 *(n=646)*	4.33 ± 4.086 *(n=184)*	3.68 ± 3.360 *(n=261)*	3.78	0.512
GI for D-DT	3.08 ± 2.559 *(n=5523)*	3.18 ± 2.696 *(n=913)*	3.49 ± 3.721 *(n=1543)*	3.25	0.214
Average GI	3.06 ± 2.567 *(N=12352)*	3.45 ± 3.319 *(N=2212)*	3.29 ± 3.057 *(N=3615)*	P-value = 0.0637	

GI: generation interval, SD: standard deviation, S-S: sire-son, S-DT: sire-daughter, D-S: dam-son, D-DT: dam-daughter.

The lengths of average GI of the different Mangalica breeds were not significantly different among the four different pathways in this study (**Table 4**). This result is different from other studies, where the sire-offspring pathways were usually longer than the dam-offspring pathways (Klein et al., 2022; Nagy et al., 2010). It was explained that in a conservation program the sires and the dams were kept in breeding as long as possible, to reduce the genetic variation loss (Klein et al., 2022). However, the contribution of male breeding animals tended to be longer in productive cycle compared to females as the sperm could be stored and artificial insemination (AI) could be implemented (Nagy et al., 2010). Since AI was not practiced in these Mangalica populations, this is likely a reason for the non-significant difference of GI among pathways. The average GI in the populations of the present study was about 3.27-years long which is about a year shorter than the GI (4.31 years) of the autochthon Moura pig (Carneiro et al., 2014). The GI value of this present study is around 1.00 to 1.50 years longer than that reported by (Krupa et al. 2021) in a local pig breed (having GI of 2.50 years) or in commercial pig breeds (Krupa et al., 2015; Melka and Schenkel, 2010; Tang et al., 2013) where the GI was generally lower than 2.00 years. The breeding animals were well maintained in this Mangalica conservation program such that the GI increased

nearly by one-year (3.27 vs 2.46 years) compared to that parameter reported by Posta et al. (2016) for the same Mangalica breeds.

4.4. Effective population size (N_e)

Trends of the estimated effective population sizes obtained from individual inbreeding increased were presented in **Table 5**. The Blonde and the Red Mangalica breeds showed the largest and the smallest population sizes throughout the whole examination period. Compared to their starting values the effective population size doubled in the Red and Swallow-Belly and tripled in the Blonde population. Then all three breeds showed erratic changes where their effective population sizes were subsequently increased and decreased several times. In the REF2021 of all Mangalica breeds the estimated effective population sizes were within the ranges of 50 and 100, respectively.

Table 5. Effective population size computed via individual increase in inbreeding through the pedigrees

Color variation	1981-1985	1986-1991	1992-1997	1998-2003	2004-2009	2010-2015	2016-2021
Blonde	45	156	92	96	71	88	86
Swallow-Belly	-	-	46	95	54	62	77
Red	-	20	45	43	50	53	58

The effective population size (N_e) is to quantify the genetic variation loss and inbreeding in real-world population (Wang et al., 2016). Some research proposed the N_e should be preserved more than 50 individuals to withstand the negative effects of inbreeding (Welsh et al., 2010, Wang et al., 2016) and a size of 500 individuals should be achieved for GD maintenance in several generations (Krupa et al., 2015). None of three effective population sizes is smaller than 50 individuals but also none of them is bigger than 500 individuals, expecting that the studied Mangalica populations are capable of avoiding inbreeding depression in a short term. Besides, comparing our results with those of Posta et al. (2016) the effective population size of every breed has been increased during the last decade which also signals the efficiency of the conducted conservation programs of these breeds. The increasing of N_e contributed to lowering the genetic variation loss in the Swallow-Belly and Red populations but not in the Blonde since the effective number of founders genome decreased in this population. The Mangalica populations of this study was comparable with that of the local Czech pig breeds having similar CGE and F_W that the Hungarian Mangalica breeds. On the other hand, the Mangalica pig breeds had much higher N_e in comparison both to Canadian (Melka and Schenkel, 2010) commercial pig breeds and to Black Slavonian (Gvozdanović et al., 2020) and to Brazilian (Bisaro) local pigs (Paixao et al, 2018) where the effective population sizes ranged between 14 and 36, respectively.

4.5. Predicting future inbreeding

Based on the criteria of inbreeding level predicted in 25 years every Mangalica pig breed was classified into degrees of endangerment (**Table 6**) ranging from "Critical" (most endangered) to "Transitional" (least endangered) categories (Alderson, 2009). It can be seen that the future inbreeding level for the next 25 years only exceeded the 10% threshold in the Red Mangalica breed which falls the least severe endangered "Transitional" category while the other two Mangalica breeds are non-endangered.

Table 6. The categorization of breeds based on predicted inbreeding coefficients

Color variation	Predicted inbreeding	Category
Blonde	9.98	non-endangered
Swallow-Belly	8.73	non-endangered
Red	13.67	transitional

From the predicted inbreeding coefficients for the next 25 years, only the Red population is in the lowest category of endangerment (Transitional) while the Blonde and Swallow-Belly breeds are not falling to this endangered scale at all. Among the reference populations, F_W of the Red population was the highest and the rate of inbreeding was also higher around 0.87% per generation. For the Blonde and Swallow-Belly Mangalica populations, although they showed similar inbreeding rate (approximately 0.60% per generation), the Blonde has higher current inbreeding coefficient. Thus, as predicting the Blonde might be likely to enter the endangered category in the future than the Swallow-Belly population. However, at present none of these two populations have reached any category of endangerment (Alderson, 2009) regarding only inbreeding coefficient, meaning that the existence and genetic diversity of these populations are in optimistic perspective at least in the next 25 years.

4.6. Probability of gene origin

The probability of gene origin parameters was presented for the Blonde, Swallow-Belly, and Red populations, respectively (**Table 7, 8, 9**). Compared to their starting values, all populations showed increased number of founders, effective number of founders, effective number of ancestors and effective number of founder genomes, respectively. Then all population witnessed decreases from 2009 for all of the above-mentioned parameters where the largest and smallest values were recorded for Blonde and the Red Mangalica breeds, respectively.

The number of effective founders (f_e) were much smaller than the total number of founders in all three REF2021, accounting for 35.51%, 39.56% and 34.21% in the Blonde, Swallow-Belly and Red, respectively. After 1986 the effective number of founder genomes (f_g) were shown a decreased tendency in the Blonde and Red populations. Concerning the Swallow-Belly population, this decrease was only detected from 2004, giving the highest f_g for the Swallow-Belly REF2021. The Blonde and Swallow-Belly reference populations shared the similar number of effective

Table 7. Parameters of GD and GD loss throughout the Blonde pedigree

	1981-1985	**1986-1991**	**1992-1997**	**1998-2003**	**2004-2009**	**2010-2015**	**2016-2021**
Total number of founders (*f*)	65	91	143	176	183	150	138
Effective number of founders (f_e)	20	38	49	50	54	49	49
Effective number of ancestors (f_a)	20	34	30	22	23	21	21
Effective number of founders genome (f_g)	16.12	20.42	16.49	12.56	12.18	10.25	8.91
Ratio f_a/f_e	1.00	0.89	0.61	0.44	0.43	0.43	0.43
GD	0.969	0.976	0.970	0.960	0.959	0.951	0.944
1-GD (GD loss)	0.031	0.024	0.030	0.040	0.041	0.049	0.056
1-GD*(GD loss due to unequal founder contributions)	0.025	0.013	0.010	0.010	0.009	0.010	0.010
GD*-GD (GD loss due to random genetic drift)	0.006	0.011	0.020	0.030	0.032	0.039	0.046
No of ancestors explaining 50% of the gene pool	8	12	11	8	8	8	7
No of ancestors explaining 80% of the gene pool	27	33	34	24	24	21	20
No of ancestors explaining 100% of the gene pool	61	83	131	156	158	131	123

Table 8. Parameters of GD and GD loss throughout the Swallow-Belly pedigree

	1981-1985	**1986-1991**	**1992-1997**	**1998-2003**	**2004-2009**	**2010-2015**	**2016-2021**
Total number of founders (*f*)	13	37	65	120	99	93	91
Effective number of founders (f_e)	10	22	29	40	38	35	36
Effective number of ancestors (f_a)	8	13	16	27	25	23	22
Effective number of founders genome (f_g)	6.45	10.49	8.83	17.84	15.13	10.87	8.74
Ratio f_a/f_e	0.80	0.59	0.55	0.68	0.66	0.66	0.61
GD	0.922	0.952	0.943	0.972	0.967	0.954	0.943
1-GD (GD loss)	0.078	0.048	0.057	0.028	0.033	0.046	0.057
1-GD*(GD loss due to unequal founder contributions)	0.050	0.023	0.017	0.013	0.013	0.014	0.014
GD*-GD (GD loss due to random genetic drift)	0.028	0.025	0.039	0.016	0.020	0.032	0.043
No of ancestors explaining 50% of the gene pool	4	5	6	10	10	8	8
No of ancestors explaining 80% of the gene pool	7	13	21	32	24	22	21
No of ancestors explaining 100% of the gene pool	9	23	44	97	78	75	78

Table 9. Parameters of GD and GD loss throughout the Red pedigree

	1981-1985	**1986-1991**	**1992-1997**	**1998-2003**	**2004-2009**	**2010-2015**	**2016-2021**
Total number of founders (*f*)	8	37	51	81	92	79	76
Effective number of founders (f_e)	4	20	28	22	27	26	26
Effective number of ancestors (f_a)	4	17	16	13	16	14	14
Effective number of founders genome (f_g)	3.20	12.99	10.98	8.40	8.92	7.02	5.72
Ratio f_a/f_e	1.00	0.85	0.57	0.59	0.59	0.54	0.54
GD	0.844	0.962	0.954	0.940	0.944	0.929	0.913
1-GD (GD loss)	0.156	0.038	0.046	0.060	0.056	0.071	0.087
1-GD*(GD loss due to unequal founder contributions)	0.125	0.025	0.018	0.023	0.019	0.019	0.019
GD*-GD (GD loss due to random genetic drift)	0.031	0.013	0.028	0.037	0.038	0.052	0.068
No of ancestors explaining 50% of the gene pool	2	6	7	5	6	6	6
No of ancestors explaining 80% of the gene pool	4	15	18	13	17	14	14
No of ancestors explaining 100% of the gene pool	-	30	35	63	72	60	57

ancestors (f_a) of 21 and 22 individuals, respectively while this number of the Red was smaller with only 14 individuals.

The ratio f_a/f_e was 1.00 between 1981–1985 in the Blonde and Red, meaning that the bottleneck had happened in these two populations afterwards. On the contrary, signals for bottlenecks were already observed in the Swallow-Belly population during the first five years of the examined period. The ratios f_a/f_e in the reference populations (2016 –2021) were ranging from 0.43 to 0.61 in the various breeds meaning that the bottleneck effects were not so severe. The Blonde Mangalica pigs were expected to be the most vulnerable to the bottleneck effects.

The whole gene pool in the Red and Swallow-Belly REF2021 could be explained only by 57 and 78 ancestors, respectively while this parameter in the Blonde REF2021 was almost double with 123. The number of ancestors contributes to 50.00% of gene pool is very small only 6 individuals in the Red, 7 individuals in the Blonde, and 8 individuals in the Swallow-Belly REF2021. From these parameters, the Red population would have suffered the most substantial genetic variability loss.

The genetic diversity of the in the Blonde and Red populations both showed similar decreasing tendencies after an initial increase while this parameter fluctuated throughout the Swallow-Belly breed. However, the GD of Swallow-Belly and Red populations was higher in their REF2021 than at the beginning of the evaluated period. In the REF2021, the Blonde and Swallow-Belly had biggest genetic diversity of approximately 94.00% comparing to the lowest of 91.30% in the Red. This means that the genetic diversity loss in the REF2021 of the Red Mangalica pigs was accounted for the highest proportion of 8.70% and these proportions of the Blonde and Swallow-Belly were 5.60 % and 5.70%, respectively. The loss of GD was dominated by random genetic drift in comparison to the unequal founder contributions.

The total number of founders (*f)* increased remarkably from 1981 to 2009 in the Blonde and Red populations and up to 2003 in the Swallow-Belly. This indicated that new founders had continuously been migrated into these three populations during a relatively long period, making population structure of the Mangalica breeds temporarily open. Consequently, the contribution of these migrated founders could have enriched the GD of these populations and may have lowered the inbreeding coefficients supposing they had not related each other and to the other members of these populations. It must be noted however, that these migrated "founders" might have caused underestimating of inbreeding coefficients to some extent if they violated the before mentioned assumptions. Only molecular genetic analyzes could clarify the possible effect of the described migration on the estimated parameters. Nevertheless, it can be noted that the CGE within the three Mangalica reference populations (2016–2021) were still quite long ranging between 6.87 and 9.73 (**Table 3**). Thus, these Mangalica pedigrees still provide sufficient information for estimating inbreeding level and genetic variability.

The f_e of three REF2021 was much smaller than the total number of founders, showing the unequal genetic contribution of founders in the current populations. This phenomenon could happen when some animals were used as parents more frequently than the others (Krupa et al., 2015). The imbalance of founder contributions was highest in the Red, followed by the Blonde population, whereas the less unequal contribution was found in the Swallow-Belly population. The

ratios between f_e/f in this study ranging from 34.21% (Red) to 39.56% (Swallow-Belly) are similar to the results of Mangalica pigs reported by Posta et al. (2016). The values in this research were higher than the results reported for Czech and Canadian pigs (Krupa et al., 2015 and Melka and Schenkel, 2010). The difference is probably due to the different breeding goals and selection intensity between the gene reserve and commercial pig breeds.

The effective number of ancestors (f_a) followed similar pattern of fe that they increased in some early periods and then decreased. The effective number of ancestors (f_a) are relatively smaller than those numbers found by Posta et al. (2016). This could be explained that in Posta et al. (2016), the pedigree reached in 2011 and the f_a numbers decreased afterwards (**Table 7, 8, 9)**, If the f_a is much lower than the f_e, being the ratio between f_a / f_e much lower than 1, that population experienced bottleneck effects (Posta et al., 2016). Among the three Mangalica populations, the Blonde reference population has got the highest bottleneck effects due to the lowest ratio f_a/f_e of 0.43, following by the Red and the Swallow-Belly.

Only seven ancestors in the Blonde and six ancestors in the Red and eight ones in the Swallow-Belly contributed to 50% of the current reference gene pool. The 100% of reference gene pool were responsible by 57, 78, 123 ancestors in the Red, Swallow-Belly, and Blonde populations, respectively. Based on the genetic contribution of ancestors, the Blonde population is expected to have higher genetic variability than the Red and Swallow-Belly breeds. However, Bâlteanu at al. (2019) found that the Blonde Mangalica had higher observed heterozygosities (H_0 = 0.31) than Swallow-Belly (H_0 = 0.29) but lower than in the Red Mangalica (H_0 = 0.32). Notably, the study did not include statistical tests to determine if these differences are significant. The most noticed discrepancy is the elevated H_0 in the Red Mangalica breed, which contrasts with its pedigree-based analysis of small population size and inbreeding. This breed also presented higher F_{ROH} (0.14), high H_0, and substantial wild-boar ancestry in admixture analysis (Bâlteanu at al. 2019). It strongly suggests unrecognized introgression from wild boars' population which simutniously increase heterozygosity at divergent loci while preserving autozygous segments from the domestic background. The GD of the Blonde retained 94.40% of its original value which was higher than the Swallow-Belly and Red with 94.30% and 91.30%, respectively. In other words, the GD loss of the Red was the highest, followed by the Swallow-Belly and the Blonde with the loss ranging between 8.70%, 5.70% and 5.60%, respectively. The GD losses observed in the present study fall in the range of results of commercial pig breeds in Czech Republic and China reported by (Krupa et al., 2015; Tang et al., 2013)) but it is lower than that proportion of Hampshire and Lacombe pig breeds (Melka and Schenkel, 2010). Wu et al. (2022) reported lower GD loss (0.80% to 1.40%, 0.10% to 0.70%, 0.30% to 1.40% for Duroc, Landrace and Yorkshire, respectively) in three commercial pigs in Taiwan. Similarly in the Czech Spotted Dog (Machová et al., 2020) the GD loss was as high as 38.20% coincided with extremely high F_W and AR values (36.45% and 74.83%). On the contrary examining the endangered Bísaro pigs (Paixão et al., 2018) the proportion of the retained GD was 99.20% contrary to the high F_W (10.48%). Nevertheles, compared to other pig related studies the population size (219,701) and the number of ancestors (4,323) were huge that kept the AR low (1.60%). The loss of GD could be experienced because of two reasons: the unequal founder contributions and the genetic drift (Lacy, 1995). The results (**Table 7, 8, 9**) showed the GD loss due to random genetic drift accounted for higher proportion than the GD loss due to unequal founder contributions. Similar tendency was in most pig related studies (Melka and Schenkel, 2010; Paixão et al., 2018; Tang et al., 2013). Although the Blonde

Mangalica population experienced more severe bottleneck effect (f_a/f_e ~ 0.43), the GD loss of the Red was still the largest among the Mangalica breeds. This can be explained that in a smaller population, the bottleneck causes more severe genetic diversity loss. In general, smaller populations are most likely to experience loss of genetic diversity. However, the results of Bâlteanu at al. (2019) did not support the pedigree-based calculation in the Red breed.

From the predicted inbreeding coefficients for the next 25 years, only the Red populations is in the lowest category of endangerment (Transitional) while the Blonde and Swallow-Belly breeds are not falling to this endangered scale at all. Among the reference populations, F_W of the Red population was the highest and the rate of inbreeding was also higher around 0.87% per generation. For the Blonde and Swallow-Belly Mangalica populations, although they showed similar inbreeding rate (approximately 0.60% per generation), the Blonde has higher current inbreeding coefficient. Thus, as predicting the Blonde might be likely to enter the endangered category in the future than the Swallow-Belly population. However, at present none of these two populations have reached any category of endangerment (Alderson, 2009), meaning that the existence and genetic diversity of these populations are in optimistic perspective at least in the next 25 years.

4.7. Population subdivision

The population differentiation of the Blonde, Swallow-Belly and Red breeds is illustrated by the pairwise F_{ST} coefficients, which are visualised in heatmap presentations (**FigureS 1, S 3, S 5 and Figures 14, 16, 18**). The distribution of the F_{ST} coefficients was not normal in any breed ($p < 0.001$). The average F_{ST} coefficients were 0.04 for the Blonde and 0.047 for the Swallow-Belly and the Red, which are significant smaller than 0.05 (p-value < 0.05), while these parameters were even smaller (0.03 and 0.04, respectively) for the active herds. The heatmaps and histogram revealed that the Swallow-Belly breed has the highest prevalence of stratification in total herds ($F_{ST} > 0.15$), followed by the Red and Blonde breeds (**FigureS 1, S 3, S 5**, and **FigureS 2(a), S 4(a), S 6(a)).** The proportion of herds with $F_{ST} > 0.15$ was 15.96%, 12.41% and 12.40% respectively. In addition, the proportion of animals with an F_{ST} bigger than 0.15 was 1.21%, 0.81% and 0.38%, respectively (**FigureS 2(b), S 4(b), S 6(b)**). In the currently active herds, highly differentiated herds with large distances ($F_{ST} > 0.15$) were only observed in the Blonde and Red breeds, accounting for 6.41% and 3.64% (**Figure 14, 16, 15a, 19a**), which represents a significant reduction compared to the total herds. A very small proportion of animal with an F_{ST} bigger than 0.15 was found in the Blonde active herds, with 0.14%, and in the Red one, with 0.09% (**Figure 15b and 19b**).

Within the Blonde Mangalica, three active herds (1645, 1630 and 1358) show considerable differentiation from each other (**Figure 14**). Despite the presence of these widely separated herds, the proportions of animals with F_{ST} values bigger than 0.15 were 0.38% and 0.14% in the overall herds and in the active herds, respectively (**FigureS 2(b) and Figure 15(b)**).

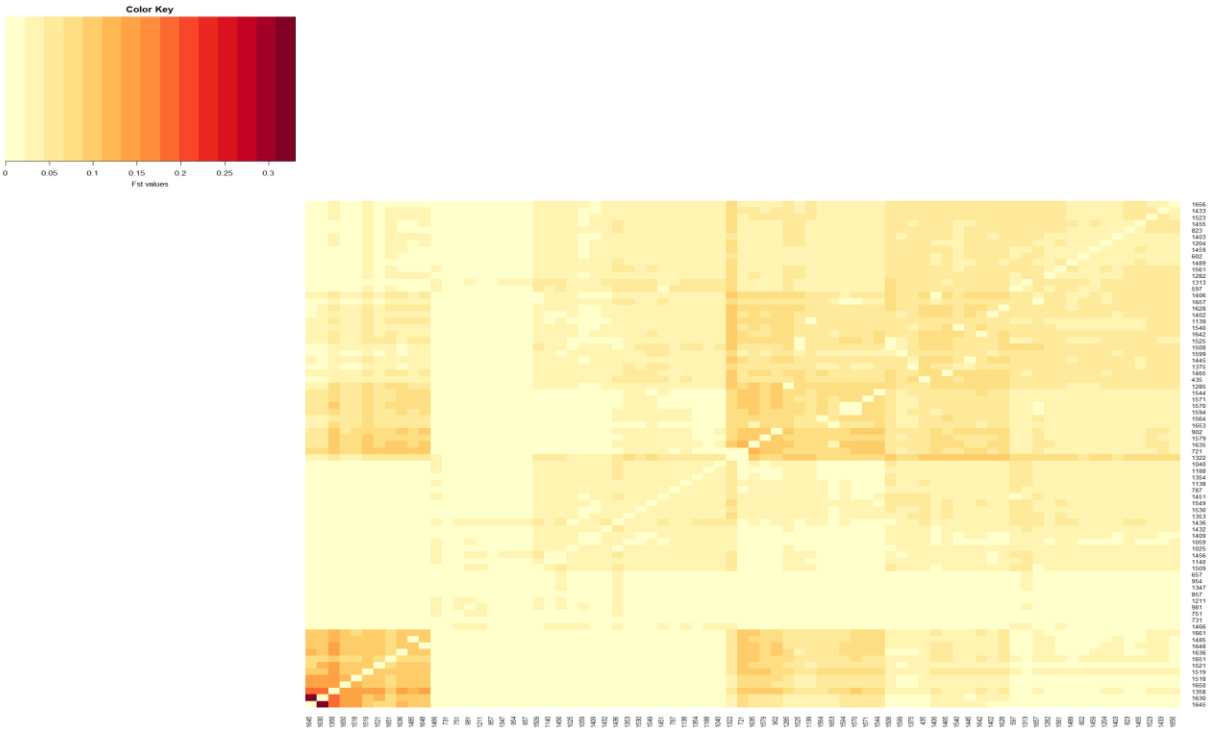


Figure 14. Heatmap based on pairwise F_{ST} coefficients between the active herds of the Blonde Mangalica breed. The color ranging from yellowish to dark red represents the scale of F_{ST} coefficients from zero onward. The x and y axes show the herd name.

In the Swallow-Belly breed, a large differentiation was observed in many overall herds (**FigureS 1**). However, all active herds in this population had an $F_{ST} < 0.15$, indicating that there was no significant genetic differentiation between the current active herds (**Figure 16 and 17**).

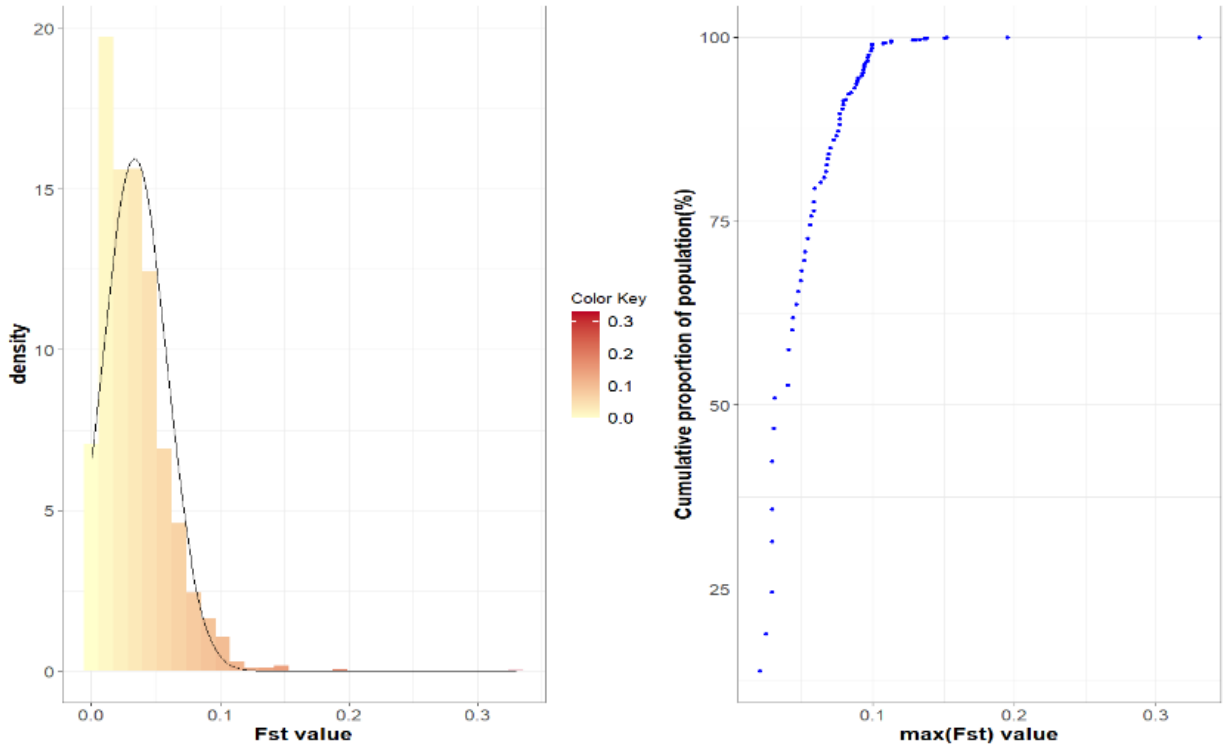


Figure 15. F_{ST} coefficients in the Blonde Mangalica active herds: (**a**) Histogram of F_{ST} values with density; (**b**) Cumulative proportion of the population related to the maximum F_{ST} of the herds.

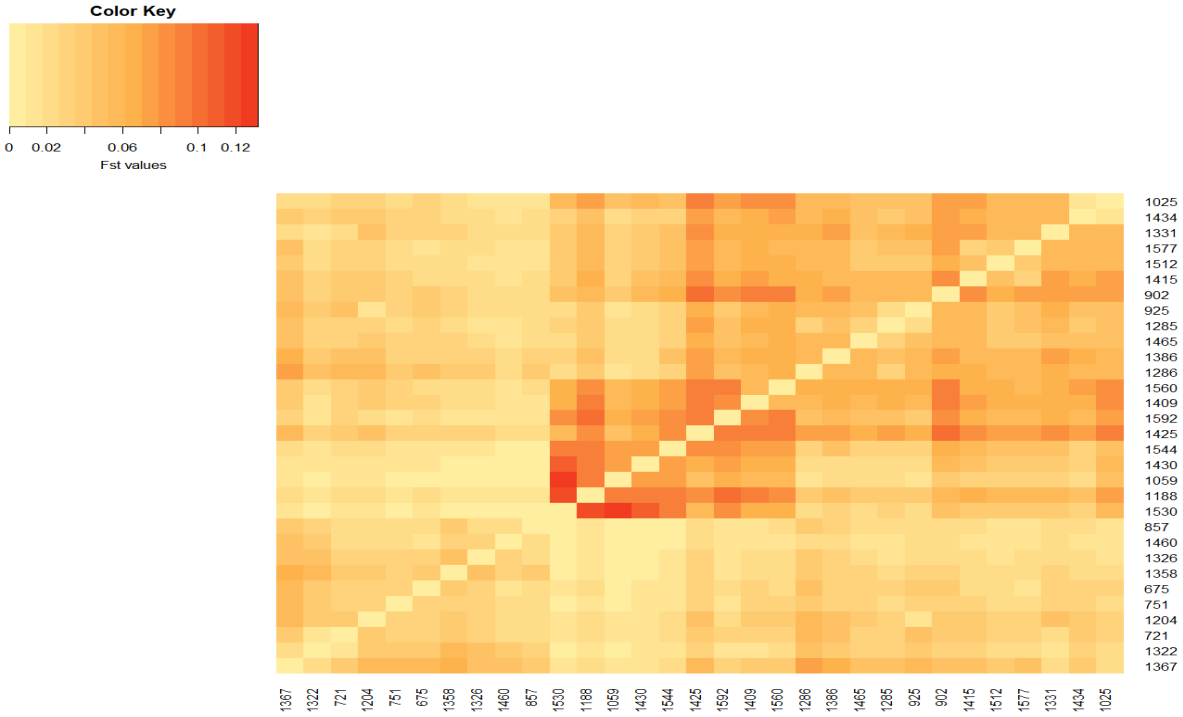
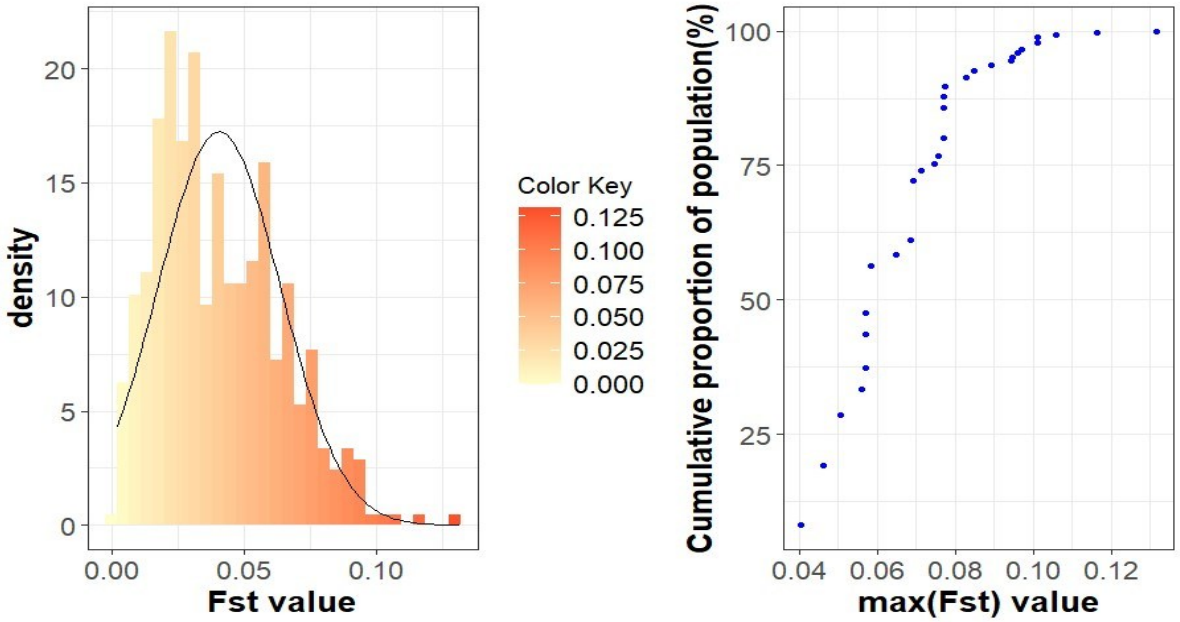


Figure 16. Heatmap based on pairwise F_{ST} coefficients between the active herds of the Swallow_Belly Mangalica breed. The color ranging from yellowish to dark red represents the scale of F_{ST} coefficients from zero onward. The x and y axes show the herd name.



(a) **(b)**

Figure 17. F_{ST} coefficients in the Swallow-Belly Mangalica active herds: **(a)** Histogram of F_{ST} values with density; **(b)** Cumulative proportion of the population related to the maximum F_{ST} of the herds

In the Red breed, large distances are observed between herds 198, 1436, 1646, 1385, 1325 and 1493 (**FigureS 5**). The active herds in this breed showed a significant differentiation between herds 1436, 1646 and 1664 (**Figure 18**). The proportions of animals with a maximum F_{ST} by 0.15 were 0.81% and 0.09% in the overall herds and in the active herds, respectively (**FigureS 6(b)** and **Figure 19(b)**).

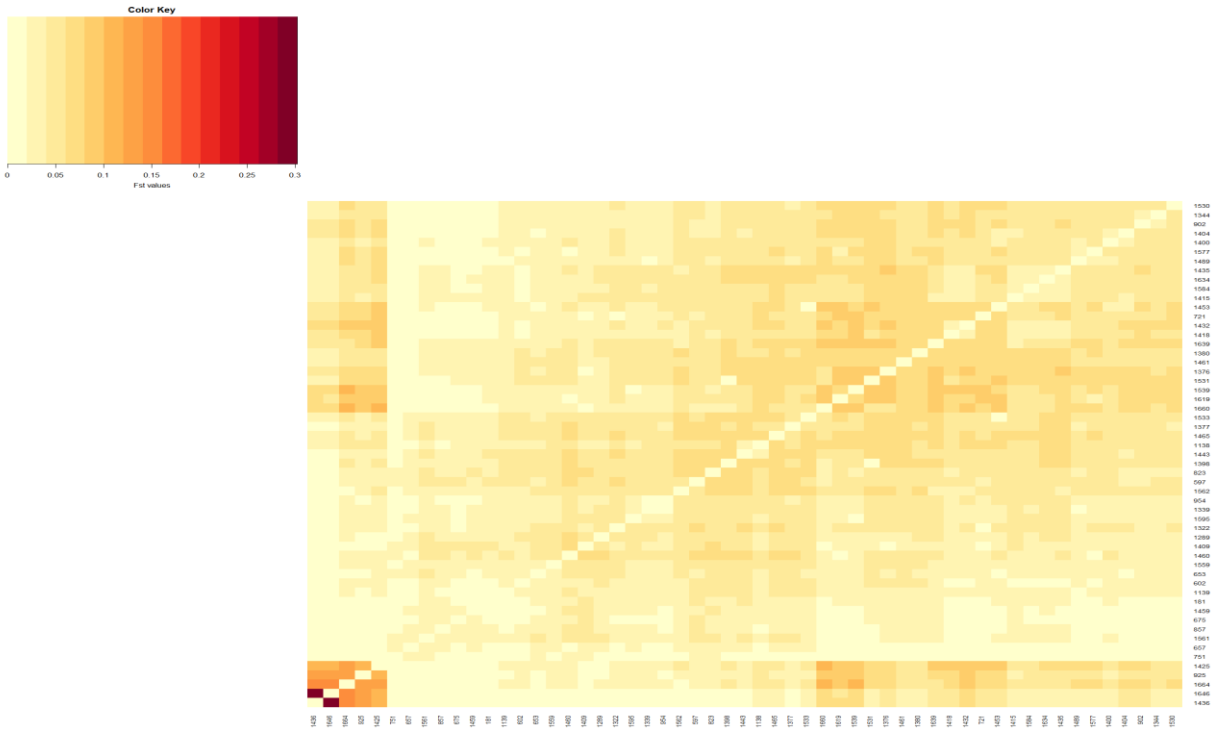


Figure 18. Heatmap based on pairwise F_{ST} coefficients between the active herds of the Red Mangalica breed. The color ranging from yellowish to dark red represents the scale of F_{ST} coefficients from zero onward. The x and y axes show the herd name.

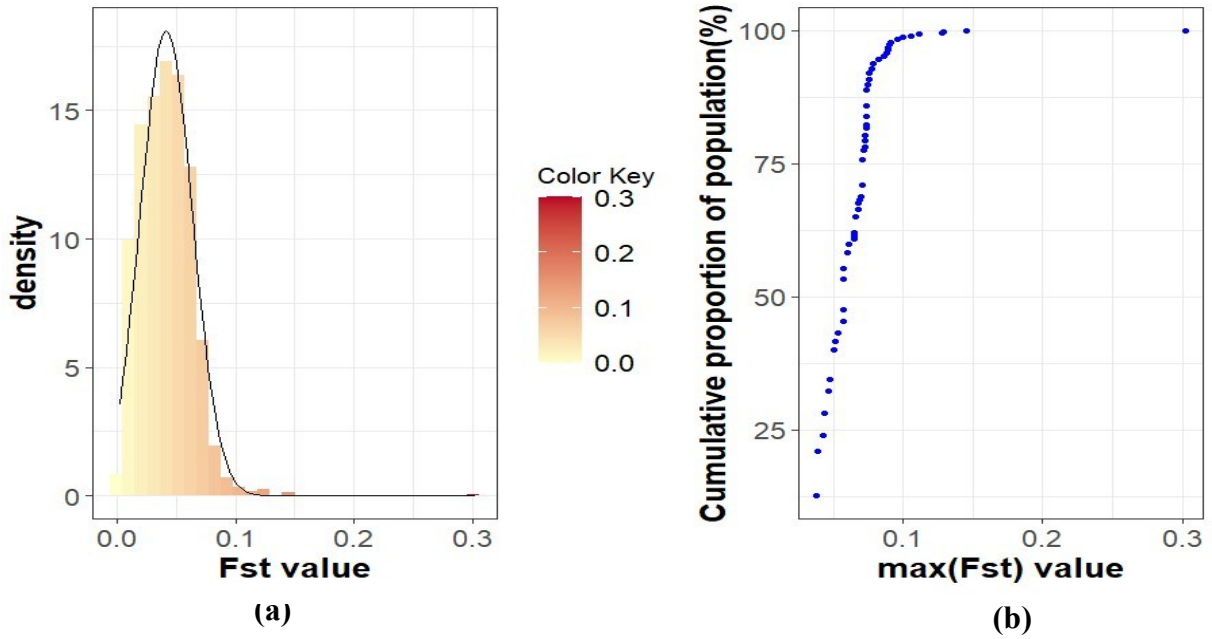


Figure 19. F_{ST} coefficients in the Red Mangalica active herd: (**a**) Histogram of F_{ST} values with density; (**b**) Cumulative proportion of the population related to the maximum F_{ST} of the herds.

The three Mangalica breeds show a uniform F_{ST} pattern between the herds. The small F_{ST} group ($F_{ST} < 0.05$) accounts for the largest proportion of more than 58% of the total, namely, 71.26%, 61.29% and 58.83% for the Blonde, Swallow-Belly and Red breeds, respectively (**Table 10**). Conversely, the large F_{ST} set ($F_{ST} > 0.15$) represents a consistently minimal percentage of around 1.00%. The Red breed has the highest percentage (40.33%) of moderate differentiation between herds ($0.05 < F_{ST} < 0.15$), followed by the Swallow-Belly breed with 37.27% and the Blonde breed with 27.55%. It is noteworthy that the Red breed shows a tendency to separate herds, with the majority of moderately differentiated herds. However, the strong stratification between herds was found in a very small proportion of only 0.84% (**Table 10**).

While the proportion of the strongly differentiated herds was below 2.00% for the three breeds, the Blonde breed stands out with the highest average distance value (average F_{ST}) within this group, which is 0.24 (between 0.15 and 0.35). In comparison, the Swallow-Belly and Red breeds are smaller, with an average F_{ST} of 0.20 (between 0.15 and 0.35) and 0.21 (between 0.15 and 0.34), respectively. Conversely, the average F_{ST} values for the small and moderate groups were approximately 0.03 and 0.07, respectively (**Table 10**).

Of the total herds, approximately 30% were active, with proportions of 30.23%, 32.98% and 35.71% for the Blonde, Swallow-Belly and Red breeds, respectively. Looking at the genetic distances between active herds, over 99.70% fall into the small and medium F_{ST} groups. This leads to a remarkable decrease in the proportion of large F_{ST} groups, which account for less than 0.30% in all three breeds, except for the Swallow-Belly breed, where the percentage is 0.00% (**Table 10**).

Some studies on genetic variability between breeds have been carried out in Mangalica pigs (Molnár et al., 2013; Zsolnai et al., 2006, Bâlteanu et al., 2019, Zsolnai et al., 2013). Analyses utilising mtDNA markers were unable to distinguish subpopulations within this Mangalica population (Molnár et al., 2013). However, a study on the Hungarian population of Mangalica pigs genotyped at 10 microsatellite loci revealed the presence of three clusters representative of three different breeds, namely, Swallow-Belly, Red and Blonde (Zsolnai et al., 2006). Bâlteanu et al. (2019) and Zsolnai et al., (2013) confirmed three distinct breeds by analysing SNPs data. Therefore, in breeding management and breed conservation, the three different coat colour variants of the Mangalica in Hungary are treated as three separated breeds.

Table 10. Average pairwise F_{ST} coefficients among herds sorted by differentiation intensity

Breed	F_{ST}_Group	Total Herds			Active Herds		
		N	Mean	Percent	N	Mean	Percent
Blonde	S	23,625	0.02 ± 0.014	71.26	2,368	0.02 ± 0.014	78.85
	M	9,133	0.07 ± 0.019	27.55	627	0.07 ± 0.017	20.88
	L	395	0.24 ± 0.077	1.19	8	0.18 ± 0.062	0.27
Swallow-Belly	S	2,679	0.03 ± 0.013	61.29	310	0.03 ± 0.012	66.67
	M	1,629	0.07 ± 0.020	37.27	155	0.07 ± 0.014	33.33
	L	63	0.20 ± 0.052	1.44	0	0	0
Red	S	6,142	0.03 ± 0.013	58.83	972	0.03 ± 0.013	65.45
	M	4,210	0.07 ± 0.018	40.33	512	0.06 ± 0.013	34.48
	L	88	0.21 ± 0.058	0.84	1	0.30	0.07

F_{ST}: Wright's F_{ST} coefficient, S: $F_{ST} \leq 0.05$, M: $0.05 < F_{ST} \leq 0.15$, L: $F_{ST} > 0.15$, N: number of observations.

There is no crossbreeding between these different breeds. A study of the genetic variability within the populations and structure within these breeds could contribute to understanding their evolutionary patterns during more than four decades of conservation efforts in numerous herds.

Traditionally, conservation efforts have focused on diversity between breeds, because according to Barker (2002), the most important goal in conserving the diversity of domestic animals is the conservation of specific breeds. However, it is argued that approaches that emphasise the component of genetic diversity between breeds may not be the most effective, as they neglect the component of variation within breeds (Barker, 2001; Caballero and Toro, 2002; Ollivier and Foulley, 2005). According to Cervantes et al. (2008), accessing genetic variability within populations, understanding population structures and analysing gene flow are crucial steps in the implementation of selection programmes. This assessment plays a central role in the formulation of efficient management strategies for genetic stock with the aim of improving the genetic basis for selection purposes. According to Molnár et al. (2013), populations within a breed that are geographically and/or ecologically isolated may acquire different physiological traits due to the specific selection criteria applied in the breeding process. Consequently, these isolated populations may differ genetically from other populations of the same breed that exhibit similar phenotypes, which may result in them being recognised as different breeds (Molnár et al., 2013). According to Wilkinson et al. (2012), the genetic substructure within a breed, as revealed by individual clustering methods, is likely to be rare in domestic species, with the presence of a limited genetic substructure typically observed in only one or two exceptional breeds. However, within-breed stratification has been detected in several livestock species, e.g., chickens (Wilkinson et al., 2012), horses (Glowatzki-Mullis et al., 2006), castles (Lazebnaya et al., 2020), goats (Martínez et al., 2015; Menezes et al., 2020), rabbits (Alves et al., 2015; Jochová et al., 2017), dogs (Chang et al., 2009; Wiener et al., 2017) and pigs (Snegin et al., 2021; Wilkinson et al., 2011).

The estimated F_{ST} coefficients provide information on the degree of differentiation between a group of populations, as applied in the present study to assess the differentiation between the herds of three Mangalica breeds. The F_{ST} coefficients, which range from 0.00 to 1.00, indicate the extent of genetic differentiation. A value of zero means that the genetic material is completely shared, allowing free crossbreeding. In contrast, a value of one indicates that all genetic variation is integrated into the population structure, meaning that there is no shared genetic divergence and populations are considered fixed or divergent (Hartl and Clark, 2007). The interpretation guidelines for Wright's F_{ST} coefficient were presented by Hartl and Clark (2007) as follows: an F_{ST} below 0.05 indicates low genetic differentiation; an F_{ST} from 0.05 to 0.15 indicates moderate genetic differentiation; an F_{ST} from 0.15 to 0.25 indicates high genetic differentiation; an F_{ST} above 0.25 indicates very high genetic differentiation. In addition, Frankham et al. (2002) reported that F_{ST} values above 0.15 indicate significant differentiation, while F_{ST} values below 0.05 indicate insignificant differentiation. In the present study, the F_{ST} coefficients between herds were between 0.00 and 0.35, as indicated by the colour spectra in the heatmap (**FigureS 1, S 3 and S 5**). Most of the analysed herds, representing more than 58.00% of the total population (**Table 10**), showed insignificant genetic differentiation according to the guidelines of Frankham et al. (2002). This group (with $F_{ST} < 0.05$) is even more dominant in active herds, with more than 65.00%. The F_{ST} range estimated in this study is broader compared to that in the research on Greek black pigs (Michailidou et al., 2014), where the F_{ST} values range from 0.06 to 0.30. Similarly, it exceeds the F_{ST} reported in studies on four commercial pig breeds and on Monteiro pigs, with F_{ST}

values ranging between 0.07 and 0.17 (Snegin et al., 2021) and from 0.01 to 0.06 (Silva et al., 2020), respectively. The variations observed may be attributed, in part, to the fact that the current study estimates F_{ST} based on pedigree data, as opposed to the molecular data used in other research. Although the F_{ST} range in this study is quite broad, with some herds reaching up to 0.35, the average F_{ST} coefficient across herds is not high (less than 0.047), which is significantly lower than 0.05 (p-value < 0.05). This F_{ST} value is higher than the F_{ST} of 0.01 observed in the study of black Slovenian pigs (Gvozdanovic et al., 2020) but lower than the inter-herd F_{ST} (F_{ST} = 0.07) within the same commercial breeds according to Snegin et al. (2021). It means that there are some divergent herds, but overall, there is a low genetic differentiation between herds in the three breeds analysed. Wilkinson et al. (2011) used a Bayesian analysis of population structure based on genotypic data to detect a substructure within the British Meishan pig breed, but this was not present in other methods. Snegin et al. (2021) found high variability between individual herds within the four commercial pig breeds, which contributed to the significant differences between the breeds analysed.

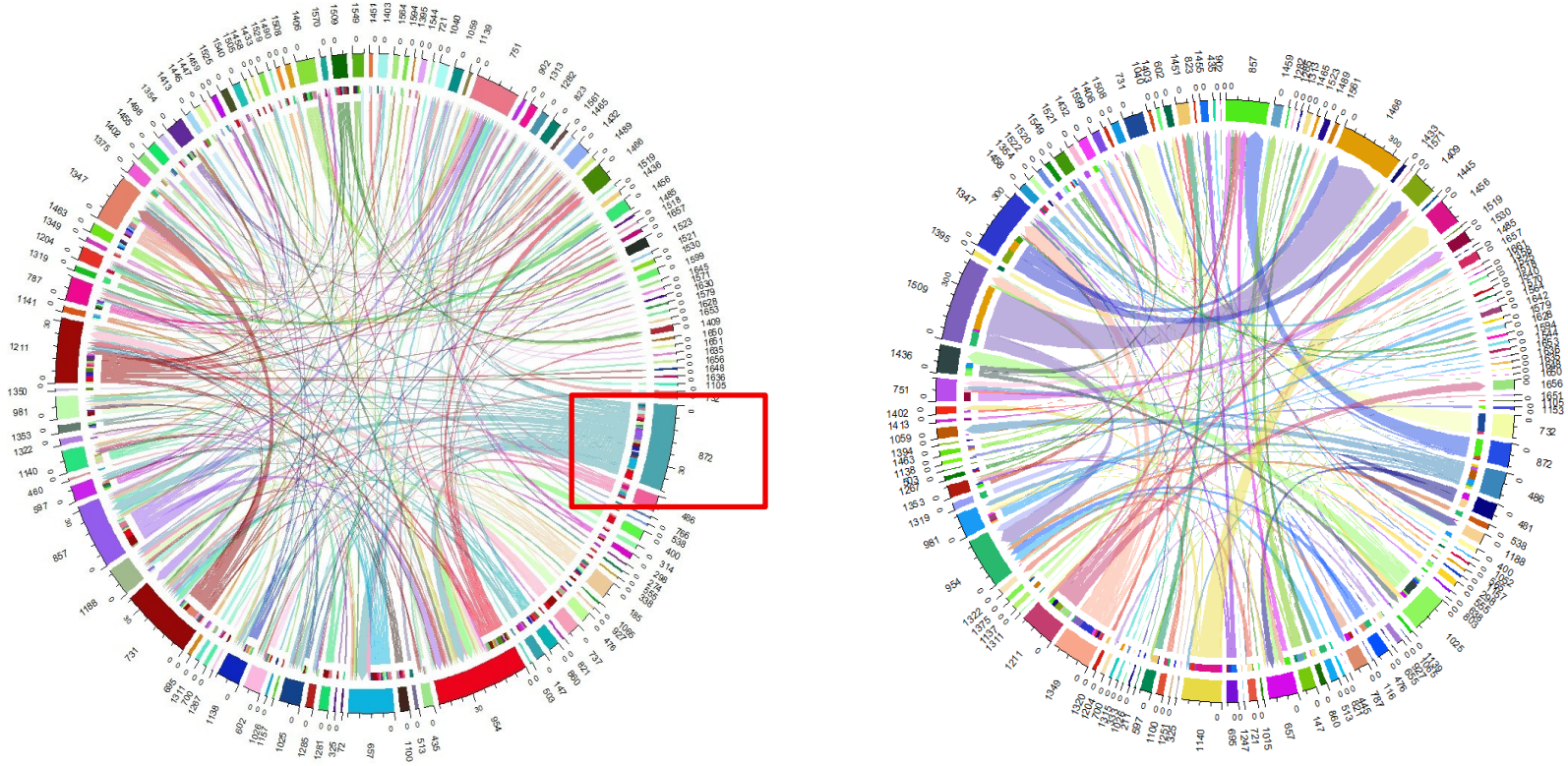
The Swallow-Belly and Red breeds showed a stronger tendency towards internal differentiation, with a larger percentage of herds showing moderate genetic differences than in the Blonde breed. Nevertheless, the average F_{ST} coefficients between herds remained similar for all three breeds (0.04). This phenomenon may be explained by the smaller population sizes of the Swallow-Belly and Red breeds.

The populations analysed, which have been listed in pedigrees since 1981, include both active and previously inactive herds. Analysing entire populations provides a comprehensive overview, but precise information on genetic subdivision depends on the active herds. Genetic differentiation was observed in certain herds across the entire populations analysed (**FigureS 1, S 3 and S 5**). However, among the active herds, these differentiated herds make up a tiny proportion, less than 0.30% (8 out of 3,003) (**Table 10**). When analysing these herds, e.g., 1645, 1630 and 1358 in the Blonde breed (**Figure 14**) and 1436, 1646 and 1664 in the Red breed (**Figure 18**), each herd had only one selected sire. When calculating the average herd coancestry, the predominance of self-coancestry contributes to high F_{ST} coefficients. However, despite this observed differentiation, the details of the substructure within the breeds remain unclear with the applied approaches.

4.8. Migration assessment

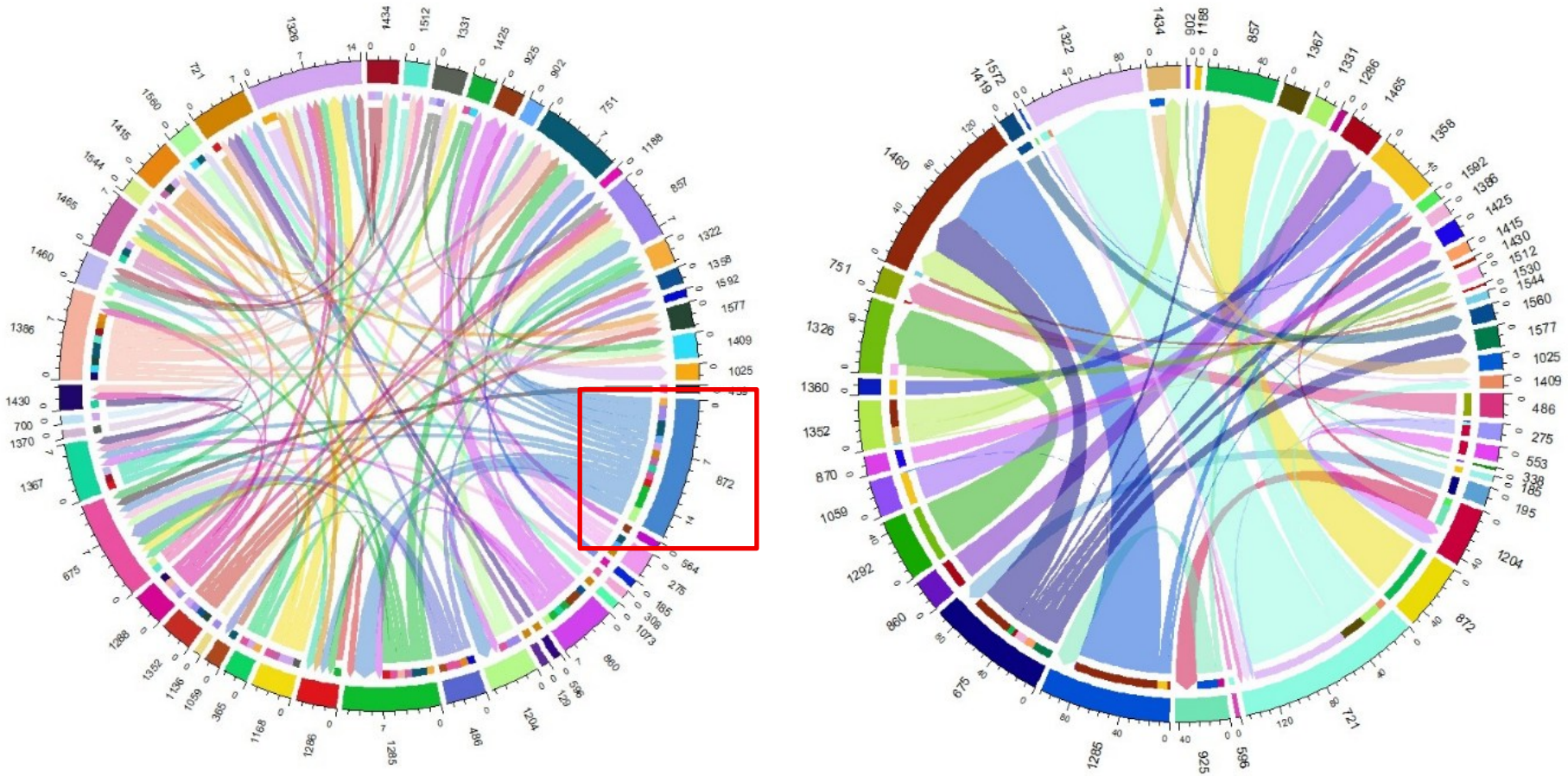
The migration of individuals within herds was considerable, affecting over 60.00% of the total current herds, specifically impacting 61.63% of the Blonde breed, 75.53% of the Swallow-Belly breed, and 63.64% of the Red breed. A consistent pattern emerged across all three breeds, suggesting that an enormous number of females were transferred between herds, while in comparison, the number of males in every moving remained relatively low. Within the three breeds, the herd numbered 872 was the most active and dominant in providing sires to neighbouring herds **(FigureS 7(a), S 8(a), S 9(a)** and **Figure 20(a), 21(a), 22(a))**

.



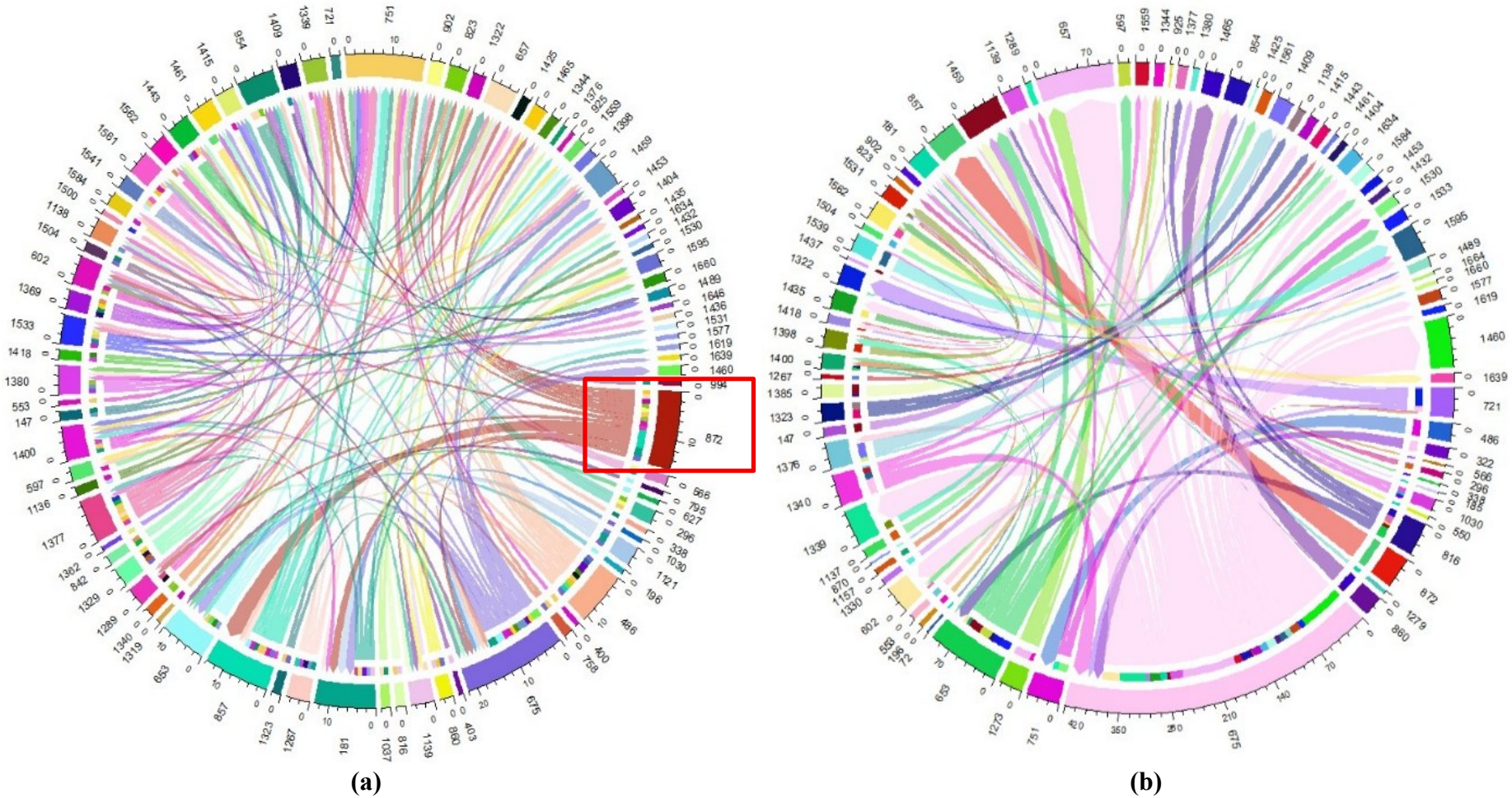
(a) **(b)**

Figure 20. Migration of the Blonde breed in active herds: (**a**) Male; (**b**) Female. Large color-coded circles represent source herds with herd IDs, smaller inner circles indicate destination herds, and arrows show the direction and volume of animal movement (thicker arrows = more animals). The red square indicates the top sire-providing herd.



(a) **(b)**

Figure 21. Migration of the Swallow-Belly breed in active herds: (**a**) Male; (**b**) Female. Large color-coded circles represent source herds with herd IDs, smaller inner circles indicate destination herds, and arrows show the direction and volume of animal movement (thicker arrows = more animals). The red square indicates the top sire-providing herd.



(a) **(b)**

Figure 22. Migration of the Red breed in active herds: (**a**) Male; (**b**) Female. Large color-coded circles represent source herds with herd IDs, smaller inner circles indicate destination herds, and arrows show the direction and volume of animal movement (thicker arrows = more animals). The red square indicates the top sire-providing herd.

In the Blonde breed, the maximum number of male pigs migrating from a particular farm to a particular herd was 10, exceeding the numbers for the Swallow-Belly and Red breeds, at 6 and 4, respectively. In contrast, the range for female pigs is much wider, reaching up to around 270 animals. In contrast the numbers for the Swallow-Belly and Red breeds were lower, with 86 and 78 individuals, respectively.

The connectivity among migrating herds revealed that more than 80% were connected by a single sire. More specifically, this percentage was 80.72% in the current Blonde herds, 87.00% in the current Swallow-Belly herds and 90.34% in the current Red herds. At the same time, 90% of these herds established connections involving more than two sows, and this pattern applied to all three breeds.

Within the Blonde breed, herd 872 stands out as the main source of sires for neighbouring herds, while herd 954 attracts the most out-migrating sires, as shown in **FigureS 7(a)** and **Figure 20(a)**. In addition, herds 1509 and 1466 play an important role in the migration of approximately 270 sows, as shown in **FigureS 7(b)** and **Figure 20(b)**.

FigureS 8(a) and **Figure 21(a)** show that herd 872 has the most significant migration, both in terms of out-migrating and incoming sires of the Swallow-Belly breed. In terms of the out-migration of females, there was significant movement from herd 721 to herd 1322, but the most significant influx was observed in herd 1460, as shown in **FigureS 8(b)** and **Figure 21(b)**.

For the Red breed, **FigureS 9(a)** and **Figure 22(a)** show that herd 872 gave most sires to neighbouring herds, while herd 751 received most sires and shared them with other breeds. For female pigs, herd 675 was the largest contributor and herd 657 is the largest recipient, as shown in **FigureS 9(b)** and **Figure 22(b)**.

The results showed a strong migration between the herds of the three breeds, as about 60.00% of the herds are connected to other herds in some way. In addition, more than 90.00% of the migration involved one sire and more than two sows. The extensive exchange of animals between individual herds could be the reason for genetic similarity between herds in this study. Achmann et al. (2004) found in the studies of Lipizzaners that the exchange of horses between studs plays a crucial role in mitigating genetic divergence between subpopulations. Dumasy et al. (2012) illustrated that an increase in genetic distance was due to a reduced connectivity between herds. This conclusion was drawn by examining the correlation between Reynolds genetic distances and the shortest path lengths calculated by the exchange network method. In addition, the Blonde breed has a lower average F_{ST} (0.04) compared to the Swallow-Belly and Red breeds (0.047), which could be due to a higher number of exchanged animals between herds within the Blonde breed. Dumasy et al. (2012) pointed out the importance of considering the number of exchanged animals when explaining genetic differentiation, and the increase in exchanged animals within the Blonde breed was consistent with its lower F_{ST} coefficient. Both male and female individuals play crucial roles in creating robust connections between herds within breeds. Significantly more females were exchanged in the breeds analysed. However, it must be noted that the two sexes show different migration characteristics. The exchange of boars between herds is a continuous process, and generally, it consists of one or few animals. On the contrary, the female exchange is occasional, and its aim can be establishing a new herd, the herd size enlargement of an existing herd or the re-establishment of a previously closed herd. In addition, the Mangalica farms do not use artificial

insemination (personal communication with HNAMB), but the boars are moved between herds under control. This could support the contribution to the gene flow between the herds of sires.

According to Snegin et al. (2021), the differentiation within the breed has been attributed to many factors, including the gene flow, geographic isolation, breeding preferences and distinctive genetic backgrounds found in the genealogical groups (sire/dam lines) of the breed's founders. Geographic isolation contributed to the emergence of intra-breed differentiation in local goats in Spain and Portugal (Martínez et al., 2015). However, there was no impact of geographical differences on genetic differentiation within the Monteiro pig breed in the Brazilian Pantanal Ecosystem. This is attributed to the presence of evidence indicating a high level of gene flow within this population (Silva et al., 2020). This can be linked to the present study; even Mangalica pigs are kept in many different regional herds, and the intensive connection between herds has contributed to the low genetic differentiation. Differentiation in dog breeds, as demonstrated by Wiener et al. (2017)**,** was driven by the direction of breeding or artificial selection (Wiener et al., 2017). This is primarily not happening in the current study, as all registered herds follow the consistent breeding strategy prescribed by the HNAMB. In addition, no barriers to gene exchange were identified in this study.

5. CONCLUSIONS AND RECOMMENDATIONS

The pedigree analysis of Blonde Mangalica (6 generations), Swallow-Belly Mangalica (5 generations), and Red Mangalica (6 generations) showed sufficient depth and completeness (CGE values of 7.08, 4.29, and 6.17, respectively) to reliably estimate key genetic diversity parameters.

In the reference population (REF2021), the number of ancestors explaining the entire gene pool was 57, 78, and 123 for the Red, Swallow-Bellied, and Blonde Mangalica breeds, respectively, with corresponding genetic diversity losses of 8.70%, 5.70%, and 5.60%. Wright's inbreeding coefficient (F_w) were 5.50 for reference population of Blonde, 4.30 for Swallow-Belly, and 7.54 for Red Mangalica while Kalinowski's new inbreeding coefficients were 2.82, 2.95, and 3.29, respectively.

The Red population has the highest genetic diversity loss, smallest effective population size, and highest inbreeding coefficient that needs to be monitored. In addition, mating plans should be focused on reducing new inbreeding in all Mangalica populations, especially in the Swallow-Belly Mangalica. The estimate inbreeding coefficients over the next 25 years were 9.98, 8.73, and 13.67 for the Blonde, Swallow-Belly, and Red Mangalica, respectively, bringing only Red Mangalica into transitional category.

The correlations between different inbreeding coefficients were calculated. Wright's inbreeding coefficient is moderately to highly correlated with F_{Kal} and F_{New} but shows a low correlation with F_{Bal}. F_{Bal} and F_{Kal} are moderately correlated, whereas F_{Bal} is negatively correlated with F_{New}. These findings indicated that different approaches to estimate inbreeding coefficients capture different aspects of inbreeding.

Analyzing Wright's F_{ST} coefficients by heatmap and calculation cumulative proportion of population relative to different levels of F_{ST}, the substructure within the Blonde, Swallow-Belly and Red breeds could not be found.

The frequency of extensive animal exchange between individual herds and the uniformity of mating strategies confirm genetic homogeneity within these breeds. The patterns observed indicate that the breeds studied, with the aim of maintaining genetic diversity and minimising the risk of inbreeding, show positive signs consistent with conservation objectives.

Pedigree analysis generally assumes that founder individuals are unrelated and non-inbred, which can underestimate inbreeding coefficients by ignoring potential background relatedness. Integrating genomic data (e.g. single nucleotide polymorphism data) overcomes this limitation, yielding more accurate estimates and revealing undocumented inbreeding or relatedness events absent from the pedigree.

Further research can decompose the inbreeding coefficient into partial inbreeding coefficients to identify ancestors with a high inbreeding load in Mangalica populations. This approach could add more information that enables breeders to develop smarter mating strategies by selecting pairs with lower inbreeding load.

6. NEW SCIENTIFIC RESULTS

1. The genealogical data, updated through 2023, now includes a more comprehensive complete generation equivalent (CGE), reported as 9.73, 6.87, and 9.03 for Blonde, Swallow-Belly, and Red Mangalica, respectively. This updated dataset provides a robust foundation for analyzing potential population struture and genetic patterns with accuracy.

2. In the reference population (REF2021), the number of ancestors explaining the entire gene pool was 57, 78, and 123 for the Red, Swallow-Bellied, and Blonde Mangalica breeds, respectively, with corresponding genetic diversity losses of 8.70%, 5.70%, and 5.60%.

3. Wright's inbreeding coefficient (F_w) were 5.50 for reference population of Blonde, 4.30 for Swallow-Belly, and 7.54 for Red Mangalica while Kalinowski's new inbreeding coefficients were 2.82, 2.95, and 3.29, respectively. Kalinowski's new inbreeding coefficient showed an increasing trend in the Swallow-Belly Mangalica reference population but presented highest value in the Red Mangalica reference population. The estimate inbreeding coefficients over the next 25 years were 9.98, 8.73, and 13.67 for the Blonde, Swallow-Belly, and Red Mangalica, respectively, bringing only Red Mangalica into transitional category.

4. Wright's inbreeding coefficient (F_w) is moderately to highly correlated with F_{Kal} and F_{New} but shows a low correlation with F_{Bal}. F_{Bal} and F_{Kal} are moderately correlated, whereas F_{Bal} is negatively correlated with F_{New}. These findings indicated that different approaches to estimate inbreeding coefficients capture different aspects of inbreeding.

5. The research did not detect the actual genetic differentiation within the breeds of Mangalica. The average Wright's F_{ST} coefficients were 0.04 for the Blonde breed and 0.047 for the Swallow-Belly and Red Mangalica breeds, while these parameters were lower in the active herds at 0.03 and 0.04, respectively.

6. The research examined migration patterns within the Mangalica breeds. The migration of individuals between herds was 61.63% for the Blonde breed and 75.53% and 63.64% for the Swallow-Belly and Red Magalica breeds, respectively.

7. SUMMARY

Maintaining genetic variability is crucial for effective genetic conservation, ensuring populations adapt to environmental changes and genetic selection, with expected heterozygosity as a key measure of diversity. Inbreeding, which increases homozygosity and reduces heterozygosity, is a major cause of allele loss, particularly in small, closed populations, leading to inbreeding depression. The inbreeding coefficient, traditionally estimated using Wright's method, measures the probability that two alleles at a locus are identical by descent, while newer methods like ancestral inbreeding consider past autozygosity. In recent decades, modern genomic technologies provide more accurate homozygosity estimates. Yet pedigree-methods remain essential for conservation management when the pedigrees are complete and sufficiently detailed.

Inbreeding depression threatens population survival, especially in small populations, and can affect various traits in wild, zoo, and domesticated animals. Standard procedures can mitigate inbreeding's adverse effects to ensure sustainable livestock production. In cases where inbreeding is unavoidable, such as in the Speke's Gazelle population at St. Louis Zoo, a small founding group led to severe inbreeding depression. Templeton and Read's breeding program for this population rapidly expanded its size and selected diverse inbred animals as parents, halving the inbreeding load in three years. This approach, though debated, demonstrated that deliberate inbreeding combined with selection can reduce inbreeding depression, which is known as purging phenomenon, offering insights for managing captive populations.

Many researchers aim to quantify inbreeding load, the hidden genetic damage in heterozygotes that manifests in homozygotes, using parameters like the inbreeding coefficient, ancestral inbreeding coefficients, likelihood of genetic death, or the number of lethal equivalents to assess its impact on population fitness. These metrics help estimate the burden of deleterious alleles that reduce survival or reproduction when expressed in homozygous individuals. However, detecting purging—the process by which natural selection removes harmful alleles from a population—requires significant effort and resources. Despite extensive studies, evidence for purging remains inconsistent or limited across different methods and populations, making it challenging to draw universal conclusions.

The Mangalica pig, an autochthonous Hungarian breed, exists in three variants—Blonde, Red, and Swallow-Belly—and has been preserved for its biological diversity despite near extinction by the 1990s. Originating in the 1830s through crosses with local and Serbian breeds, Mangalica pigs are valued for fat production and adaptability but have low reproductive capacity. The National Association of Mangalica Breeders, re-established in 1994, has significantly increased the population, with 6,723 sows and 354 boars registered by 2019. Recent studies on Mangalica genetic diversity and population structure, based on pedigree data up to 2011, require updates to reflect changes over the past decade. Key metrics like inbreeding coefficients, effective population size, and gene origin probabilities will be calculated using updated pedigree data to assess genetic diversity and historical breeding patterns. Genetic differentiation between herds will be evaluated using Wright's F_{ST} to monitor potential subpopulation isolation. Migration patterns between herds will be analyzed using pedigree data to understand their impact on genetic diversity and population structure.

The research found that the pedigrees of Mangalica breeds range from 5 generations for Swallow-Belly to 6 generations for Blonde and Red Mangalica, with complete generation equivalents of 4.29 for Swallow-Belly, 7.08 for Blonde, and 6.17 for Red breeds.

Wright's inbreeding coefficient of reference population (REF2021) is highest in Red Mangalica (7.54%) and 4.30% and 5.50% for Swallow-Belly and Blonde, respectively. In which Swallow-Belly is the only population having Kalinowski new inbreeding being higher than Kalinowski inbreeding (2.95% vs. 1.35%). The inbreeding coefficient F_W is strongly correlated with F_{New} but weakly with F_{Bal}, while F_{Bal} and F_{Kal} show a moderate to strong correlation across all studied breeds. F_{New} and F_{Bal} have a slightly negative correlation in all breeds.

The average generation intervals ranged from 3.06 years for Blonde, 3.45 years for Swallow-Belly, and 3.29 year for Red Mangalica, but the differences are not statistically significant. In the REF2021, the estimated effective population sizes (N_e) were within the ranges of 50 and 100, with Blonde Mangalica at 85.57, Swallow-Belly Mangalica at 76.91, and Red Mangalica at 57.74. Based on predicted breeding levels over 25 years, only Red Mangalica was classified in transitional category (least endangered), while the other breeds were out of categories.

The f_a/f_e ratios in the REF2021 of Mangalica breeds ranged from 0.43 to 0.60, indicating that the bottleneck effects happened but were not so severe. The whole gene pool in the Red and Swallow-Belly REF2021 could be explained only by 57 and 78 ancestors, respectively while this parameter in the Blonde REF2021 was almost double with 123. The number of ancestors contributes to 50.00% of gene pool is very small only 6 individuals in the Red, 7 individuals in the Blonde, and 8 individuals in the Swallow-Belly REF2021. The genetic diversity loss in the REF2021 of the Red Mangalica pigs was accounted for the highest proportion of 8.70% and these proportions of the Blonde and Swallow-Belly were 5.60 % and 5.70%, respectively.

No population subdivision was detected in Mangalica breeds, with only 0.27% of active Blonde Mangalica herds, 0.00% of Swallow-Belly Mangalica herds, and 0.07% of Red Mangalica herds having Wright's F_{ST} coefficients greater than 0.15. Considerable migration between herds, at 61.63% for Blonde Mangalica, 75.53% for Swallow-Belly Mangalica, and 63.64% for Red Mangalica, likely contributes to this genetic homogeneity.

The pedigree of Mangalica pigs were explicit depth and completeness to reliably estimate key genetic diversity parameters. The Blonde, Swallow-Belly, and Red Mangalica breeds are not at risk of endangerment from inbreeding over the next 25 years, supported by prolonged keeping sires and dams without using artificial insemination. Using different approaches to estimate inbreeding coefficients and calculating their correlations enables a comprehensive assessment of inbreeding load, enhancing understanding of genetic diversity and inbreeding dynamics in these breeds. The Red population shows the highest genetic diversity loss, the smallest effective population size, and the highest inbreeding coefficient that need to be monitored. In addition, mating plans should be focused on reducing new inbreeding in all Mangalica populations, especially in the Swallow-Belly Mangalica. The potential genetic differenciation within the Blonde, Swallow-Belly and Red breeds could not be detected that could be partly explained by the frequent migration of individuals between herds.

8. ACKNOWLEDGMENT

This thesis represents more than three years of hard-working and effort, made possible by the support, guidance and encouragement of many individuals. I am grateful to everyone who contributed, whether directly or indirectly, and I sincerely apologize to anyone whose name may not be mentioned in the acknowledgements.

My initial gratitude goes to my PhD supervisors for their support and guidance throughout this academic journey. First of all, I would like to thank Prof. Dr. Nagy István for your enormous support not only in my research, but also in my career orientation and overall well-being. You have always made time for me when I needed it, provided the necessary resources, and involved me in the research network. I sincerely acknowledge your kindness, continued encouragement and unwavering support. I also would like to thank my co-supervisor, Ass. Prof. Dr. Kövér György, who taught and supported me in statistics and data analysis and connected me to the Hungarian National Association of Mangalica Breeders' data source for this research.

I would like to acknowledge with gratitude Dr. Bokor Árpád, who assisted me in accessing the Endog software and provided valuable support in the data analysis for this study. My heartfelt gratitude goes to Prof. Dr. Farkas János, who, despite being retired, enthusiastically contributed to the data analysis. A special thank you to Prof. Dr. Juan Pablo Gutiérrez García from University of Madrid, who helped me solve problems while using the Endog software, even though we have not yet met in person. I would like to sincerely thank Prof. Dr. Čurik Ino, who has provided me with materials, broadened my horizons, and offered financial support, as well as the opportunity to engage in academic research at the University of Zagreb. Your guidance has been important in bridging the gap between quantitative genetics and genomics.

I would also like to extend my sincere thanks to Prof. Dr. Szabó András, who taught me, shared his expertise in writing scientific papers and research publication, and supported my participation in seminars and internships throughout my studies. I sincerely appreciate Dr. Tóth Péter, director of the Hungarian National Association of Mangalica Breeders, for the organization's support in providing information on Mangalica pig breeds and the data used in this study. I would like to thank Dr. Áprily Szilva, Head of the Animal Husbandry Institute, for giving me the opportunity to take on short-term work that helped me gain practical experience and partially finance my studies. I am sincerely grateful to the Stipendium Hungaricum scholarship for providing the financial support that enabled me to pursue my studies and research.

Last but not least I am genuinely appreciative to my family who have always supported, cared for, encouraged, and accompanied me throughout my past and future journeys. I also want to thank my friends and colleagues, whose presence and participation in various activities have made my life more meaningful besides my academic activities.

9. REFERENCES

1. ACHMANN, R., CURIK, I., DOVC, P., KAVAR, T., BODO, I., HABE, F., MARTI, E., SÖLKNER, J., BREM, G. (2004): Microsatellite diversity, population subdivision and gene flow in the Lipizzan horse. *Animal Genetics*, *35*(4), 285–292. https://doi.org/10.1111/j.1365-2052.2004.01157.x.

2. ÁCS, V., KÖVÉR, G., FARKAS, J., BOKOR, Á., NAGY, I. (2020): Effects of long-term selection in the Border Collie dog breed: Inbreeding purge of canine hip and elbow dysplasia. *Animals*, *10*(10), 1743.

3. ADDO, S., SCHÄLER, J., HINRICHS, D., THALLER, G. (2017): Genetic Diversity and Ancestral History of the German Angler and the Red-and-White Dual-Purpose Cattle Breeds Assessed through Pedigree Analysis. *Agricultural Sciences*, *8*(9), Article 9. https://doi.org/10.4236/as.2017.89075.

4. ALDERSON, L. (2009): Breeds at risk: Definition and measurement of the factors which determine endangerment. *Livestock Science*, *123*(1), 23–27.

5. ALMEIDA, F. R. C. L., DIAS, A. L. N. A. (2022): Pregnancy in pigs: The journey of an early life. *Domestic Animal Endocrinology*, *78*, 106656. https://doi.org/10.1016/j.domaniend.2021.106656.

6. ALVES, J. M., CARNEIRO, M., AFONSO, S., LOPES, S., GARREAU, H., BOUCHER, S., ALLAIN, D., QUENEY, G., ESTEVES, P. J., BOLET, G. (2015): Levels and patterns of genetic diversity and population structure in domestic rabbits. *PLoS One*, *10*(12), e0144687.

7. ANDERSSON, E., FRÖSSLING, J., ENGBLOM, L., ALGERS, B., GUNNARSSON, S. (2016): Impact of litter size on sow stayability in Swedish commercial piglet producing herds. *Acta Veterinaria Scandinavica*, *58*, 31. https://doi.org/10.1186/s13028-016-0213-8

8. ARGENTE, M-J. (2016): Major components in limiting litter size. 87–114 p. In: Carreira R. P. (Ed.) *Insights from Animal Reproduction.* InTech: London, UK, 242p.

9. BALLOU, J. D. (1997): Ancestral inbreeding only minimally affects inbreeding depression in mammalian populations. *Journal of Heredity*, *88*(3), 169–178.

10. BALLOU, J.D., LACY, R.C. (1995) Identifying genetically important individuals for management of genetic variation in pedigreed populations. 76-111p. In: *Population Management for Survival and Recovery, Analytical Methods and Strategies in Small Population Management*. Columbia University Press, New York, 375 p.

11. BALOGH, E. E., GÁBOR, G., BODÓ, S., RÓZSA, L., RÁTKY, J., ZSOLNAI, A., ANTON, I. (2019): Effect of single-nucleotide polymorphisms on specific reproduction parameters in Hungarian Large White sows. *Acta Veterinaria Hungarica, 67*(2), 256-273.

12. BÂLTEANU, V. A., CARDOSO, T. F., AMILLS, M., EGERSZEGI, I., ANTON, I., BEJA-PEREIRA, A., ZSOLNAI, A. (2019): The footprint of recent and strong demographic decline in the genomes of Mangalitza pigs. *Animal*, *13*(11), 2440–2446.

13. BARKER, J. S. (2001): Conservation and management of genetic diversity: A domestic animal perspective. *Canadian Journal of Forest Research*, *31*(4), 588–595. https://doi.org/10.1139/x00-180.

14. BARKER, J. S. F. (2002): Relevance of animal genetic resources and differences to the plant sector. *Animal Breeding and Animal Genetic Resources*, 15–21.

15. BATES, D., MÄCHLER, M., BOLKER, B., WALKER, S. (2015): Fitting Linear Mixed-Effects Models using lme4. *Journal of statistical software*, *67*, 1-48. https://doi.org/10.18637/jss.v067.i01.

16. BATES, D., RODRIGUEZ, P.P., VAZQUEZ, A. I. (2023): pedigreemm: Pedigree-based mixed-effects models, R package version 0.3-4. https://github.com/anainesvs /pedigreemm/.

17. BAUMUNG, R., FARKAS, J., BOICHARD, D., MÉSZÁROS, G., SÖLKNER, J., CURIK, I. (2015): GRAIN: A computer program to calculate ancestral and partial inbreeding coefficients using a gene dropping approach. *Journal of Animal Breeding and Genetics*, *132*(2), 100–108. https://doi.org/10.1111/jbg.12145.

18. BAXTER, E. M., JARVIS, S., SHERWOOD, L., FARISH, M., ROEHE, R., LAWRENCE, A. B., EDWARDS, S. A. (2011): Genetic and environmental effects on piglet survival and maternal behaviour of the farrowing sow. *Applied Animal Behaviour Science*, *130*(1–2), 28–41.

19. BERGFELDER-DRÜING, S., GROSSE-BRINKHAUS, C., LIND, B., ERBE, M., SCHELLANDER, K., SIMIANER, H., THOLEN, E. (2015): A Genome-Wide Association Study in Large White and Landrace Pig Populations for Number Piglets Born Alive. *PLoS ONE*, *10*(3), e0117468. https://doi.org/10.1371/journal.pone.0117468.

20. BERSABÉ, D., GARCÍA‐DORADO, A. (2013): On the genetic parameter determining the efficiency of purging: An estimate for *D rosophila* egg-to-pupae viability. *Journal of Evolutionary Biology*, *26*(2), 375–385. https://doi.org/10.1111/jeb.12054.

21. BIJLSMA, BUNDGAARD, PUTTEN, V. (1999): Environmental dependence of inbreeding depression and purging in Drosophila melanogaster. *Journal of Evolutionary Biology*, *12*(6), 1125–1137.

22. BOAKES, E. H., WANG, J., AMOS, W. (2007): An investigation of inbreeding depression and purging in captive pedigreed populations. *Heredity*, *98*(3), 172–182.

23. BOAKES, E., WANG, J. (2005): A simulation study on detecting purging of inbreeding depression in captive populations. *Genetics Research*, *86*(2), 139–148.

24. BOICHARD, D. (2002): Pedig: A Fortran package for pedigree analysis suited for large populations. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France, August, 2002. Session 28*, 1–2. https://www.cabdirect.org/cabdirect/abstract/20033053742.

25. BOICHARD, D., MAIGNEL, L., VERRIER, E. (1997): The value of using probabilities of gene origin to measure genetic variability in a population. *Genetics Selection Evolution*, *29*(1), 5–23.

26. BOTHA, M., OROIAN, I. G., PETRESCU-MAG, I. V., GAVRILOAIE, C. (2014): Mangalitsa: The recovery of a rustic genetic heritage. *Porcine Research*, *4*(2), 30–36.

27. CABALLERO, A., BRAVO, I., WANG, J. (2017): The risk of forcing inbreeding in conservation programmes: A reply to Theodorou and Couvet. *Heredity*, *119*(1), 51–53.

28. CABALLERO, A., TORO, M. A. (2000): Interrelations between effective population size and other pedigree tools for the management of conserved populations. *Genetics Research*, *75*(3), 331–343.

29. CABALLERO, A., TORO, M. A. (2002): Analysis of genetic diversity for the management of conserved subdivided populations. *Conservation Genetics*, *3*(3), 289–299. https://doi.org/10.1023/A:1019956205473.

30. CABRERA, R. A., LIN, X., CAMPBELL, J. M., MOESER, A. J., ODLE, J. (2012): Influence of birth order, birth weight, colostrum and serum immunoglobulin G on neonatal piglet survival. *Journal of Animal Science and Biotechnology*, *3*(1), 42. https://doi.org/10.1186/2049-1891-3-42.

31. CANARIO, L., CANTONI, E., LE BIHAN, E., CARITEZ, J. C., BILLON, Y., BIDANEL, J. P., FOULLEY, J. L. (2006): Between-breed variability of stillbirth and its relationship with sow and piglet characteristics. *Journal of Animal Science*, *84*(12), 3185–3196.

32. CARNEIRO, H., PAIVA, S.R., LEDUR, M., FIGUEIREDO, E.A.P., GRINGS, V.H., SILVA, F.C.P., MCMANUS, C. (2014): Pedigree and population viability analyses of a conservation herd of Moura pig. *Animal Genetic Resources*, 54, 127–134.

33. CAROLINO, N., VITORINO, A., CAROLINO, I., PAIS, J., HENRIQUES, N., SILVEIRA, M., VICENTE, A. (2020): Genetic diversity in the Portuguese Mertolenga cattle breed assessed by pedigree analysis. *Animals*, *10*(11), 1990.

34. CASELLAS, J., VARONA, L., IBÁÑEZ-ESCRICHE, N., QUINTANILLA, R., NOGUERA, J. L. (2008): Skew distribution of founder-specific inbreeding depression effects on the longevity of Landrace sows. *Genetics Research*, *90*(6), 499–508. https://doi.org/10.1017/S0016672308009907.

35. CASSADY J.P., JOHNSON R.K., POMP D., ROHRER G.A., VAN VLECK L.D., SPIEGEL E.K., GILSON K.M. (2001): Identification of Quantitative Trait Loci affecting

reproduction in pigs. Journal of animal science, 79 (3): 623-633. doi: 10.2527/2001.793623x.

36. CECCHINATO, A., BONFATTI, V., GALLO, L., CARNIER, P. (2008): Survival analysis of preweaning piglet survival in a dry-cured ham-producing crossbred line. *Journal of Animal Science*, *86*(10), 2486–2495.

37. CERVANTES, I., GOYACHE, F., MOLINA, A., VALERA, M., GUTIÉRREZ, J. P. (2008a): Application of individual increase in inbreeding to estimate realized effective sizes from real pedigrees. *Journal of Animal Breeding and Genetics*, *125*(5), 301–310.

38. CERVANTES, I., MOLINA, A., GOYACHE, F., GUTIÉRREZ, J. P., VALERA, M. (2008b): Population history and genetic variability in the Spanish Arab Horse assessed via pedigree analysis. *Livestock Science*, *113*(1), 24–33.

39. CHANG, M. L., YOKOYAMA, J. S., BRANSON, N., DYER, D. J., HITTE, C., OVERALL, K. L., HAMILTON, S. P. (2009): Intrabreed Stratification Related to Divergent Selection Regimes in Purebred Dogs May Affect the Interpretation of Genetic Association Studies. *Journal of Heredity*, *100*(Suppl 1), S28–S36. https://doi.org/10.1093/jhered/esp012.

40. CHE, L., YANG, Z., XU, M., XU, S., CHE, L., LIN, Y., FANG, Z., FENG, B., LI, J., CHEN, D. (2017): Maternal nutrition modulates fetal development by inducing placental efficiency changes in gilts. *BMC Genomics*, *18*, 1–14.

41. CHEN, Z., YE, S., TENG, J., DIAO, S., YUAN, X., CHEN, Z., ZHANG, H., LI, J., ZHANG, Z. (2019): Genome-wide association studies for the number of animals born alive and dead in duroc pigs. *Theriogenology*, *139*, 36–42. https://doi.org/10.1016/j.theriogenol ogy.2019.07.013.

42. CHEN, Z., ZHANG, Z., WANG, Z., ZHANG, Z., WANG, Q., PAN, Y. (2022): Heterozygosity and homozygosity regions affect reproductive success and the loss of reproduction: A case study with litter traits in pigs. *Computational and Structural Biotechnology Journal*, *20*, 4060–4071. https://doi.org/10.1016/j.csbj.2022.07.039.

43. COSTER, A. (2022): pedigree: Pedigree Functions (Version 1.4.2) [Computer software]. https://cran.r-project.org/web/packages/pedigree/index.html.

44. CRNOKRAK, P., ROFF, D. A. (1999): Inbreeding depression in the wild. *Heredity*, *83*(3), 260–270. https://doi.org/10.1038/sj.hdy.6885530.

45. CULBERTSON, M. S., MABRY, J. W., MISZTAL, I., BERTRAND, J. K., LARSON, L., CUNDIFF, L. V., FLATT, W. (1997): Effects of inbreeding and outbreeding in purebred Hampshire and Duroc Swine. *The Professional Animal Scientist*, *13*(4), 194–197.

46. CURIK, I., FERENČAKOVIĆ, M., SÖLKNER, J. (2017): Genomic dissection of inbreeding depression: A gate to new opportunities. *Revista Brasileira de Zootecnia*, *46*, 773–782.

47. CURIK, I., KÖVÉR, G., FARKAS, J., SZENDRŐ, Z., ROMVÁRI, R., SÖLKNER, J., NAGY, I. (2020): Inbreeding depression for kit survival at birth in a rabbit population under long-term selection. *Genetics Selection Evolution*, *52*(1), 39. https://doi.org/10.1186/s12711-020-00557-3.

48. DAMGAARD, L. H., RYDHMER, L., LØVENDAHL, P., GRANDINSON, K. (2003): Genetic parameters for within-litter variation in piglet birth weight and change in within-litter variation during suckling. *Journal of Animal Science*, *81*(3), 604–610.

49. DARWIN, C., TANGLEY, L. (1984): The Zoo Ark—Charting a New Course. *BioScience*, *34*(10), 606–612. https://doi.org/10.1093/bioscience/34.10.606.

50. DE CARA, M. Á. R., VILLANUEVA, B., TORO, M. Á., FERNÁNDEZ, J. (2013): Purging deleterious mutations in conservation programmes: Combining optimal contributions with inbred matings. *Heredity*, *110*(6), 530–537.

51. DE OLIVEIRA, L. F., LOPES, P. S., DIAS, L. C. D. C. M., SILVA, L. M. D. E., SILVA, H. T., GUIMARÃES, S. E. F., MARQUES, D. B. D., SILVA, D. A. D., VERONEZE, R. (2022): Estimation of genetic parameters and inbreeding depression in Piau breed pigs [Preprint]. In Review. https://doi.org/10.21203/rs.3.rs-1619371/v1.

52. DISTL, O. (2007): Mechanisms of Regulation of Litter Size in Pigs on the Genome Level. *Reproduction in Domestic Animals*, *42*(s2), 10–16. https://doi.org/10.1111/j.1439-0531.2007.00887.x.

53. DOEKES, H. P., BIJMA, P., WINDIG, J. J. (2021): How Depressing Is Inbreeding? A Meta-Analysis of 30 Years of Research on the Effects of Inbreeding in Livestock. *Genes*, *12*(6), Article 6. https://doi.org/10.3390/genes12060926.

54. DOEKES, H. P., CURIK, I., NAGY, I., FARKAS, J., KÖVÉR, G., WINDIG, J. J. (2020): Revised Calculation of Kalinowski's Ancestral and New Inbreeding Coefficients. *Diversity*, *12*(4), Article 4. https://doi.org/10.3390/d12040155.

55. DOEKES, H. P., VEERKAMP, R. F., BIJMA, P., DE JONG, G., HIEMSTRA, S. J., WINDIG, J. J. (2019): Inbreeding depression due to recent and ancient inbreeding in Dutch Holstein–Friesian dairy cattle. *Genetics Selection Evolution*, *51*(1), 54. https://doi.org/10.1186/s12711-019-0497-z.

56. DUMASY, J.-F., DANIAUX, C., DONNAY, I., BARET, P. V. (2012): Genetic diversity and networks of exchange: A combined approach to assess intra-breed diversity. *Genetics Selection Evolution*, *44*(1), 17. https://doi.org/10.1186/1297-9686-44-17.

57. DUSSEX, N., VAN DER VALK, T., MORALES, H. E., WHEAT, C. W., DÍEZ-DEL-MOLINO, D., VON SETH, J., FOSTER, Y., KUTSCHERA, V. E., GUSCHANSKI, K., RHIE, A. (2021): Population genomics of the critically endangered kākāpō. *Cell Genomics*, *1*(1). https://doi.org/10.1016/j.xgen.2021.100002.

58. EGERSZEGI, I., RÁTKY, J., SOLTI, L., BRÜSSOW, K.-P. (2003): Mangalica–an indigenous swine breed from Hungary. *Archives Animal Breeding*, *46*(3), 245–256.

59. ERNST, C. W., STEIBEL, J. P. (2013): Molecular advances in QTL discovery and application in pig breeding. *Trends in Genetics*, *29*(4), 215–224. https://doi.org/10.1016/j.tig.2013.02.002.

60. FALCONER, D. S., MACKAY, T. F. C. (1996): Introduction to quantitative genetics, 4th edition. Longman. *Essex, England*, 254–256.

61. FARKAS, J., CURIK, I., CSATÓ, L., CSÖRNYEI, Z., BAUMUNG, R., NAGY, I. (2007): Bayesian inference of inbreeding effects on litter size and gestation length in Hungarian Landrace and Hungarian Large White pigs. *Livestock Science*, *112*(1–2), 109–114.

62. FELDPAUSCH, J. A., JOURQUIN, J., BERGSTROM, J. R., BARGEN, J. L., BOKENKROGER, C. D., DAVIS, D. L., GONZALEZ, J. M., NELSSEN, J. L., PULS, C. L., TROUT, W. E., RITTER, M. J. (2019): Birth weight threshold for identifying piglets at risk for preweaning mortality. *Translational Animal Science*, *3*(2), 633–640. https://doi.org/10.1093/tas/txz076.

63. FRANK, K., MOLNÁR, J., BARTA, E., MARINCS, F. (2017): The full mitochondrial genomes of Mangalica pig breeds and their possible origin. *Mitochondrial DNA Part B*, *2*(2), 730–734. https://doi.org/10.1080/23802359.2017.1390415.

64. FRANKHAM, R. (1995): Conservation genetics. *Annual Review of Genetics*, *29*(Volume 29, 1995), 305–327. https://doi.org/10.1146/annurev.ge.29.120195.001513

65. FRANKHAM, R., BRISCOE, D. A., BALLOU, J. D. (2002): Introduction to conservation genetics. *Cambridge university press*. 640 p. 309 – 335.

66. FRANKHAM, R., GILLIGAN, D. M., MORRIS, D., BRISCOE, D. A. (2001): Inbreeding and extinction: Effects of purging. *Conservation Genetics*, *2*(3), 279–284. https://doi.org/10.1023/A:1012299230482.

67. NOVOZÁNSZKY, G., ZSIGMOND, R. F. (2019): A Sertéstenyésztés 2019. Évi Eredményei from Nemzeti Élelmiszerlánc-Biztonsági Hivatal. https://portal.nebih.gov.hu/documents/10182/43858/Sert%C3%A9s+%C3%A9vk%C3%B6nyv2019.pdf/. Search engine: Google. Date of search: 2023.06.25.

68. GALLA, S. J., BROWN, L., COUCH-LEWIS (NGĀI TAHU: TE HAPŪ O NGĀTI WHEKE, Y., NGĀTI WAEWAE), CUBRINOVSKA, I., EASON, D., GOOLEY, R. M., HAMILTON, J. A., HEATH, J. A., HAUSER, S. S., LATCH, E. K., MATOCQ, M. D., RICHARDSON, A., WOLD, J. R., HOGG, C. J., SANTURE, A. W., STEEVES, T. E. (2022): The relevance of pedigrees in the conservation genomics era. *Molecular Ecology*, *31*(1), 41–54. https://doi.org/10.1111/mec.16192.

69. GARCÍA-ATANCE, M. A., CARLEOS, C., ANDRINO, S., JUSTO, J. R., RIVERO, C. J., FERNÁNDEZ, M., CAÑON, J., CORTES, O. (2023): Genetic Diversity of Five Galician (Northwestern Spain) Local Primitive Bovine Breeds Using Pedigree Records. *Diversity*, *15*(2), 252.

70. GARCÍA-DORADO, A. (2012): Understanding and predicting the fitness decline of shrunk populations: Inbreeding, purging, mutation, and standard selection. *Genetics*, *190*(4), 1461–1476.

71. GARCÍA-DORADO, A., WANG, J., LÓPEZ-CORTEGANO, E. (2016): Predictive model and software for inbreeding-purging analysis of pedigreed populations. *G3: Genes, Genomes, Genetics*, *6*(11), 3593–3601.

72. GEBREGIWERGIS, G. T., SØRENSEN, A. C., HENRYON, M., MEUWISSEN, T. (2020): Controlling Coancestry and Thereby Future Inbreeding by Optimum-Contribution Selection Using Alternative Genomic-Relationship Matrices. *Frontiers in Genetics*, *11*. https://doi.org/10.3389/fgene.2020.00345.

73. GEISERT, R. D., SCHMITT, R. A. M. (2001): Early embryonic survival in the pig: Can it be improved? *J Anim Sci*, *80*(E-suppl_1), E54–E65.

74. GILMOUR, A. R., R.B.J., G., CULLIS, B. R., THOMPSON, R. (2009): Asreml User Guide Release 3.0. *VSN International Ltd, Hemel Hemptead, HP1 1ES, UK*.

75. GLOWATZKI ‐ MULLIS, M. L., MUNTWYLER, J., PFISTER, W., MARTI, E., RIEDER, S., PONCET, P. A., GAILLARD, C. (2006): Genetic diversity among horse populations with a special focus on the Franches-Montagnes breed. *Animal Genetics*, *37*(1), 33–39. https://doi.org/10.1111/j.1365-2052.2005.01376.x.

76. GONZÁLEZ-CANO, R., GONZÁLEZ-MARTÍNEZ, A., MUÑOZ-MEJÍAS, M. E., VALERA, P., RODERO, E. (2022): Analyses of Genetic Diversity in the Endangered "Berrenda" Spanish Cattle Breeds Using Pedigree Data. *Animals*, *12*(3), 249.

77. GOURLEY, K. M., CALDERON, H. I., WOODWORTH, J. C., DEROUCHEY, J. M., TOKACH, M. D., DRITZ, S. S., GOODBAND, R. D. (2020): Sow and piglet traits associated with piglet survival at birth and to weaning. *Journal of Animal Science*, *98*(6), skaa187. https://doi.org/10.1093/jas/skaa187.

78. GU, Z., GU, L., EILS, R., SCHLESNER M., BRORS B. (2014): Circlize implements and enhances circular visualization in R. *Bioinformatics, 30*(19), 2811-2812.

79. GULISIJA, D., CROW, J. F. (2007): Inferring purging from pedigree data. *Evolution*, *61*(5), 1043–1051.

80. GUTIÉRREZ, J. P., CERVANTES, I., GOYACHE, F. (2009): Improving the estimation of realized effective population sizes in farm animals. *Journal of Animal Breeding and Genetics*, *126*(4), 327–332.

81. GUTIÉRREZ, J. P., GOYACHE, F. (2005): A note on ENDOG: A computer program for analysing pedigree information. *Journal of Animal Breeding and Genetics*, *122*(3), 172–176. https://doi.org/10.1111/j.1439-0388.2005.00512.x.

82. GUTIÉRREZ-REINOSO, M. A., APONTE, P. M., GARCÍA-HERREROS, M. (2022): A review of inbreeding depression in dairy cattle: Current status, emerging control strategies,

and future prospects. *Journal of Dairy Research*, *89*(1), 3–12. https://doi.org/10.1017/S0022029922000188.

83. GVOZDANOVIĆ, K., ŠKORPUT, D., KUŠEC, I. D., SALAJPAL, K., KUŠEC, G. (2020): Estimation of population differentiation using pedigree and molecular data in Black Slavonian pig. *Acta Fytotechn Zootechn*, *23*, 241–249. https://doi.org/10.15414 /afz.2020.23.mi-fpap.241-249.

84. HAIG, S. M., BALLOU, J. D., DERRICKSON, S. R. (1990): Management Options for Preserving Genetic Diversity: Reintroduction of Guam Rails to the Wild. *Conservation Biology*, *4*(3), 290–300. https://doi.org/10.1111/j.1523-1739.1990.tb00291.x.

85. HANKÓ, B. (1940): Ancient domestic animals of Hungary (Ősi magyar háziállataink). Tiszántúli Mg-i Kamara, Debrecen, Hungary.

86. HARTL, D. L., CLARK, A. G. (2007): Principles of population genetics. 4th edition. *Sinauer associates*. Sunderland, Massachusetts. 671p.

87. HEDRICK, P. W. (1994): Purging inbreeding depression and the probability of extinction: Full-sib mating. *Heredity*, *73*(4), 363–372.

88. HEDRICK, P. W., GARCIA-DORADO, A. (2016): Understanding inbreeding depression, purging, and genetic rescue. *Trends in Ecology & Evolution*, *31*(12), 940–952.

89. HELLBRÜGGE, B., TÖLLE, K.-H., BENNEWITZ, J., HENZE, C., PRESUHN, U., KRIETER, J. (2008): Genetic aspects regarding piglet losses and the maternal behaviour of sows. Part 1. Genetic analysis of piglet mortality and fertility traits in pigs. *Animal*, *2*(9), 1273–1280.

90. HENDERSON, C. R. (1975): Best linear unbiased estimation and prediction under a selection model. *Biometrics*, 423–447.

91. HERPIN, P., HULIN, J. C., LE DIVIDICH, J., FILLAUT, M. (2001): Effect of oxygen inhalation at birth on the reduction of early postnatal mortality in pigs. *Journal of Animal Science*, *79*(1), 5–10.

92. HEUß, E. M., PRÖLL-CORNELISSEN, M. J., NEUHOFF, C., THOLEN, E., GROßE-BRINKHAUS, C. (2019): Invited review: Piglet survival: benefits of the immunocompetence. *Animal*, *13*(10), 2114–2124. https://doi.org/10.1017 /S1751731119000430.

93. HINES, E. (2021): Developmental Milestones during Pig Gestation. Search engine: Google. https://extension.psu.edu/developmental-milestones-during-pig-gestation. Date of search: 2023. 06. 23.

94. HINRICHS, D., BENNEWITZ, J., WELLMANN, R., THALLER, G. (2015): Estimation of ancestral inbreeding effects on stillbirth, calving ease and birthweight in German Holstein dairy cattle. *Journal of Animal Breeding and Genetics*, *132*(1), 59–67. https://doi.org/10.1111/jbg.12114.

95. HINRICHS, D., MEUWISSEN, T. H., ØDEGARD, J., HOLT, M., VANGEN, O., WOOLLIAMS, J. A. (2007): Analysis of inbreeding depression in the first litter size of mice in a long-term selection experiment with respect to the age of the inbreeding. *Heredity*, *99*(1), 81–88.

96. HOECK, P. E., WOLAK, M. E., SWITZER, R. A., KUEHLER, C. M., LIEBERMAN, A. A. (2015): Effects of inbreeding and parental incubation on captive breeding success in Hawaiian crows. *Biological Conservation*, *184*, 357–364.

97. HOLLEMA, B. L., ZWIERS, S., HERMESCH, S. (2020): Genetic parameters for haemoglobin levels in sows and piglets as well as sow reproductive performance and piglet survival. *Animal*, *14*(4), 688–696. https://doi.org/10.1017/S1751731119002532.

98. HONDA, T., NOMURA, T., YAMAGUCHI, Y., MUKAI, F. (2004): Monitoring of genetic diversity in the Japanese Black cattle population by the use of pedigree information. *Journal of Animal Breeding and Genetics*, *121*(4), 242–252.

99. HOSHINO, Y., KOKETSU, Y. (2009): An evaluation of the impact of increased lactation length on the reproductive efficiency of sows in commercial herds. *Journal of Veterinary Medical Science*, *71*(3), 299–303.

100. IMAEDA, N., ANDO, A., MATSUBARA, T., TAKASU, M., NISHII, N., MIYAMOTO, A., OHSHIMA, S., KAMETANI, Y., SUZUKI, S., SHIINA, T., ONO, T., KULSKI, J. K., KITAGAWA, H. (2021): Stillbirth rates and their association with swine leucocyte antigen class II haplotypes in Microminipigs. *Animal Bioscience*, *34*(11), 1749–1756. https://doi.org/10.5713/ab.20.0763.

101. JATFA, J. W., WACHIDA, N. M., IJABO, H. M., ADAMU, S. S. (2018): Aflatoxicosis Associated with Swine Stillbirth in the Piggery Farm University of Agriculture Makurdi. *Curr. Trends Biomedical. Eng. Biosci*, *13*, 555873.

102. JI, Y., WU, Z., DAI, Z., WANG, X., LI, J., WANG, B., WU, G. (2017): Fetal and neonatal programming of postnatal growth and feed efficiency in swine. *Journal of Animal Science and Biotechnology*, *8*. https://doi.org/10.1186/s40104-017-0173-5.

103. JIANG, Y.-L., LI, N., FAN, X.-Z., XIAO, L.-R., XIANG, R.-L., HU, X.-X., DU, L.-X., WU, C.-X. (2002): Associations of T→A Mutation in the Promoter Region of Myostatin Gene with Birth Weight in Yorkshire Pigs. *Asian-Australasian Journal of Animal Sciences*, *15*(11), 1543–1545.

104. JOCHOVÁ, M., NOVÁK, K., KOTT, T., VOLEK, Z., MAJZLÍK, I., TŮMOVÁ, E. (2017): Genetic characterization of Czech local rabbit breeds using microsatellite analysis. *Livestock Science*, *201*, 41–49. https://doi.org/10.1016/j.livsci.2017.03.025.

105. JUSTINSKI, C., WILKENS, J., DISTL, O. (2023): Genetic Diversity and Trends of Ancestral and New Inbreeding in German Sheep Breeds by Pedigree Data. *Animals*, *13*(4), 623.

106. KALINOWSKI, S. T., HEDRICK, P. W., MILLER, P. S. (2000): Inbreeding Depression in the Speke's Gazelle Captive Breeding Program. *Conservation Biology*, *14*(5), 1375–1384. https://doi.org/10.1046/j.1523-1739.2000.98209.x.

107. KARDOS, M., HUSBY, A., MCFARLANE, S. E., QVARNSTRÖM, A., ELLEGREN, H. (2016): Whole-genome resequencing of extreme phenotypes in collared flycatchers highlights the difficulty of detecting quantitative trait loci in natural populations. *Molecular Ecology Resources*, *16*(3), 727–741. https://doi.org/10.1111/1755-0998.12498.

108. KARDOS, M., LUIKART, G., ALLENDORF, F. W. (2015): Measuring individual inbreeding in the age of genomics: Marker-based measures are better than pedigrees. *Heredity*, *115*(1), 63–72. https://doi.org/10.1038/hdy.2015.17.

109. KAUFMANN, D., HOFER, A., P. BIDANEL, J., KÜNZI, N. (2000): Genetic parameters for individual birth and weaning weight and for litter size of Large White pigs. *Journal of Animal Breeding and Genetics*, *117*(2), 121–128. https://doi.org/10.1111/j.1439-0388.2000x.00238.x.

110. KELLER, L. F., WALLER, D. M. (2002): Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, *17*(5), 230–241. https://doi.org/10.1016/S0169-5347(02)02489-8

111. KENNEDY, E. S., GRUEBER, C. E., DUNCAN, R. P., JAMIESON, I. G. (2014): Severe inbreeding depression and no evidence of purging in an extremely inbred wild species—The Chatham Island black robin. *Evolution*, *68*(4), 987–995.

112. KHAN, A., PATEL, K., SHUKLA, H., VISWANATHAN, A., VAN DER VALK, T., BORTHAKUR, U., NIGAM, P., ZACHARIAH, A., JHALA, Y. V., KARDOS, M., RAMAKRISHNAN, U. (2021): Genomic evidence for inbreeding depression and purging of deleterious genetic variation in Indian tigers. *Proceedings of the National Academy of Sciences*, *118*(49), e2023018118. https://doi.org/10.1073/pnas.2023018118.

113. KITKHA, S., BOONSOONGNERN, A., RATANAVANICHROJN, N., JIRAWATTANAPONG, P., PINYOPUMMIN, A. (2017): Effects of the higher parity and litter size on piglet birth weight and survival rate of later born piglets. *Thai Journal of Veterinary Medicine*, *17*(1), 78 – 86. https://doi.org/10.56808/2985-1130.2815.

114. KLEIN, R., OLÁH, J., MIHÓK, S., POSTA, J. (2022): Pedigree-Based Description of Three Traditional Hungarian Horse Breeds. *Animals, 12*(16), 2071. https://doi.org/10.3390/ani12162071.

115. KLEINMAN-RUIZ, D., LUCENA-PEREZ, M., VILLANUEVA, B., FERNÁNDEZ, J., SAVELJEV, A. P., RATKIEWICZ, M., SCHMIDT, K., GALTIER, N., GARCÍA-DORADO, A., GODOY, J. A. (2022): Purging of deleterious burden in the endangered Iberian lynx. *Proceedings of the National Academy of Sciences*, *119*(11), e2110614119. https://doi.org/10.1073/pnas.2110614119.

116. KNOL, E. F., DUCRO, B. J., VAN ARENDONK, J. A. M., VAN DER LENDE, T. (2002a): Direct, maternal and nurse sow genetic effects on farrowing-, pre-weaning- and total piglet survival. *Livestock Production Science*, *73*(2), 153–164. https://doi.org/10.1016/S0301-6226(01)00248-2.

117. KNOL, E. F., LEENHOUWERS, J. I., VAN DER LENDE, T. (2002c): Genetic aspects of piglet survival. *Livestock Production Science*, *78*(1), 47–55.

118. KNOL, E. F., VAN DER SPEK, D., ZAK, L. J. (2022b): Genetic aspects of piglet survival and related traits: A review. *Journal of Animal Science*, *100*(6), skac190. https://doi.org/10.1093/jas/skac190.

119. KÖCK, A., FUERST-WALTL, B., BAUMUNG, R. (2009): Effects of inbreeding on number of piglets born total, born alive and weaned in Austrian Large White and Landrace pigs. *Archives Animal Breeding*, *52*(1), 51–64.

120. KOENIG, S., SIMIANER, H. (2006): Approaches to the management of inbreeding and relationship in the German Holstein dairy cattle population. *Livestock Science*, *103*(1), 40–53. https://doi.org/10.1016/j.livsci.2005.12.009.

121. KÖVÉR, G., CURIK, I., VOSTRY, L., FARKAS, J., MEZŐSZENTGYÖRGYI, D., NAGY, I. (2023): Analysis of inbreeding effects on survival at birth of Pannon White rabbits using the Inbreeding-Purging Model. *Diversity*, *15*(1), 71.

122. KRISTENSEN, T. N., SØRENSEN, A. C. (2005): Inbreeding – lessons from animal breeding, evolutionary biology and conservation genetics. *Animal Science*, *80*(2), 121–133. https://doi.org/10.1079/ASC41960121.

123. KRUPA, E., ŽÁKOVÁ, E., KRUPOVÁ, Z. (2015): Evaluation of inbreeding and genetic variability of five pig breeds in Czech Republic. *Asian-Australasian Journal of Animal Sciences*, *28*(1), 25–36. https://doi.org/10.5713/ajas.14.0251.

124. KRUPA, E., MORAVČÍKOVÁ, N., KRUPOVÁ, Z., ŽÁKOVÁ, E. (2021): Assessment of the genetic diversity of a local pig breed using pedigree and SNP data. *Genes*, *12*(12), 1972.

125. LACY, R. C. (1989): Analysis of founder representation in pedigrees: Founder equivalents and founder genome equivalents. *Zoo Biology*, *8*(2), 111–123.

126. LACY, R. C. (1995): Clarification of genetic terms and their use in the management of captive populations. *Zoo Biology*, *14*(6), 565–577. https://doi.org/10.1002/zoo.1430140609.

127. LACY, R. C., BALLOU, J. D. (1998): Effectiveness of selection in reducing the genetic load in populations of Peromyscus polionotus during generations of inbreeding. *Evolution*, *52*(3), 900–909.

128. LANFERDINI, E., ANDRETTA, I., FONSECA, L. S., MOREIRA, R. H. R., CANTARELLI, V. S., FERREIRA, R. A., SARAIVA, A., ABREU, M. L. T. (2018): Piglet birth weight, subsequent performance, carcass traits and pork quality: A meta-

analytical study. *Livestock Science*, *214*, 175–179. https://doi.org/10.1016/j.livsci.2018.05.019.

129. LANGENDIJK, P. (2021): Latest Advances in Sow Nutrition during Early Gestation. *Animals : An Open Access Journal from MDPI*, *11*(6), 1720. https://doi.org/10.3390/ani11061720.

130. LANGENDIJK, P., PLUSH, K. (2019): Parturition and Its Relationship with Stillbirths and Asphyxiated Piglets. *Animals*, *9*(11), Article 11. https://doi.org/10.3390/ani9110885

131. LANH, D. T. K., NAM, N. H. (2022): High stillbirth rate in a swine farm in Vietnam and associated risk factors. *Journal of Advanced Veterinary and Animal Research*, *9*(1), 13–18. https://doi.org/10.5455/javar.2022.i564.

132. LAZEBNAYA, I. V., PERCHUN, A. V., LAZEBNY, O. E. (2020): Intrabreed and interbreed variation of the BOLA-DRB3.2 gene in the Kostroma and Yaroslavl indigenous Russian cattle breeds. *Immunogenetics*, *72*(6–7), 355–366. https://doi.org/10.1007/s00251-020-01173-7.

133. LE COZLER, Y., GUYOMARC'H, C., PICHODO, X., QUINIO, P.-Y., PELLOIS, H. (2002): Factors associated with stillborn and mummified piglets in high-prolific sows. *Animal Research*, *51*(3), 261–268.

134. LEE, J., LEE, S.-M., LIM, B., PARK, J., SONG, K.-L., JEON, J.-H., NA, C.-S., KIM, J.-M. (2020): Estimation of Variance Components and Genomic Prediction for Individual Birth Weight Using Three Different Genome-Wide SNP Platforms in Yorkshire Pigs. *Animals*, *10*(12), Article 12. https://doi.org/10.3390/ani10122219.

135. LEENHOUWERS, J. I., VAN DER LENDE, T., KNOL, E. F. (1999): Analysis of stillbirth in different lines of pig. *Livestock Production Science*, *57*(3), 243–253.

136. LEENHOUWERS, J. I., WISSINK, P., VAN DER LENDE, T., PARIDAANS, H., KNOL, E. F. (2003): Stillbirth in the pig in relation to genetic merit for farrowing survival1. *Journal of Animal Science*, *81*(10), 2419–2424. https://doi.org/10.2527/2003.81102419x.

137. LEROY, G. (2014): Inbreeding depression in livestock species: Review and meta-analysis. *Animal Genetics*, *45*(5), 618–628. https://doi.org/10.1111/age.12178.

138. LI, Y., LI, B., YANG, M., HAN, H., CHEN, T., WEI, Q., MIAO, Z., YIN, L., WANG, R., SHEN, J., LI, X., XU, X., FANG, M., ZHAO, S. (2020): Genome-Wide Association Study and Fine Mapping Reveals Candidate Genes for Birth Weight of Yorkshire and Landrace Pigs. *Frontiers in Genetics*, *11*. https://www.frontiersin.org/articles/10.3389/fgene.2020.00183.

139. LÓPEZ-CORTEGANO, E. (2022): purgeR: Inbreeding and purging in pedigreed populations. *Bioinformatics*, *38*(2), 564–565.

140. LÓPEZ-CORTEGANO, E., BERSABÉ, D., WANG, J., GARCÍA-DORADO, A. (2018): Detection of genetic purging and predictive value of purging parameters estimated in pedigreed populations. *Heredity*, *121*(1), 38–51.

141. LÓPEZ-CORTEGANO, E., MORENO, E., GARCÍA-DORADO, A. (2021): Genetic purging in captive endangered ungulates with extremely low effective population sizes. *Heredity*, *127*(5), 433–442.

142. LÓPEZ-CORTEGANO, E., VILAS, A., CABALLERO, A., GARCÍA-DORADO, A. (2016): Estimation of genetic purging under competitive conditions. *Evolution*, *70*(8), 1856–1870.

143. LUKOVIĆ Z., ŠKORPUT D. (2015): Factors Influencing Litter Size in Pigs. *Cabi Reviews* 2015: 1-9. doi: 10.1079/PAVSNNR201510006.

144. MACCLUER, J. W., BOYCE, A. J., DYKE, B., WEITKAMP, L. R., PFENNING, D. W., PARSONS, C. J. (1983): Inbreeding and pedigree structure in Standardbred horses. *Journal of Heredity*, *74*(6), 394–399.

145. MACCLUER, J. W., VANDEBERG, J. L., READ, B., RYDER, O. A. (1986): Pedigree analysis by computer simulation. *Zoo Biology*, *5*(2), 147–160. https://doi.org/10.1002/zoo.1430050209.

146. MACHOVÁ, K., KRANJČEVIČOVÁ, A., VOSTRÝ, L., KRUPA, E. (2020): Analysis of genetic diversity in the czech spotted dog. *Animals*, *10*(8), 1416.

147. MAIGNEL, L., BOICHARD, D., VERRIER, E. (1996): Genetic variability of French dairy breeds estimated from pedigree information. *Interbull Bulletin*, *14*, 49–49.

148. MANDAL, A., BANEH, H., SUBRAMANYAM, B. V., NOTTER, D. R. (2020): Genetic variability and population structure based on pedigree information for Muzaffarnagari sheep in India. *Small Ruminant Research*, *191*, 106182.

149. MARINCS, F., MOLNÁR, J., TÓTH, G., STÉGER, V., BARTA, E. (2013): Introgression and isolation contributed to the development of Hungarian Mangalica pigs from a particular European ancient bloodline. *Genetics Selection Evolution*, *45*(1), 22. https://doi.org/10.1186/1297-9686-45-22.

150. MARTÍNEZ, A. M., GAMA, L. T., DELGADO, J. V., CAÑÓN, J., AMILLS, M., DE SOUSA, C. B., GINJA, C., ZARAGOZA, P., MANUNZA, A., LANDI, V., SEVANE, N. (2015): The Southwestern fringe of Europe as an important reservoir of caprine biodiversity. *Genetics Selection Evolution*, *47*(1), 86. https://doi.org/10.1186/s12711-015-0167-8.

151. MC PARLAND, S., KEARNEY, F., BERRY, D. P. (2009): Purging of inbreeding depression within the Irish Holstein-Friesian population. *Genetics Selection Evolution*, *41*(1), 16. https://doi.org/10.1186/1297-9686-41-16.

152. MELKA, M. G., SCHENKEL, F. (2010): Analysis of genetic diversity in four Canadian swine breeds using pedigree data. *Canadian journal of animal science, 90*(3), 331-340.

153. MENEZES, M. P. C., MARTINEZ, A. M., PIMENTA FILHO, E. C., VEGA-PLA, J. L., DELGADO, J. V., ARANDAS, J. K. G., ROCHA, L. L. DA, RIBEIRO, M. N. (2020): Diversity Analysis and Genetic Relationships among Local Brazilian Goat Breeds Using SSR Markers. *Animals*, *10*(10), Article 10. https://doi.org/10.3390/ani10101842.

154. MEUWISSEN, T. H. E., LUO, Z. (1992): Computing inbreeding coefficients in large populations. *Genetics Selection Evolution*, *24*(4), 305–313.

155. MICHAILIDOU, S., KALIVAS, A., GANOPOULOS, I., STEA, E., MICHAILIDIS, G., TSAFTARIS, A., ARGIRIOU, A. (2014): A multi-farm assessment of Greek black pig genetic diversity using microsatellite molecular markers. *Genetics and Molecular Research*, *13*(2), 2752–2765.

156. MICHELS, P. W., DISTL, O. (2022): Genetic Diversity and Trends of Ancestral and New Inbreeding in Deutsch Drahthaar Assessed by Pedigree Data. *Animals*, *12*(7), 929.

157. MILLER, P. S., HEDRICK, P. W. (2001): Purging of inbreeding depression and fitness decline in bottlenecked populations of Drosophila melanogaster. *Journal of Evolutionary Biology*, *14*(4), 595–601.

158. MO, J., LU, Y., ZHU, S., FENG, L., QI, W., CHEN, X., XIE, B., CHEN, B., LAN, G., LIANG, J. (2022): Genome-Wide Association Studies, Runs of Homozygosity Analysis, and Copy Number Variation Detection to Identify Reproduction-Related Genes in Bama Xiang Pigs. *Frontiers in Veterinary Science*, *9*.

159. MOLNÁR, J., TÓTH, G., STÉGER, V., ZSOLNAI, A., JÁNOSI, A., MOHR, A., SZÁNTÓ-EGÉSZ, R., TÓTH, P., MICSINAI, A., RÁTKY, J., MARINCS, F. (2013): Mitochondrial D-loop analysis reveals low diversity in Mangalica pigs and their relationship to historical specimens. *Journal of Animal Breeding and Genetics*, *130*(4), 312–320. https://doi.org/10.1111/j.1439-0388.2012.01014.x.

160. MOREIRA, R. H. R., PÉREZ PALENCIA, J. Y., MOITA, V. H. C., CAPUTO, L. S. S., SARAIVA, A., ANDRETTA, I., FERREIRA, R. A., DE ABREU, M. L. T. (2020): Variability of piglet birth weights: A systematic review and meta-analysis. *Journal of Animal Physiology and Animal Nutrition*, *104*(2), 657–666. https://doi.org/10.1111/jpn.13264.

161. MORENO, E., PEREZ-GONZALEZ, J., CARRANZA, J., MOYA-LARANO, J. (2015): Better fitness in captive Cuvier's gazelle despite inbreeding increase: Evidence of purging? *PLoS One*, *10*(12), e0145111.

162. MORTON, N. E., CROW, J. F., MULLER, H. J. (1956): An estimate of the mutational damage in man from data on consanguineous marriages. *Proceedings of the National Academy of Sciences*, *42*(11), 855–863. https://doi.org/10.1073/pnas.42.11.855.

163. MOTA-ROJAS, D., TRUJILLO, M. E., MARTÍNEZ, J., ROSALES, A. M., OROZCO, H., RAMÍREZ, R., SUMANO, H., ALONSO-SPILSBURY, M. (2006): Comparative routes of oxytocin administration in crated farrowing sows and its effects on fetal and postnatal asphyxia. *Animal Reproduction Science*, *92*(1–2), 123–143.

164. MUGNIER, A., CHASTANT, S., LYAZRHI, F., SAEGERMAN, C., GRELLET, A. (2023): Definition of low birth weight in domestic mammals: A scoping review. *Animal Health Research Reviews*, 1–8.

165. NAGY, I., CURIK, I., RADNAI, I., CERVANTES, I., GYOVAI, P., BAUMUNG, R., FARKAS, J., SZENDRŐ, Z. (2010): Genetic diversity and population structure of the synthetic Pannon White rabbit revealed by pedigree analyses. *Journal of Animal Science*, *88*(4), 1267–1275.

166. NAM, N. H., SUKON, P. (2021): Non-infectious risk factors for intrapartum stillbirth in a swine farm in the North of Vietnam. *Veterinary World*, *14*(7), 1829–1834. https://doi.org/10.14202/vetworld.2021.1829-1834.

167. NEI, M. (1973): Analysis of Gene Diversity in Subdivided Populations. *Proceedings of the National Academy of Sciences*, *70*(12), 3321–3323. https://doi.org/10.1073/pnas.70.12.3321.

168. NEI, M. (1987): Molecular evolutionary genetics. Columbia university press. 524p.

169. NGUYEN, T. Q., KNAP, P. W., SIMM, G., EDWARDS, S. A., ROEHE, R. (2021): Evaluation of direct and maternal responses in reproduction traits based on different selection strategies for postnatal piglet survival in a selection experiment. *Genetics Selection Evolution*, *53*(1), 28. https://doi.org/10.1186/s12711-021-00612-7.

170. NYMAN, S., JOHANSSON, A. M., PALUCCI, V., SCHÖNHERZ, A. A., GULDBRANDTSEN, B., HINRICHS, D., DE KONING, D.-J. (2022): Inbreeding and pedigree analysis of the European red dairy cattle. *Genetics Selection Evolution*, *54*(1), 70.

171. OGAWA, S., KONTA, A., KIMATA, M., ISHII, K., UEMOTO, Y., SATOH, M. (2019): Estimation of genetic parameters for farrowing traits in purebred Landrace and Large White pigs. *Animal Science Journal*, *90*(1), 23–28. https://doi.org/10.1111/asj.13120.

172. OLLIVIER, L., FOULLEY, J.-L. (2005): Aggregate diversity: New approach combining within-and between-breed genetic diversity. *Livestock Production Science*, *95*(3), 247–254.

173. PAIXÃO, G., MARTINS, Â., ESTEVES, A., PAYAN-CARREIRA, R., CAROLINO, N. (2019): Genetic parameters for reproductive, longevity and lifetime production traits in Bísaro pigs. *Livestock Science*, *225*, 129–134. https://doi.org/10.1016 /j.livsci.2019.05.010.

174. PAIXÃO, G., ESTEVES, A., PAYAN-CARREIRA, R., CAROLINO, N. (2018): Demographic structure and genetic diversity of the endangered Bísaro pig: evolution and current status. *Czech Journal of Animal Science 63*(11), 452–461.

175. PELTONIEMI, O., YUN, J., BJÖRKMAN, S., HAN, T. (2021): Coping with large litters: The management of neonatal piglets and sow reproduction. *Journal of Animal Science and Technology*, *63*(1), 1–15. https://doi.org/10.5187/jast.2021.e3

176. PERDOMO-GONZÁLEZ, D. I., LASECA, N., DEMYDA-PEYRÁS, S., VALERA, M., CERVANTES, I., MOLINA, A. (2022): Fine-tuning genomic and pedigree inbreeding rates in equine population with a deep and reliable stud book: The case of the Pura Raza Española horse. *Journal of Animal Science and Biotechnology*, *13*(1), 1–14.

177. PERDOMO-GONZÁLEZ, D. I., SÁNCHEZ-GUERRERO, M. J., MOLINA, A., VALERA, M. (2020): Genetic structure analysis of the pura raza español horse population through partial inbreeding coefficient estimation. *Animals*, *10*(8), 1360.

178. PÉREZ-PEREIRA, N., CABALLERO, A., GARCÍA-DORADO, A. (2022): Reviewing the consequences of genetic purging on the success of rescue programs. *Conservation Genetics*, *23*(1), 1–17. https://doi.org/10.1007/s10592-021-01405-7.

179. PÉREZ-PEREIRA, N., POUSO, R., RUS, A., VILAS, A., LÓPEZ-CORTEGANO, E., GARCÍA-DORADO, A., QUESADA, H., CABALLERO, A. (2021): Long-term exhaustion of the inbreeding load in Drosophila melanogaster. *Heredity*, *127*(4), 373–383.

180. PILES, M., SÁNCHEZ, J. P., PASCUAL, M., RODRÍGUEZ‐RAMILO, S. T. (2023): Inbreeding depression on growth and prolificacy traits in two lines of rabbit. *Journal of Animal Breeding and Genetics*, *140*(1), 39–48. https://doi.org/10.1111/jbg.12745.

181. PORTER, V. (2020): Mason's world dictionary of livestock breeds, types and varieties. CABI. 451p. 235 – 235.

182. POSTA, J., SOMOGYVÁRI, E., MIHÓK, S. (2020): Historical changes and description of the current Hungarian Hucul horse population. *Animals*, *10*(7), 1242.

183. POSTA, J., SZABÓ, P., KOMLÓSI, I. (2016): Pedigree analysis of Mangalica pig breeds. *Annals of Animal Science*, *16*(3), 701.

184. RALLS, K., SUNNUCKS, P., LACY, R. C., FRANKHAM, R. (2020): Genetic rescue: A critique of the evidence supports maximizing genetic diversity rather than minimizing the introduction of putatively harmful genetic variation. *Biological Conservation*, *251*, 108784.

185. RÁTKY, J., TÓTH, P., EGERSZEGI, I., SARLÓS, P., MANABE, N., BRUSSOW, K.-P. (2007): Multifunctional aspects of Mangalica breeding. *Proceeding of the 5th Vietnamese-Hungarian International Conference on "Animal Production and Aquqculture for Sustainable Farming", Can Tho University, Can Tho, Vietnam*, 11–15.

186. READ, B., FRUEH, R. J. (1980): Management and breeding of Speke's gazelle *Gazella spekei* at the St Louis Zoo, with a note on artificial insemination. *International Zoo Yearbook*, *20*(1), 99–104. https://doi.org/10.1111/j.1748-1090.1980.tb00950.x.

187. RIDDERSHOLM, K. V., BAHNSEN, I., BRUUN, T. S., DE KNEGT, L. V., AMDI, C. (2021): Identifying risk factors for low piglet birth weight, high within-litter variation and occurrence of intrauterine growth-restricted piglets in hyperprolific sows. *Animals*, *11*(9), Article 9. https://doi.org/10.3390/ani11092731.

188. RODRIGÁÑEZ, J., TORO, M. A., RODRÍGUEZ, M. C., SILIÓ, L. (1998): Effect of founder allele survival and inbreeding depression on litter size in a closed line of Large White pigs. *Animal Science*, *67*(3), 573–582.

189. RODRÍGUEZ, C., CASCO, J. M. G., SILIÓ, L. (2013): Measuring effects of new and fast inbreeding on the litter size of Iberian pigs. *Acta Agric Slov*, *4*, 22.

190. RODRÍGUEZ-RAMILO, S. T., ELSEN, J. M., LEGARRA, A. (2019): Inbreeding and effective population size in French dairy sheep: Comparison between genomic and pedigree estimates. *Journal of Dairy Science*, *102*(5), 4227–4237.

191. ROEHE, R., SHRESTHA, N. P., MEKKAWY, W., BAXTER, E. M., KNAP, P. W., SMURTHWAITE, K. M., JARVIS, S., LAWRENCE, A. B., EDWARDS, S. A. (2010): Genetic parameters of piglet survival and birth weight from a two-generation crossbreeding experiment under outdoor conditions designed to disentangle direct and maternal effects1. *Journal of Animal Science*, *88*(4), 1276–1285. https://doi.org/10.2527/jas.2009-2287.

192. ROONGSITTHICHAI, A., OLANRATMANEE, E. (2021): Fetal mortality associated with backfat thickness at first mating and first farrowing of the primiparous sows raised in a commercial herd in Thailand. *Tropical Animal Health and Production*, *53*, 1–8.

193. RUTHERFORD, K. M. D., BAXTER, E. M., D'EATH, R. B., TURNER, S. P., ARNOTT, G., ROEHE, R., ASK, B., SANDØE, P., MOUSTSEN, V. A., THORUP, F., EDWARDS, S. A., BERG, P., LAWRENCE, A. B. (2013): The welfare implications of large litter size in the domestic pig I: Biological factors. *Animal Welfare*, *22*(2), 199–218. https://doi.org/10.7120/09627286.22.2.199.

194. SAURA, M., FERNÁNDEZ, A., VARONA, L., FERNÁNDEZ, A. I., DE CARA, M. Á. R., BARRAGÁN, C., VILLANUEVA, B. (2015): Detecting inbreeding depression for reproductive traits in Iberian pigs using genome-wide data. *Genetics Selection Evolution*, *47*(1), 1–9.

195. SCHÄLER, J., KRÜGER, B., THALLER, G., HINRICHS, D. (2020): Comparison of ancestral, partial, and genomic inbreeding in a local pig breed to achieve genetic diversity. *Conservation Genetics Resources*, *12*(1), 77–86. https://doi.org/10.1007/s12686-018-1057-5.

196. SELL-KUBIAK, E., DOBRZANSKI, J., DERKS, M. F. L., LOPES, M. S., SZWACZKOWSKI, T. (2022): Meta-analysis of SNPs determining litter traits in pigs. *Genes*, *13*(10), 1730. https://doi.org/10.3390/genes13101730.

197. SEWALEM, A., JOHANSSON, K., WILHELMSON, M., LILLPERS, K. (1999): Inbreeding and inbreeding depression on reproduction and production traits of White Leghorn lines selected for egg production traits. *British Poultry Science*, *40*(2), 203–208. https://doi.org/10.1080/00071669987601.

198. SHI, L., WANG, L., ZHANG, P., MO, J., LI, Y., WANG, L., ZHAO, F. (2021): Evaluation of inbreeding depression on the total numbers of piglets born in different

groups of Large White pigs. https://www.cabidigitallibrary.org/doi/full/10.5555/20210504851.

199. SILIÓ, L., BARRAGÁN, C., FERNÁNDEZ, A. I., GARCÍA-CASCO, J., RODRÍGUEZ, M. C. (2016): Assessing effective population size, coancestry and inbreeding effects on litter size using the pedigree and SNP data in closed lines of the Iberian pig breed. *Journal of Animal Breeding and Genetics*, *133*(2), 145–154.

200. SILVA, E. C., MCMANUS, C., PIOVEZAN, U., FARIA, D. A., SOUZA, C. A., CAETANO, A. R., PAIVA, S. R. (2020): Phylogeography of feral Monteiro pig in the Brazilian Pantanal Ecosystem. *Genetica*, *148*(3–4), 183–193. https://doi.org/10.1007/s10709-020-00099-y.

201. SIRAZIEV, R., GRUZDOVA, O. (2020): The State of Litter of Pigs in the Conditions of the Complex. *E3S Web of Conferences*, *203*, 01008.

202. SLATIS, H. M. (1960): An analysis of inbreeding in the European bison. *Genetics*, *45*(3), 275.

203. SNEGIN, E. A., KRAMARENKO, A. S., ARTEMCHUK, O. Y., KRAMARENKO, S. S. (2021): Intra- and interbreed genetic heterogeneity and divergence in four commercial pig breeds based on microsatellite markers. *Regulatory Mechanisms in Biosystems*, *12*(1), Article 1. https://doi.org/10.15421/022120

204. SONESSON, A. K., GJERDE, B., MEUWISSEN, T. H. E. (2005): Truncation selection for BLUP-EBV and phenotypic values in fish breeding schemes. *Aquaculture*, *243*(1), 61–68. https://doi.org/10.1016/j.aquaculture.2004.09.024.

205. SONESSON, A. K., MEUWISSEN, T. H. E. (2000): Mating schemes for optimum contribution selection with constrained rates of inbreeding. *Genetics Selection Evolution*, *32*(3), 231–248.

206. SONESSON, A. K., MEUWISSEN, T. H. E. (2001): Minimization of rate of inbreeding for small populations with overlapping generations. *Genetics Research*, *77*(3), 285–292.

207. STRANGE, T., ASK, B., NIELSEN, B. (2013): Genetic parameters of the piglet mortality traits stillborn, weak at birth, starvation, crushing, and miscellaneous in crossbred pigs1. *Journal of Animal Science*, *91*(4), 1562–1569. https://doi.org/10.2527/jas.2012-5584.

208. SUWANLEE, S., BAUMUNG, R., SÖLKNER, J., CURIK, I. (2007): Evaluation of ancestral inbreeding coefficients: Ballou's formula versus gene dropping. *Conservation Genetics*, *8*(2), 489–495. https://doi.org/10.1007/s10592-006-9187-9.

209. TAN, C., HUANG, Z., XIONG, W., YE, H., DENG, J., YIN, Y. (2022): A review of the amino acid metabolism in placental function response to fetal loss and low birth weight in pigs. *Journal of Animal Science and Biotechnology*, *13*(1), 28.

210. TANG, G.Q., XUE, J., LIAN, M.J., YANG, R.F., LIU, T.F., ZENG, Z.Y., JIANG, A.A., JIANG, Y.Z., ZHU, L., BAI, L. (2013): Inbreeding and genetic diversity in three imported

swine breeds in China using pedigree data. *Asian-Australasian journal of animal sciences, 26*(6), 755.

211. TE PAS, M. F. W., SOUMILLION, A., HARDERS, F. L., VERBURG, F. J., VAN DEN BOSCH, T. J., GALESLOOT, P., MEUWISSEN, T. H. E. (1999): Influences of myogenin genotypes on birth weight, growth rate, carcass weight, backfat thickness, and lean weight of pigs. *Journal of Animal Science*, *77*(9), 2352–2356. https://doi.org/10.2527/1999.7792352x.

212. TEMPLETON, A. R. (2002): The Speke's gazelle breeding program as an illustration of the importance of multilocus genetic diversity in conservation biology: Response to Kalinowski et al. *Conservation Biology*, *16*(4), 1151–1155.

213. TEMPLETON, A. R., READ, B. (1983): The elimination of inbreeding depression in a captive herd of Speke's gazelle. *Genetics and Conservation.*, 241–261.

214. TEMPLETON, A. R., READ, B. (1984): Factors eliminating inbreeding depression in a captive herd of speke's gazelle (*Gazella spekei*): *Zoo Biology*, *3*(3), 177–199. https://doi.org/10.1002/zoo.1430030302.

215. TEMPLETON, A. R., READ, B. (1998): Elimination of inbreeding depression from a captive population of Speke's gazelle: Validity of the original statistical analysis and confirmation by permutation testing. *Zoo Biology*, *17*(2), 77–94. https://doi.org/10.1002/(SICI)1098-2361(1998)17:2<77::AID-ZOO4>3.0.CO;2-6.

216. THEODOROU, K., COUVET, D. (2015): The efficiency of close inbreeding to reduce genetic adaptation to captivity. *Heredity*, *114*(1), 38–47.

217. THREADGOLD, T., GREENWOOD, E. C., VAN WETTERE, W. (2021): Identifying Suitable Supplements to Improve Piglet Survival during Farrowing and Lactation. *Animals*, *11*(10), Article 10. https://doi.org/10.3390/ani11102912.

218. TOMÁS, A., CASELLAS, J., RAMÍREZ, O., PÉREZ-ENCISO, M., RODRÍGUEZ, C., NOGUERA, J. L., SÁNCHEZ, A. (2006): Polymorphisms of the porcine dopamineβ-hydroxylase gene and their relation to reproduction and piglet survivability in an Iberian × Meishan F2 intercross. *Animal Genetics*, *37*(3), 279–282. https://doi.org/10.1111/j.1365-2052.2006.01457.x.

219. TOWN, S. C., PUTMAN, C. T., TURCHINSKY, N. J., DIXON, W. T., FOXCROFT, G. R. (2004): Number of conceptuses in utero affects porcine fetal muscle development. *Reproduction*, *128*(4), 443–454.

220. TSE, W.-Y., TOWN, S. C., MURDOCH, G. K., NOVAK, S., DYCK, M. K., PUTMAN, C. T., FOXCROFT, G. R., DIXON, W. T. (2008): Uterine crowding in the sow affects litter sex ratio, placental development and embryonic myogenin expression in early gestation. *Reproduction, Fertility, and Development*, *20*(4), 497–504. https://doi.org/10.1071/rd07200.

221. TUCKER, B. S., CRAIG, J. R., MORRISON, R. S., SMITS, R. J., KIRKWOOD, R. N. (2021): Piglet Viability: A Review of Identification and Pre-Weaning Management Strategies. *Animals*, *11*(10), Article 10. https://doi.org/10.3390/ani11102902.

222. UDOMCHANYA, J., SUWANNUTSIRI, A., SRIPANTABUT, K., PRUCHAYAKUL, P., JUTHAMANEE, P., NUNTAPAITOON, M., TUMMARUK, P. (2019): Association between the incidence of stillbirths and expulsion interval, piglet birth weight, litter size and carbetocin administration in hyper-prolific sows. *Livestock Science*, *227*, 128–134. https://doi.org/10.1016/j.livsci.2019.07.013.

223. VAISHNAV, S., CHAUHAN, A., AJAY, A., SAINI, B. L., KUMAR, S., KUMAR, A., BHUSHAN, B., GAUR, G. K. (2023): Allelic to genome wide perspectives of swine genetic variation to litter size and its component traits. *Molecular Biology Reports*, *50*(4), 3705–3721. https://doi.org/10.1007/s11033-022-08168-5.

224. VAN DEN BOSCH, M., SOEDE, N., KEMP, B., VAN DEN BRAND, H. (2023): Sow Nutrition, Uterine Contractions, and Placental Blood Flow during the Peri-Partum Period and Short-Term Effects on Offspring: A Review. *Animals*, *13*(5), 910. https://doi.org/10.3390/ani13050910.

225. VAN DEN BOSCH, M., VAN DE LINDE, I. B., KEMP, B., VAN DEN BRAND, H. (2022): Disentangling Litter Size and Farrowing Duration Effects on Piglet Stillbirth, Acid–Base Blood Parameters and Pre-Weaning Mortality. *Frontiers in Veterinary Science*, *9*, 836202. https://doi.org/10.3389/fvets.2022.836202.

226. VAN RENS, B. T., VAN DER LENDE, T. (2004): Parturition in gilts: Duration of farrowing, birth intervals and placenta expulsion in relation to maternal, piglet and placental traits. *Theriogenology*, *62*(1–2), 331–352.

227. VANDERHAEGHE, C., DEWULF, J., DE KRUIF, A., MAES, D. (2013): Non-infectious factors associated with stillbirth in pigs: A review. *Animal Reproduction Science*, *139*(1–4), 76–88.

228. VANDERHAEGHE, C., DEWULF, J., DE VLIEGHER, S., PAPADOPOULOS, G. A., DE KRUIF, A., MAES, D. (2010): Longitudinal field study to assess sow level risk factors associated with stillborn piglets. *Animal Reproduction Science*, *120*(1–4), 78–83.

229. VEGA-TREJO, R., DE BOER, R. A., FITZPATRICK, J. L., KOTRSCHAL, A. (2022): Sex-specific inbreeding depression: A meta-analysis. *Ecology Letters*, *25*(4), 1009–1026. https://doi.org/10.1111/ele.13961.

230. VITEZICA, Z. G., VARONA, L., ELSEN, J.-M., MISZTAL, I., HERRING, W., LEGARRA, A. (2016): Genomic BLUP including additive and dominant variation in purebreds and F1 crossbreds, with an application in pigs. *Genetics Selection Evolution*, *48*(1), 6. https://doi.org/10.1186/s12711-016-0185-1.

231. VOSTRA-VYDROVA, H., HOFMANOVA, B., MORAVCIKOVA, N., RYCHTAROVA, J., KASARDA, R., MACHOVA, K., BRZAKOVA, M., VOSTRY, L.

(2020): Genetic diversity, admixture and the effect of inbreeding on milk performance in two autochthonous goat breeds. *Livestock Science*, *240*, 104163.

232. WANG, X., LIU, X., DENG, D., YU, M., LI, X. (2016): Genetic determinants of pig birth weight variability. *BMC Genetics*, *17*(Suppl 1), 15. https://doi.org/10.1186/s12863-015-0309-6.

233. WANG, Y., DONG, R., LI, X., CUI, C., YU, G. (2022): Analysis of the Genetic Diversity and Family Structure of the Licha Black Pig Population on Jiaodong Peninsula, Shandong Province, China. *Animals*, *12*(8). https://doi.org/10.3390/ani12081045.

234. WEIGEL, K. A. (2001): Controlling Inbreeding in Modern Breeding Programs. *Journal of Dairy Science*, *84*, E177–E184. https://doi.org/10.3168/jds.S0022-0302(01)70213-5.

235. WELSH, C. S., STEWART, T. S., SCHWAB, C., BLACKBURN, H. D. (2010): Pedigree analysis of 5 swine breeds in the United States and the implications for genetic conservation1. *Journal of Animal Science*, *88*(5), 1610–1618. https://doi.org/10.2527/jas.2009-2537.

236. WIENER, P., SÁNCHEZ-MOLANO, E., CLEMENTS, D. N., WOOLLIAMS, J. A., HASKELL, M. J., BLOTT, S. C. (2017): Genomic data illuminates demography, genetic structure and selection of a popular dog breed. *BMC Genomics*, *18*(1), 609. https://doi.org/10.1186/s12864-017-3933-x.

237. WIENTJES, J. G. M., SOEDE, N. M., KNOL, E. F., VAN DEN BRAND, H., KEMP, B. (2013): Piglet birth weight and litter uniformity: Effects of weaning-to-pregnancy interval and body condition changes in sows of different parities and crossbred lines. *Journal of Animal Science*, *91*(5), 2099–2107.

238. WILKINSON, S., HALEY, C., ALDERSON, L., WIENER, P. (2011): An empirical assessment of individual-based population genetic statistical techniques: Application to British pig breeds. *Heredity*, *106*(2), 261–269.

239. WILKINSON, S., WIENER, P., TEVERSON, D., HALEY, C. S., HOCKING, P. M. (2012): Characterization of the genetic diversity, structure and admixture of British chicken breeds. *Animal Genetics*, *43*(5), 552–563. https://doi.org/10.1111/j.1365-2052.2011.02296.x.

240. WILLIS, K., WIESE, R. J. (1997): Elimination of inbreeding depression from captive populations: Speke's gazelle revisited. *Zoo Biology*, *16*(1), 9–16. https://doi.org/10.1002/(SICI)1098-2361(1997)16:1<9::AID-ZOO3>3.0.CO;2-E.

241. WILMOT, H., MOTA, R. R., VANDERICK, S., GENGLER, N. (2020): Pedigree relatedness and pseudo-phenotypes as a first approach to assess and maintain genetic diversity of the Walloon Piétrain pig population. *Livestock Science*, *233*, 103950.

242. WITTENBURG, D., GUIARD, V., TEUSCHER, F., REINSCH, N. (2008): Comparison of statistical models to analyse the genetic effect on within-litter variance in pigs. *Animal*, *2*(11), 1559–1568. https://doi.org/10.1017/S1751731108002851.

243. WOOLLIAMS, J. (2007): Chapter. Genetic contributions and inbreeding. *Genetic Resources*, 147-165. https://doi.org/10.3920/9789086865925_008.

244. WRIGHT, S. (1922): Coefficients of inbreeding and relationship. *The American Naturalist*, *56*(645), 330–338.

245. WRIGHT, S. (1931): Evolution in Mendelian populations. *Genetics*, *16*(2), 97-159.

246. WRIGHT, S. (1965): The Interpretation of Population Structure by F-Statistics with Special Regard to Systems of Mating. *Evolution*, *19*(3), 395–420. https://doi.org/10.2307/2406450.

247. WRIGHT, S. (1978): Evolution and the genetics of populations, volume 4: Variability within and among natural populations. University of Chicago press.

248. WU, P., WANG, K., ZHOU, J., YANG, Q., YANG, X., JIANG, A., JIANG, Y., LI, M., ZHU, L., BAI, L, LI, X., TANG, G. (2019): A genome wide association study for the number of animals born dead in domestic pigs. *BMC genetics*, *20*(1), 4.

249. WU, R.S., WANG, H.C., SU, C.L., WANG, P.H., LIN, E.C. (2022): Pedigree-based analyses of changes in genetic variability in three major swine breeds in Taiwan after a disease outbreak, *Translational Animal Science, 6*(2), txac043, https://doi.org/10.1093/tas/txac043

250. YU, G., WANG, C., WANG, Y. (2022): Genetic parameter analysis of reproductive traits in Large White pigs. *Animal Bioscience*, *35*(11), 1649–1655. https://doi.org/10.5713/ab.22.0119

251. ZAALBERG, R. M., CHU, T. T., BOVBJERG, H., JENSEN, J., VILLUMSEN, T. M. (2023): Genetic parameters for early piglet weight, litter traits and number of functional teats in organic pigs. *Animal*, *17*(3), 100717.

252. ZAK, L. J., GAUSTAD, A. H., BOLARIN, A., BROEKHUIJSE, M. L. W. J., WALLING, G. A., KNOL, E. F. (2017): Genetic control of complex traits, with a focus on reproduction in pigs. *Molecular Reproduction and Development*, *84*(9), 1004–1011. https://doi.org/10.1002/mrd.22875.

253. ZALESKI, H. M., HACKER, R. R. (1993): Variables related to the progress of parturition and probability of stillbirth in swine. *The Canadian Veterinary Journal*, *34*(2), 109.

254. ZHANG, L., ZHOU, X., MICHAL, J. J., DING, B., LI, R., JIANG, Z. (2014): Genome Wide Screening of Candidate Genes for Improving Piglet Birth Weight Using High and Low Estimated Breeding Value Populations. *International Journal of Biological Sciences*, *10*(3), 236–244. https://doi.org/10.7150/ijbs.7744.

255. ZHANG, Q., CALUS, M. P., GULDBRANDTSEN, B., LUND, M. S., SAHANA, G. (2015): Estimation of inbreeding using pedigree, 50k SNP chip genotypes and full sequence data in three cattle breeds. *BMC Genetics*, *16*(1), 88. https://doi.org/10.1186/s12863-015-0227-7

256. ZHANG, S., ZHANG, J., OLASEGE, B. S., MA, P., QIU, X., GAO, H., WANG, C., WANG, Y., ZHANG, Q., YANG, H., WANG, Z., DING, X., PAN, Y. (2020): Estimation of genetic parameters for reproductive traits in connectedness groups of Duroc, Landrace and Yorkshire pigs in China. *Journal of Animal Breeding and Genetics*, *137*(2), 211–222. https://doi.org/10.1111/jbg.12431

257. ZHANG, Y., ZHUO, Y., NING, C., ZHOU, L., LIU, J.-F. (2022): Estimate of inbreeding depression on growth and reproductive traits in a Large White pig population. *G3*, *12*(7), jkac118.

258. ZSOLNAI, A., RADNÓCZY, L., FÉSÜS, L., ANTON, I. (2006): Do Mangalica pigs of different colours really belong to different breeds? *Archives Animal Breeding*, *49*(5), 477–483.

259. ZSOLNAI, A., TOTH, G., MOLNAR, J., STEGER, V., MARINCS, F., JANOSI, A., UJHELYI, G., KOPPÁNYNÉ SZABÓ, E., MOHR, A., ANTON, I. (2013): Looking for breed differentiating SNP loci and for a SNP set for parentage testing in Mangalica. *Archives Animal Breeding*, *56*(1), 200–207.

References with no authors

1. The Hungarian National Association of Mangalica Breeders (HNAMB, n.a.): The breeds that are bred. Search engine: Google. https://moe.org.hu/en/breeding/breeds/. Date of search 2025. 08. 29.

10. PUBLICATIONS AND PRESENTATIONS

10.1 Publications on the thesis topic

1. **NGUYEN, A. T**., KÖVÉR, G., FARKAS, J., BOKOR, Á., TÓTH, P., NAGY, I. (2023): Analysis of genetic variability and population structure of the Mangalica pig breed using pedigree data. *Livestock Science*, *273*, 105265.

2. NAGY, I., **NGUYEN, T. A.** (2023): Characterizing and Eliminating the Inbreeding Load. *Veterinary Sciences*, *11*(1), 8.

3. **NGUYEN, A. T.**, KÖVÉR, G., TÓTH, P., CURIK, I., BOKOR, Á., NAGY, I. (2024): Population Subdivision and Migration Assessment of Mangalica Pig Breeds Based on Pedigree Analysis. *Animals*, *14*(4), 653.

4. **NGUYEN, A. T.**, NAGY, I. (2024): Physiological and Genetic Aspects of some Fitness Traits Performance in Pigs. *Agriculturae Conspectus Scientificus*, *89*(2), 95-103.

10.2 Publications outside the scope of the thesis

1. NAGY, I., BOKOR, Á., FARKAS, J., **NGUYEN, A. T.**, POSTA, J., KÖVÉR, G. (2024): Correlation Analysis among the Various Inbreeding Coefficients of Pannon Ka Rabbits. *Diversity*, 16(9), 524.

2. NAGY, I., CURIK, I., **NGUYEN, A. T.**, FARKAS, J., KÖVÉR, G. (2025): The importance of random effects in detecting purging of inbreeding depression: A model comparison in Pannon White rabbits. *Animal*, *19*(2), 101412.

10.3 Oral presentations

1. **NGUYEN, A. T.,** KÖVÉR, G., NAGY, I. (2023): Insight the population structure and genetic diversity of the Red Mangalica pig by pedigree analysis. *Program and Abstract Book of the 32nd Annual Meeting of DAGENE*. 26 p. pp. 15-15, 1 p.

2. **NGUYEN, A. T.,** NAGY, I., FARKAS, J., CURIK, I., KOVER, G. (2023): Ancestral inbreeding and inbreeding-purging models' comparative analysis based on their classification efficiency of the Pannon white rabbit kits' survival at birth. *Book of Abstracts of the 1st Regional Meeting of the European Federation of Animal Science.* 102 p. pp. 90-90, 1 p.

3. **NGUYEN, A. T.**, KÖVÉR, G., TÓTH, P., BOKOR, A., NAGY, I. (2024): Analyzing population subdivision of the Blonde Mangalica breed. *7th Fatty pig & 12th Mediterranean pig meeting*. 74p. pp. 12-12, 1p.

APPENDICES

TableS 1. The observed purging cases in different species

Species/Breeds	Analyzed trait	Used methodology	Reference
Sumatran tiger	Neonatal survival rate	Ancestral inbreeding	(Ballou, 1997)
Peromyscus polinatus rhoadsi	Litter size	–	(Lacy and Ballou, 1998)
Peromyscus polinatus rhoadsi	Litter weight and weaning	–	(Lacy and Ballou, 1998)
Amur tiger	Survival to 7 days	–	(E. H. Boakes et al., 2007)
Black-footed ferret	Survival to 7 days	–	(E. H. Boakes et al., 2007)
Lesser kudu	Survival to 7 days	–	(E. H. Boakes et al., 2007)
Grey dorcopsis wallaby	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Hippopotamus	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Congo peafowl	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Black-footed ferret	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Bontebok	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Goeldi's marmoset	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Wied's Black-tufted-ear marmoset	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Wyoming toad	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Golden lion tamarin	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Reindeer	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Gunther's dik-dik	Survival to 30 days	–	(E. H. Boakes et al., 2007)
Irish Holstein-Frisean	Milk yield	–	(Mc Parland et al., 2009)
	Protein yield	–	(Mc Parland et al., 2009)
German Holstein-Frisean	Birthweight	–	(Hinrichs et al., 2015)
Border collie dog	Hip dysplasia	–	(Ács et al., 2020)
Pannon white rabbit	Survival at birth	–	(Curik et al., 2020)

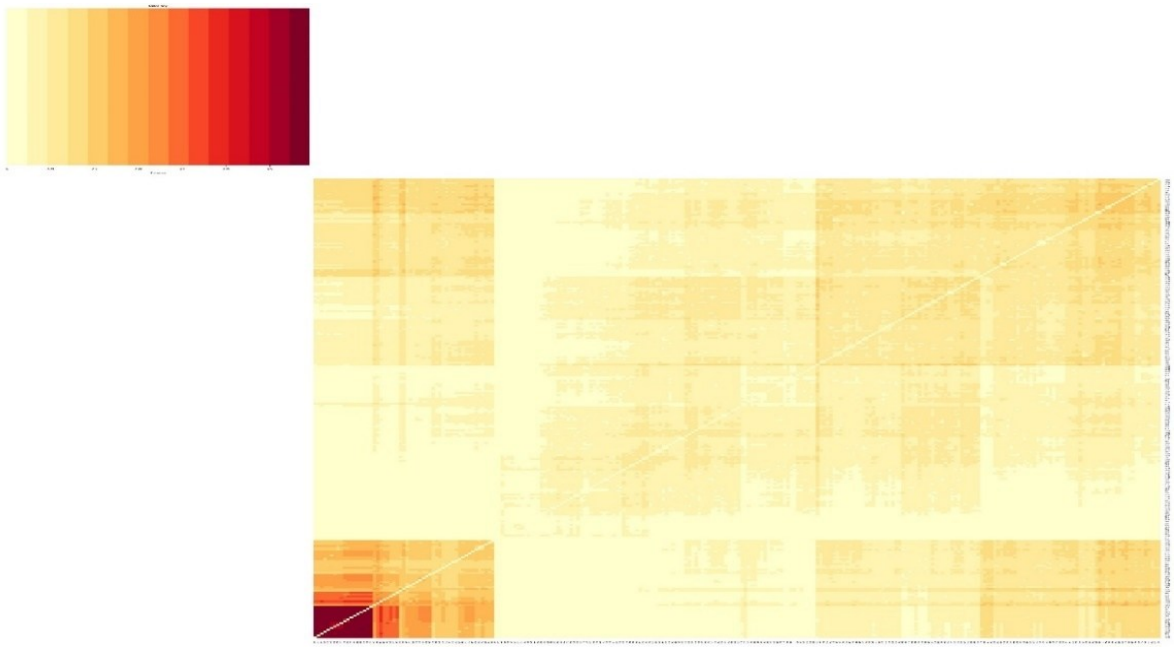
Pura Raza Espanola mares	AFF, I12, AIF	–	(Perdomo-González et al., 2020)
White shorthair goat	Milk production	–	(Vostra-Vydrova et al., 2020)
Prat rabbit line	Weaning weight	–	(Piles et al., 2023)
Prat rabbit line	Slaughter weight	–	(Piles et al., 2023)
Drosophila melanogaster	Egg to pupae viability	Inbreeding-Purging Model	(Bersabé and García-Dorado, 2013)
Drosophila melanogaster	Noncompetitive pupae productivity	–	(López-Cortegano et al., 2016)
Drosophila melanogaster	Competitive productivity	–	(López-Cortegano et al., 2016)
Gazella cuvieri	Early survival	–	(López-Cortegano et al., 2021)
Nanger dama	Early survival	–	(López-Cortegano et al., 2021)
Pannon white rabbit	Survival at birth	–	(Kövér et al., 2023)
Pannon white rabbit	Survival at birth	Expressed opportunity for purging	(Kövér et al., 2023)
Jersey cattle	Fitness	–	(Gulisija and Crow, 2007)
Indian tiger	NA	Whole genome analysis	(Khan et al., 2021)
Kākāpō	NA	–	(Dussex et al., 2021)
Iberian lynx	NA	–	(Kleinman-Ruiz et al., 2022)

AFF: age at first foaling in months; I12: average interval between first and second foaling in months; AIF: average interval between foaling in months; NA: non-applicable; (–) characters indicate that a given cell contains the same methodology as it appears above.

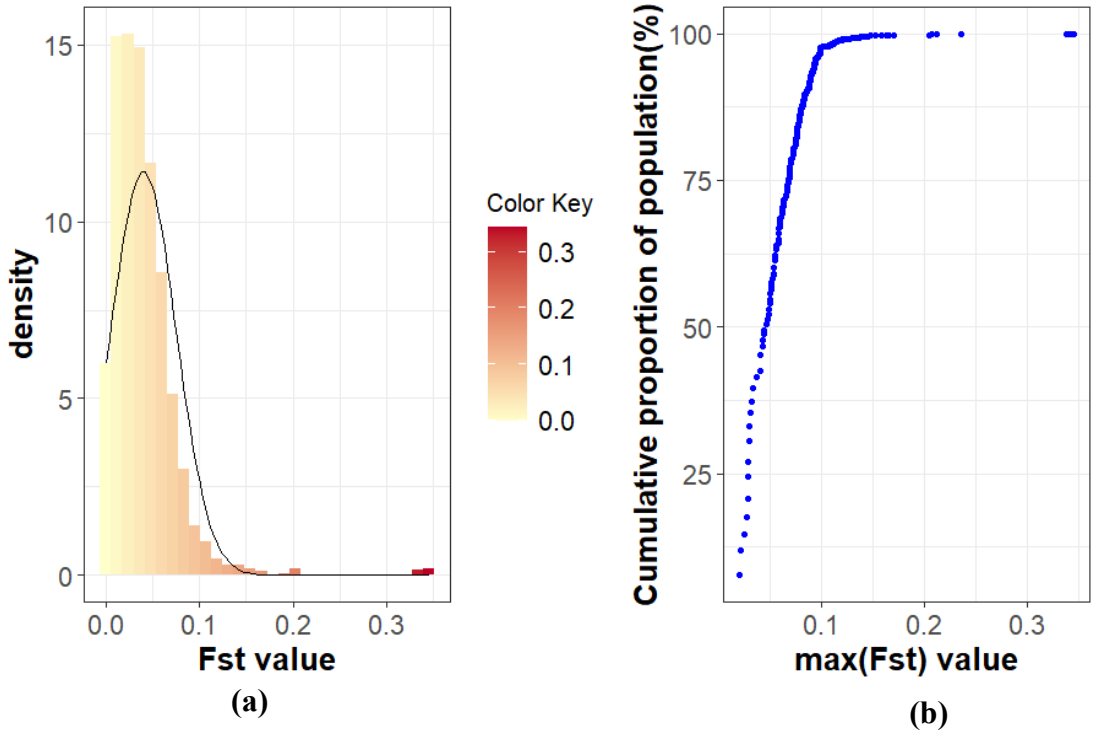
TableS 2. Studies reported average birth weight of piglets

Study	Journal	Genetics	Parity	Obs. (piglets)	Avg. Birth weight (kg)	Avg. litter weight (kg)
Lanferdini et al. (2018)	Livestock science	NA	All	3,294	1.45 (0.8 – 2.1)	NA
Feldpausch et al. (2019)	Translational Animal Science	Large White x Landrace; Triumph TR4 x PIC 1050	1 – 9	4,068	1.51 ± 0.38 (0.5 – 2.3)	NA
Moreira et al. (2020)	Animal Physiology and Animal Nutrition	Yorkshire, Landrace, Large White	All	7,148	1.53 (1.23 – 1.89)	NA
Baxter et al. (2011)	Applied Animal Behaviour Science	Landrace x (Large White x Duroc)	All	757	1.46 ± 0.02	19.98 ± 1.04
Hellbrügge et al. (2008)	Animal	German Landrace	NA	13,971	1.5 ± 0.4 (0.3 – 3.3)	11.2 ± 3.6
De Oliveira et al. (2022)	Tropical Animal Health and Production	Piau breed	NA	3,548	0.997 ± 0.271 (0.3 – 1.766)	NA
Nam and Sukon (2021)	Veterinary World	(Landrace xYorkshire) x Duroc	All	1,257	1.4 ± 0.4	NA
Riddersholm et al. (2021)	Animals	Danish Landrace x Danish Yorkshire (DanBred Duroc)	1 – 10	8,677	1.235 ± 0.335 (0.29 – 2.91)	NA

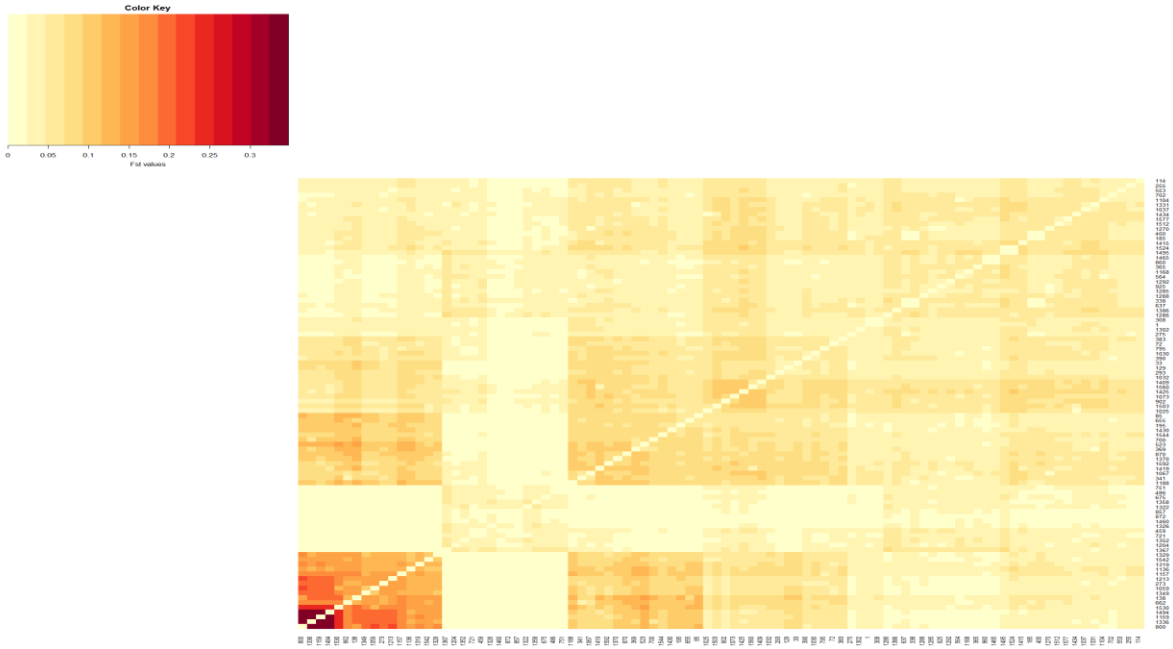
NA: not available information; Obs: Observations; Avg: average



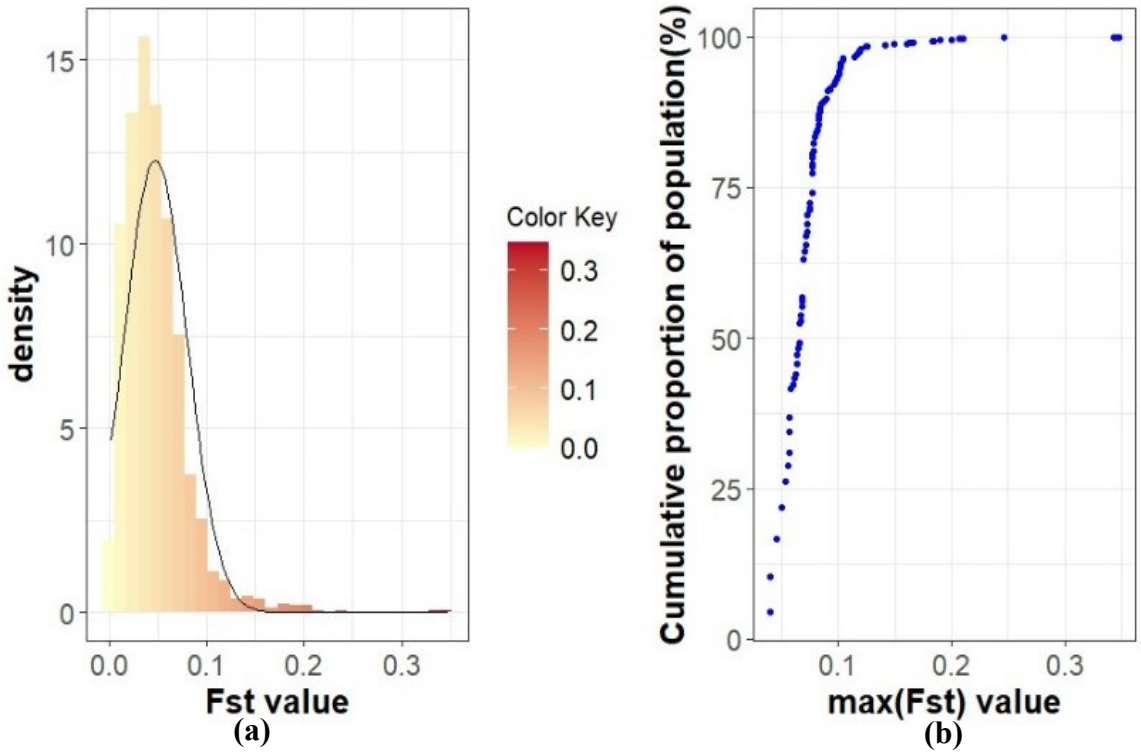
FigureS 1. Heatmap based on pairwise F_{ST} coefficients between the herds of Blonde Mangalica breed. The color ranging from yellowish to dark red represents the scale of F_{ST} coefficients from zero onward. The x and y axis show herd name.



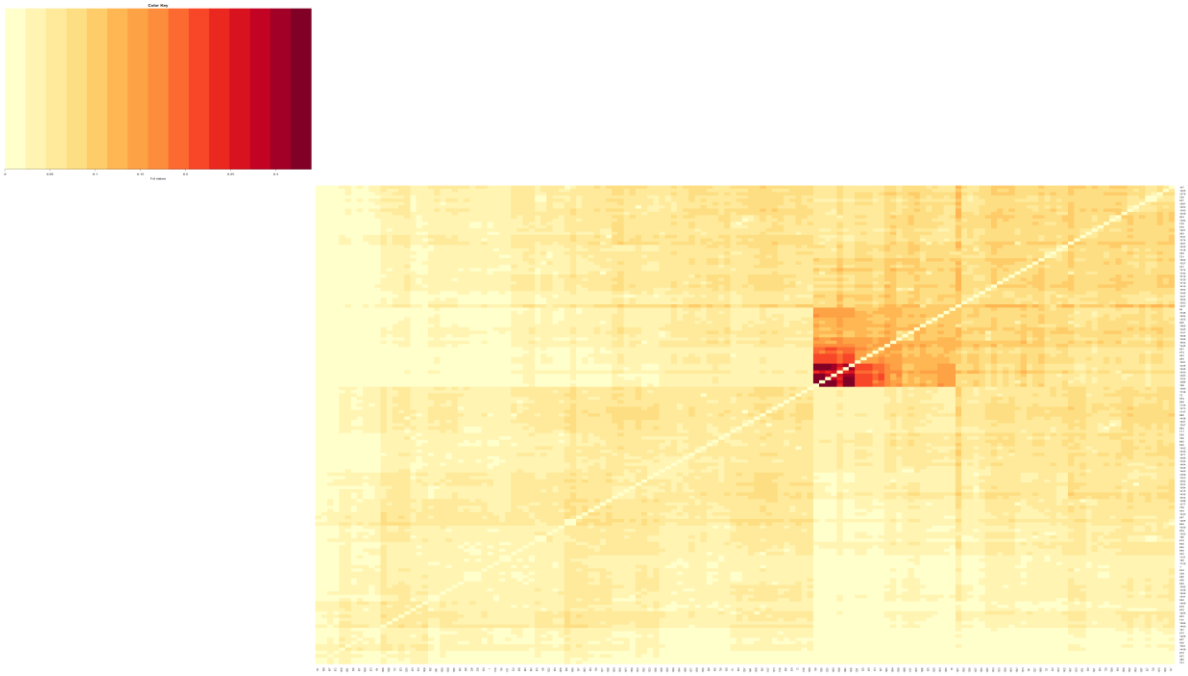
FigureS 2. F_{ST} coefficients in the Blonde Mangalica total herds: **(a)** Histogram of F_{ST} values with density; **(b)** Cumulative proportion of population related to the max F_{ST} of the herds.



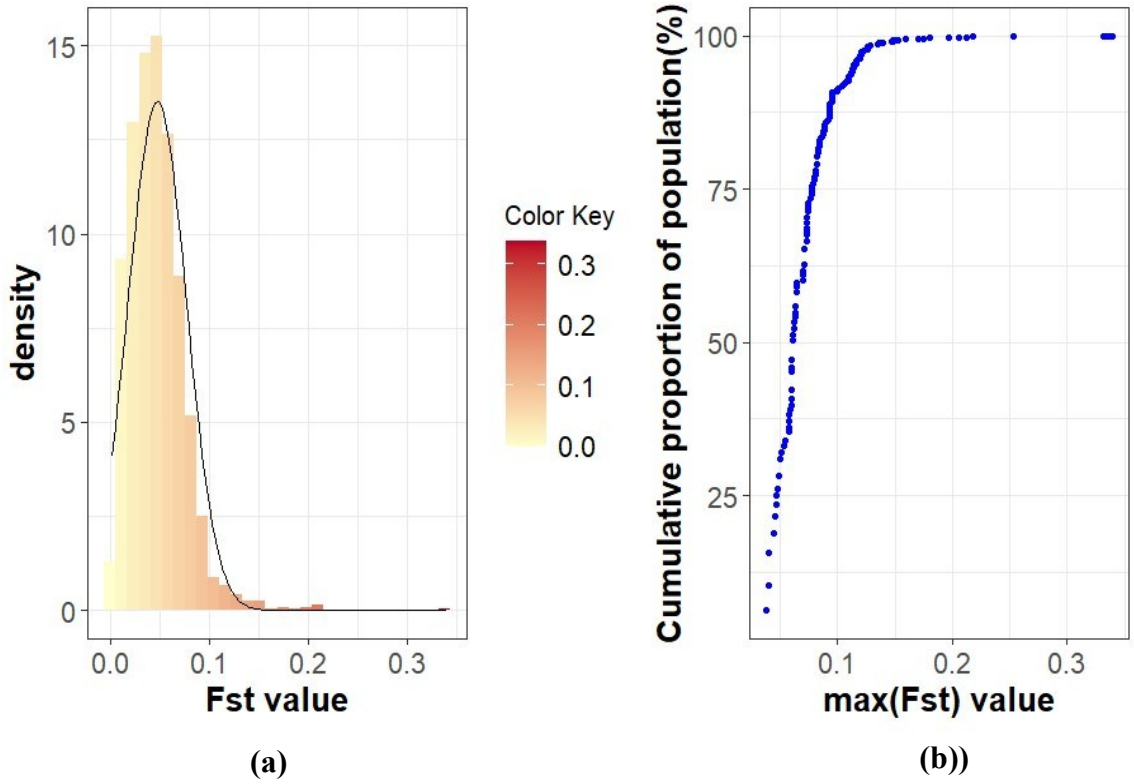
FigureS 3. Heatmap based on pairwise F_{ST} coefficients between the herds of Swallow-Belly Mangalica breed. The color ranging from yellowish to dark red represents the scale of F_{ST} coefficients from zero onward. The x and y axis show herd name.



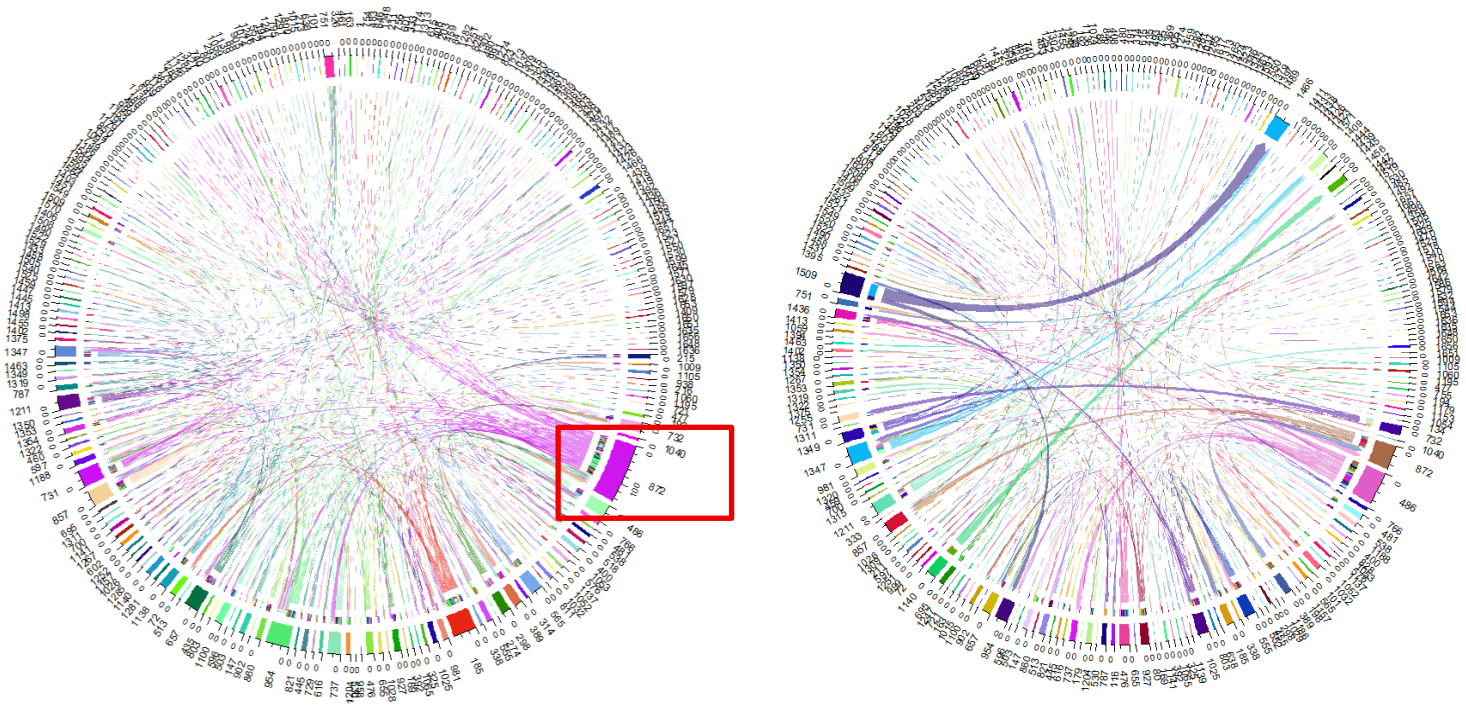
FigureS 4. F_{ST} coefficients in the Swallow-Belly Mangalica total herds: **(a)** Histogram of F_{ST} values with density; **(b)** Cumulative proportion of population related to the max F_{ST} of the herds.



FigureS 5. Heatmap based on pairwise F_{ST} coefficients between the herds of Red Mangalica breed. The color ranging from yellowish to dark red represents the scale of F_{ST} coefficients from zero onward. The x and y axis show herd name.

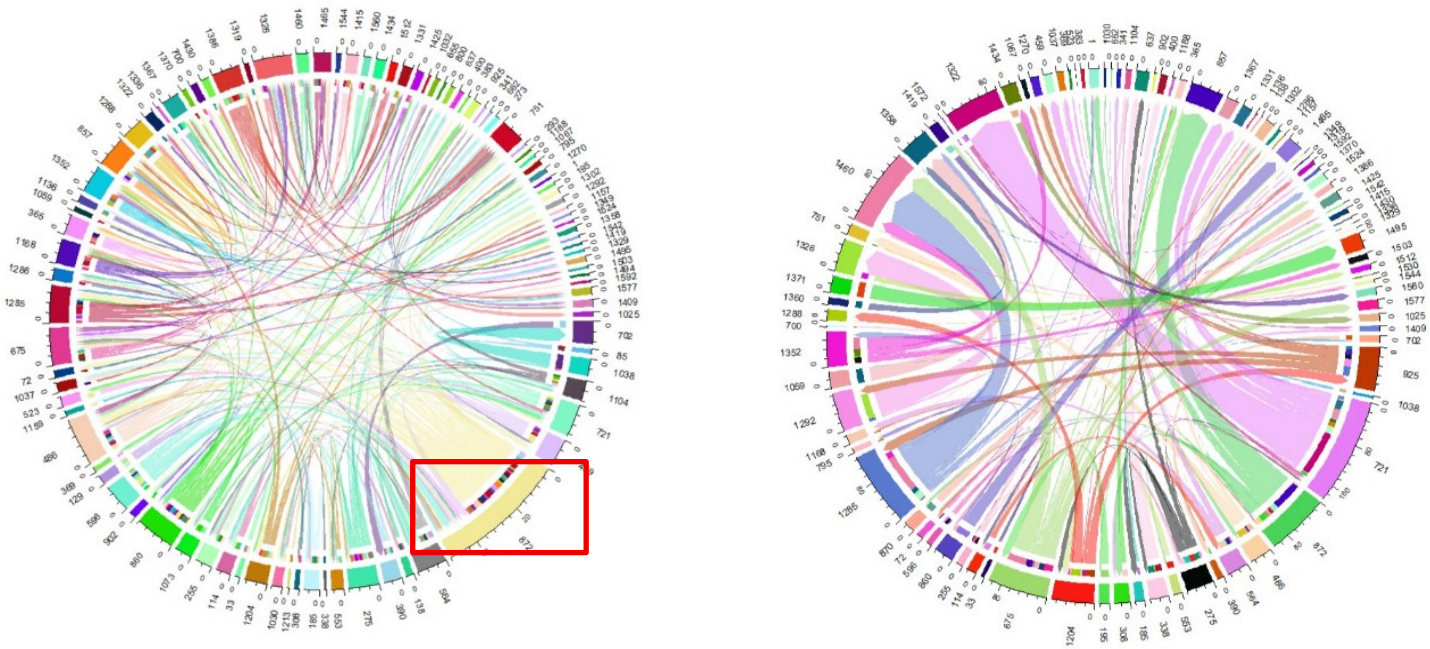


FigureS 6. F_{ST} coefficients in the Red Mangalica total herds: **(a)** Histogram of F_{ST} values with density; **(b)** Cumulative proportion of population related to the max F_{ST} of the herds.



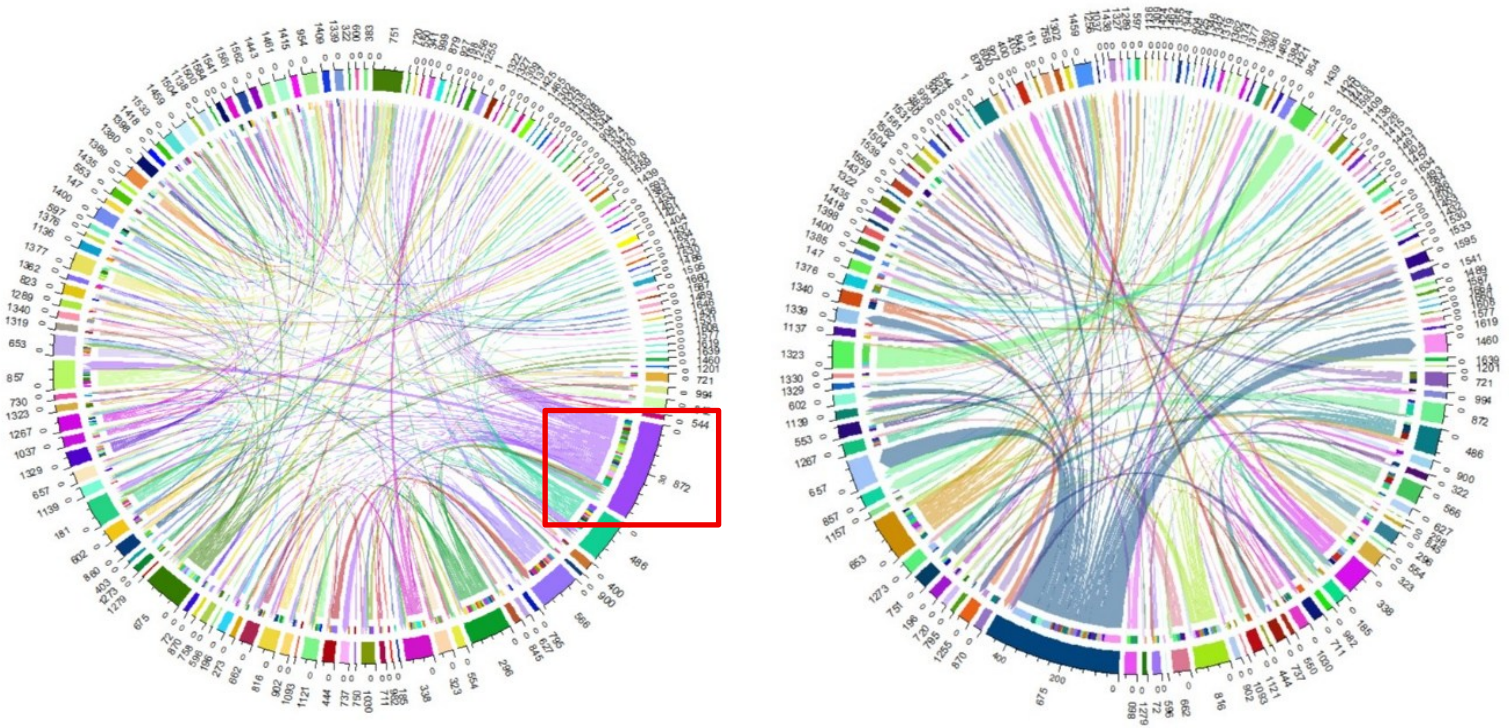
(a) **(b)**

FigureS 7. Migration of the Blonde Mangalica in total herds: **(a)** Male; **(b)** Female. Large color-coded circles represent source herds with herd IDs, smaller inner circles indicate destination herds, and arrows show the direction and volume of animal movement (thicker arrows = more animals). The red square indicates the top sire-providing herd.



(a) **(b)**

FigureS 8. Migration of the Swallow-Belly in total herds: **(a)** Male; **(b)** Female. Large color-coded circles represent source herds with herd IDs, smaller inner circles indicate destination herds, and arrows show the direction and volume of animal movement (thicker arrows = more animals). The red square indicates the top sire-providing herd.



(a) **(b)**

FigureS 9. Migration of the Red in total herds: **(a)** Male; **(b)** Female. Large color-coded circles represent source herds with herd IDs, smaller inner circles indicate destination herds, and arrows show the direction and volume of animal movement (thicker arrows = more animals). The red square indicates the top sire-providing herd.