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RESEARCH

Genetic analysis of juvenile survival in the captive population of Mhorr gazelle (*Nanger Dama Mhorr*) and the effect of inbreeding

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Abstract
Minimizing the effects of inbreeding is one of the main challenges facing conservation managers of small populations. When inbreeding negatively affects the offspring survival, the short- and long-term viability of the species can be severely compromised. In the present study, we evaluated the genetic parameters affecting calf survival during the perinatal period (PS) and between the perinatal period and weaning (WS) in the captive population of the critically endangered mhorr gazelle (*Nanger dama mhorr*). The dataset analysed included 2185 calf records from a total pedigree of 2739 animals born between 1971 and 2021. The models with the best predictive value showed heritabilities of the direct genetic effect of 0.259 (SD = 0.052) for the PS and 0.123 (SD = 0.047) for the WS. Only the WS was affected by maternal permanent environmental effect ($c^2 = 0.035$, SD = 0.026). No genetic correlation was observed between the direct genetic effects of both traits. The maximum inbreeding coefficient of the calf was shown to reduce the PS almost 30% points and the inbreeding coefficient of the dam, around 15% points of the WS. Despite this, the genetic and phenotypic trends over the years of both traits were positive, which demonstrates the effectiveness of the mating strategy applied and the effect of no artificial selection that has occurred in this captive population.

Keywords Captive breeding program · Critically endangered · Dama gazelle · Heritability · Inbreeding · Juvenile survival

Introduction

Offspring survival is a critical aspect for long-term viability in threatened species. Conservation breeding programs play an important role in preventing extinction, but their sustainability may be impeded by generational fitness changes (Farquharson et al. 2021). Inbreeding depression has been shown to be one of the main factors affecting various life history traits over time in small populations, such as fertilisation, embryo survival, offspring survival and total lifetime reproductive success (Grueber et al. 2010; Harrisson et al. 2019), putting all global conservation efforts at risk even under the best captive management practices. Consequently, increased juvenile mortality in offspring of related parents, one of the extreme results of inbreeding depression, has become a major concern for managers of small captive populations (Ralls et al. 1979). Population models suggest that the levels of inbreeding depression observed in captivity could decrease the viability of wild populations (O'Grady et al. 2006), so ensuring that released animals have the adaptive potential necessary to cope with their natural environment is essential to guarantee the lasting persistence of populations in their habitat and should be considered in species conservation management strategies.

A common measure of the evolutionary potential of populations is narrow sense heritability (h^2), that indicates the proportion of the phenotypic variance attributable to additive genetic variance (Falconer and Mackay 1996). Estimating heritability is required to predict the response to selection and is useful in species that are managed using trait information. Traits with high heritability values provide a higher ability to respond to selection, as a large range of phenotypes will be available in the population to evolve

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in response to environmental changes. In contrast, traits with low heritabilities show a more restricted response to selection (Koffler et al. 2017). Fitness-related traits, such as offspring survival, generally exhibit low heritability estimates, since fixation of advantageous traits reduces additive genetic variance (Frankham et al. 2002). Hence, knowing accurate heritability estimates of these fitness traits is a conservation priority to both, determine the long-term viability of a population, and predict an endangered species' ability to respond to new environments such as, for example, those found after reintroductions.

However, the quantitative genetic variation measured in a trait is not only due to its additive genetic variance. In addition to the genetic direct effect of the individual, there are other components of quantitative genetic variation determining the ability of a trait to undergo adaptive evolution. Parents, as close relatives, can influence offspring performance. Thus, parental effects are defined as the influence of parent's genotype and phenotype to their offspring phenotype, independent of additive genetic effects (Kruuk and Hadfield 2007). In polygynous mammals mature males intensely compete for the control of females and territory, so most, or all, parental care falls on the mothers (Dubost 2016). In these cases, it would be expected that the maternal effect usually has greater relevance in the offspring survival than paternal effects (Martin et al. 2022). Within the maternal effect, a distinction is made between maternal genetic effect, which refers to the influence that the mother's genes have on the development of the embryo and the phenotype of the offspring; and the maternal permanent environmental effect, which is defined as the non-genetic part of the maternal effect that is shared by all descendants of the same mother.

The dama gazelle is a North African species currently classified as critically endangered (IUCN 2016). Specifically, one of its three subspecies (Cano 1984), the mhorr gazelle (*Nanger dama mhorr*), is considered extinct in the wild since 1968 (Valverde 2004). The creation of an *ex situ* breeding program with the last living specimens at "La Hoya" Experimental Field Station, belonging to the "Estación Experimental de Zonas Áridas" of the "Consejo Superior de Investigaciones Científicas" (EEZA-CSIC), prevented the complete disappearance of this subspecies (Abáigar 2018). Today, this captive population continues to grow and is managed at the European Association of Zoos and Aquaria (EAZA) as an Ex-situ Programme (EEP), with the main purpose of restoring mhorr gazelle populations in their natural habitat. The mating strategy applied within EEP, following the criteria of minimizing coancestry between mating individuals, aimed to maximize the retention of genetic variability of the population and minimized its levels of inbreeding (Domínguez et al. 2024).

The objective of this work was to ascertain for the first time the genetic parameters affecting calf survival traits (perinatal and weaning survival) in the captive population of mhorr gazelle (EEP population). We also investigated the effect of inbreeding on the evolution of these fitness traits along the history of this conservation program. As the rate of evolutionary change in response to selection is proportional not only to the amount of additive genetic variance (Fisher 1930) but also to the pattern of covariances among genetic effects and phenotypes that they determine (Arnold 1994), here we also discussed the relative importance of these two drivers of phenotypic variance. This issue is relevant for the long-term viability of this captive population as well as for its use as founder source in future reintroduction programs.

Materials and methods

Study population

Dama gazelle (*Nanger dama*) is the largest species of gazelle, with adult individuals weighing up to 75 kg. Differences between sexes are mainly based on body mass and thickness of the horns, all of which are greater in males. Females reach sexual maturity earlier, between 9 and 12 months, while males are sexually mature between 18 and 24 months (Barbosa and Espeso 2005). Lifespan in captivity ranges between 16 and 19 years. Females can leave offspring up to 16 years old and males up to 15 years old (Domínguez 2022). The gestation period lasts 6.5 months and only one calf is produced per birth. The weight of newborns is usually around 4 kg in females and 5 kg in males. The longest lactation period observed in this species is 6 months (Barbosa and Espeso 2005).

Data of juvenile survival from birth to 6 months old were obtained from the mhorr gazelle studbook (Domínguez 2022), where a total of 2739 records between 1971 and 2021 were included. According to this pedigree information, the first week of life is the period of highest mortality in the captive population (29.84%). Considering this critical stage and the age of weaning in the study species, two juvenile survival traits were differentiated throughout the lactation period of the offspring:

- Perinatal survival (PS): characterizes the ability of a calf to be born alive and survive until the seventh day of life.
- Weaning survival (WS): characterizes the ability of the calves to survive from the eighth day of life until 6 months of age.

Only records including exact birth date, birth location, sex of calf, age of the dam and calving number of the dam were considered. Calves with incomplete records or ambiguous death dates were eliminated from the analyses. All comparison groups had at least 10 records to ensure reliable results. The final dataset analysed included a total of 2185 calf records, of which 1114 were males and 1071 females. The number of dams with progeny in the database was 478.

Description of the models

Mixed linear model methodology was used to analyse the calf survival traits, with the equation under matrix notation of the more complex models used being:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Md} + \mathbf{Wp} + \mathbf{e}$$

with

$$\begin{pmatrix} \mathbf{u} \\ \mathbf{d} \\ \mathbf{p} \\ e \end{pmatrix} \sim \mathbf{N}\left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \mathbf{A}\boldsymbol{\sigma}_{\mathbf{u}}^{2} & \mathbf{A}\boldsymbol{\sigma}_{\mathbf{ud}} & 0 & 0 \\ \mathbf{A}\boldsymbol{\sigma}_{\mathbf{ud}} & \mathbf{A}\boldsymbol{\sigma}_{\mathbf{d}}^{2} & 0 & 0 \\ 0 & 0 & \mathbf{I}\boldsymbol{\sigma}_{\mathbf{p}}^{2} & 0 \\ 0 & 0 & 0 & \mathbf{I}\boldsymbol{\sigma}_{\mathbf{e}}^{2} \end{bmatrix}\right)$$

where **y** is the vector of phenotypic measurements of offspring survival; **X** is an incidence matrix relating the values of **y** to the systematic effects given in the vector **b**; **Z** is an incidence matrix relating each individual's phenotype to an additive genetic effect, **u** is a vector describing the additive genetic effects; **M** is the incidence matrix of maternal genetic effects (*m*), with **d** as their vector; **W** is the incidence matrix of maternal permanent environmental effects (*c*), with **p** as their vector; **e** is a vector of residuals effects; $\boldsymbol{\sigma}_{u}^{2}$ the additive genetic variance, $\boldsymbol{\sigma}_{d}^{2}$ the maternal genetic variance due to *m*, $\boldsymbol{\sigma}_{ud}$ the genetic covariance between the direct and maternal genetic effect, $\boldsymbol{\sigma}_{p}^{2}$ is the variance associated with maternal permanent environmental effects (*c*), **I** is an identity matrix, and **A** is the numerator relationship matrix.

This relationship matrix based on genealogical records assumes that the founder animals are unrelated, which has already been described as not being the case in this captive European population (Al Ain Zoo et al. 2019). However, the influence of the founders' relatedness on the kinship matrix is limited after several generations have passed, since kinship depends mainly on close common ancestors in the genealogy between individuals.

Regarding random effects considered, six different models were defined:

- Calf model: a univariate animal model including, for each analysed trait, the additive genetic effect, besides the residual.
- Dam model: includes the maternal genetic effect, besides the residual.
- Calf-dam model: includes the additive genetic effect, the maternal genetic effect and the covariance between them, besides the residual effect.
- Calf-permanent model: model 1, but also including the permanent environment associated with dam as a random environmental effect.
- Dam permanent model: model 2, but also including the permanent environment associated with dam.
- Calf-dam-permanent model: model 3, but also including the permanent environment associated with dam.

The systematic effects included in the fitted models were: number of calving (primiparous or multiparous), season of birth (winter, spring, summer and autumn), year of birth (from 1973 to 2021; years 1973, 1974 and 1975 were pooled since only 2 records were available in 1973 and 3 in 1974), birth location (24 different institutions, see details in Table 1; locations with less than 10 records were excluded), sex of calf (male or female), and age of the dam at calving in days, as a linear and quadratic covariate. Additionally, the inbreeding coefficient of the calf and the inbreeding coefficient of the dam were also included as covariates in some models, as detailed below, to ascertain the possible influence of inbreeding on the mhorr gazelle genetic background. This individual inbreeding coefficient (Wright 1923) was computed from the pedigree information using the ENDOG program v4.8 (Gutiérrez and Goyache 2005), that implements the algorithm described by Meuwissen and Luo (1992). According to the inbreeding covariates considered, four groups of models were distinguished for each of the models described above:

- Model I: includes the inbreeding coefficient of the calf and the inbreeding coefficient of the dam as linear covariates.
- Model II: includes just the inbreeding coefficient of the calf.
- Model III: includes just the inbreeding coefficient of the dam.
- Model IV: does not include neither of the two inbreeding coefficients.

PS and WS are both discrete and dichotomous traits: live calf (1) and dead calf (0). However, they were modelled according to two different statistical approaches:

- Continuous models (CM): they assume that the analysed trait is a continuous variable with a normal distribution (Meyer et al. 2001).
- Threshold models (TM): it is assumed that an underlying nonobservable variable exists defining the different categories of the categorical trait if this underlying

Table 1 Location, situation and number of records of the institutions included in the dataset. "Active" institution means it is participating in the captive breeding program at the time the study was conducted, and "historical" means that the institution was not participating in the captive breeding program at the time the study was conducted, but in the past it did

Institution name	Country	Situation	Number of records
Schoenbrunner Tiergarten	Austria	Active	22
Mountain View Conservation and Beeding Centre	Canada	Historical	53
Zoo de Montpellier	France	Active	37
Münchner Tierpark Hellabrunn	Germany	Active	208
Tierpark Berlin	Germany	Active	119
Zoo Frankfurt	Germany	Active	126
Budapest Zoo and Botanical Garden	Hungary	Active	17
Zoom Torino	Italy	Active	10
Rotterdam Zoo	Netherlands	Active	56
Bioparc Valencia	Spain	Active	20
Estación Experimental de Zonas Áridas	Spain	Active	1059
Zoo Aquarium de Madrid	Spain	Active	37
Zoobotánico Jerez	Spain	Active	44
Zoo de Barcelona	Spain	Active	41
National Zoological Gardens of South Africa	South Africa	Historical	19
Belfast Zoological Gardens	United Kingdom	Historical	12
Busch Gardens Tampa Bay	United States	Historical	20
Cincinnati Zoo and Botanical Garden	United States	Historical	37
Oregon Wildlife Foundation	United States	Historical	28
Philadelphia Zoo	United States	Historical	10
Phoenix Zoo	United States	Historical	12
Saint Louis Zoological Park	United States	Historical	21
San Diego Zoo	United States	Historical	152
San Diego Zoo Safari Park	United States	Historical	25

variable exceeds a particular threshold value (Gianola 1982).

Estimates of genetic parameters in dichotomous traits may depend on the population mean of the trait, so threshold models would better account for the probabilistic structure of categorical data than linear models (Gianola and Foulley 1983). But when the amount of information for fixed effects is small, threshold models can have problems in estimating variance components and providing reliable results (Altarriba et al. 1998). Therefore, all models were solved with a continuous and a threshold approach, and then compared by the logarithm of the conditional predictive ordinate (logCPO) (Pettit and Young 1990; Varona et al. 1997; Varona and Sorensen 2010; Pun et al. 2012). This is a cross-validated predictive method, that relies on predictive distributions conditioned on the observed data with a single data point removed. The lower the logCPO value, the better the fit between the observations and the model. A total of 48 different models were fitted for each trait, considering the combination of the 6 models defined according to the random effects (Models 1–6) with the 4 models defined by the inbreeding covariates (Models I-IV) and the two statistical approaches (continuous and threshold models). Finally, when the models with the best predictive value for each of the calf survival traits were identified, a bitrait model was computed to determine the genetic correlation between both traits.

All analyses were performed in a Bayesian frame using the TM program (Legarra 2008). Due to the dichotomous nature of the studied traits, in threshold models, a restriction was set so that residual variance was 1 and threshold was 0. For all models, a Gibbs chain length of 1,000,000 samples, a burn-in period of 100,000, and a thinning interval of 100 were defined.

Estimates of systematic effects and genetic trends

Since Bayesian approach was applied, inferences of systematic effects were based on probabilities obtained from the marginal posterior distributions of the parameters. The mean of such marginal posterior distributions will be considered as the estimation across the text. Therefore, and to ensure that the combination of solutions is an estimable function (Formoso-Rafferty et al. 2017), the probability of survival for a particular level l of a systematic effect s was calculated by adding the solution of that desired level $\widehat{b}_{sl}$ to the sum the rest of the averaged systematic effects, as indicated in the following expression:

$$y_{sl} = \sum_{i=1,n_s} \frac{\widehat{b}_{ij}}{n_s} + \widehat{b}_{sl}$$

For threshold models, the parameters obtained correspond to the underlying variable, so they should be converted to the area below the threshold y_{sl} in a normal distribution. To determine if there were differences in terms of probability between the levels of each systematic effect, the marginal posterior distributions of the differences between levels were calculated. In this Bayesian context, all the resulting solutions were assessed with a 95% highest posterior density interval, considering values above this interval to be significant.

In a similar way, estimates of genetic trends were computed from the sum of all averaged systematic effects and the mean of the genetic effects by year of birth of the individuals. The mean inbreeding coefficient was subsequently included in the calculations to determine its effect on these survival traits. For the estimation of the genetic and phenotypic trends expressed by year of birth, the records of historical institutions were removed and only the calf records of the 13 active institutions were used (Table 1), with the aim of representing a more realistic situation of the population that is currently managed in the captive breeding program.

Results

Mean and standard deviation of the marginal posterior distribution of the genetic and environmental effects concerning the juvenile survival traits analysed in the mhorr gazelle captive population (PS and WS) are given in Appendix S1. Considering inbreeding covariates, changes of less than 6% were observed in the estimated heritabilities for the direct genetic effect (h^2) between the four models, and less than 3% for the maternal genetic effect (m^2) and the maternal permanent environmental effect (c^2). In all cases, threshold models showed a better predictive value than their continuous counterparts (lower logCPO value). Correlations between direct and maternal genetic effects were always positive for PS and negative for WS, although in many cases the standard deviations of these correlations were very high.

Among all fitted models, the worst predictive values were always for the dam models and the dam-permanent models, regardless of the approach considered. On the contrary, the best predictive values were for the calf model in the PS and the calf-permanent model in the WS (Table 2), both obtained with a threshold approach. The best calf model included the inbreeding coefficient of the calf as linear covariate (Model II) and the best calf-permanent model, the inbreeding coefficient of the dam (Model III). Computing them together as a bitrait model, the genetic correlations of direct genetic effects between traits were 0.201 (SD = 0.296).

Table 2 Mean and standard deviation (in brackets) of the marginal posterior distribution of the genetic and environmental parameters obtained in the models with the best predictive value

Trait	Model	Inbreeding covariate	Statistical approach	h^2	c^2
PS	Calf model	Calf	Threshold	0.259 (0.052)	
WS	Calf-permanent model	Dam	Threshold	0.123 (0.047)	0.035 (0.026)

h^2 = ratio of variance explained by the direct genetic effect to the total phenotypic variance

c^2 = ratio of variance explained by the maternal permanent environmental effect to the total phenotypic variance

The solutions of systematic effects shown following belong to the models with the best predictive values. As Bayesian approach was applied, inferences will be expressed in terms of the percentage of the marginal posterior distribution in each case. Regarding the number of calving, the calf of a primiparous female had a lower probability of PS than the calves of multiparous females (Fig. 1a), with 100% of probability of being lower. The probability of the multiparous providing more survivability than primiparous was 67% in the WS. Calves born in winter had a lower PS than those born in the other three seasons (Fig. 1b), with 100% of probability of being lower. However, for the WS the probability of the difference in survivability between seasons was less than 95% in all cases. Female calves had a higher probability of survival than males (Fig. 1c), with 96% of probability of being higher in the PS and 92% in the WS. Concerning the age of the mother, it was observed that the calves with the highest PS were those born to dams between 10 and 13 years old, with an optimal age of 12.2 years (Fig. 1d). In the case of the WS, the offspring born from young and old gazelles were less likely to survive than those born from middle-aged gazelles, the optimal age being 8.4 years. Significant differences were also observed depending on the birth location (Fig. 1e), PS ranging between 54.72% and 96.10%, and WS between 48.24 and 96.79%. Finally, a relevant finding was that calf and dam inbreeding had a negative effect on these juvenile survival traits (Fig. 2). The maximum inbreeding coefficient of the calf reduced almost 30% points of the PS and the maximum inbreeding coefficient of the mother, around 15% points of the WS.

Figure 3 shows the phenotypic and the genetic trends in active institutions for the PS and the WS by year of birth according to the models with the best predictive value, which includes the direct genetic effect as the only genetic effect. Both traits showed a positive genetic trend over time, increasing the probability of survival due to the genetic effect of the calf from 81.17 to 93.55% in the PS, and from 83.11 to 87.22% in the WS (Fig. 3a). However, when the mean inbreeding coefficients of the animal and the dam were included (Fig. 3b), the PS decreased by around 15% points and the WS by almost 10% points, respectively. Regarding the phenotypic probability of survival, a fluctuation was observed by year of birth, suggesting that changes in the environment across the years of the study affected phenotypic variation. Despite this fluctuation, a positive phenotypic trend was noticed in both survival traits. It can also be seen the individual inbreeding trend by year of birth in Fig. 4, where this coefficient has clearly slowed its growth rate in recent decades.

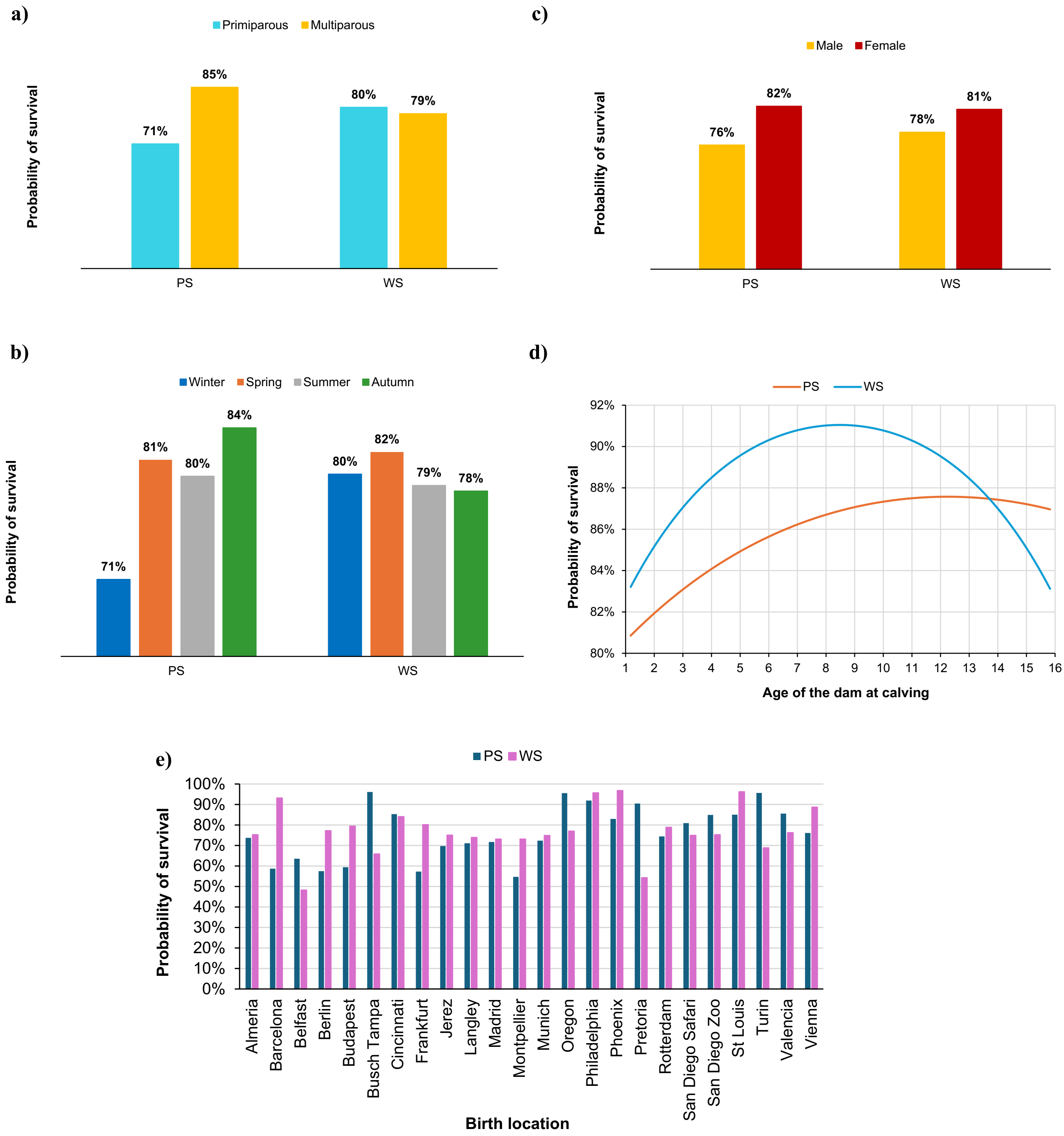

Fig. 1 Probability of perinatal (PS) and weaning (WS) survival for the mhorr gazelle calves considering the mother's number of calving (**a**), the season of birth (**b**), the sex of the calf (**c**) and the age of the dam at calving in years (**d**)

Discussion

The models with the best predictive values showed moderate heritability values (h^2) for the PS (0.259) and low ones for the WS (0.123) of this mhorr gazelle population. These magnitudes of heritability are, however, significant, indicating that both calf survival traits can be transferred from parents to offspring, although genetic progress will be predictably faster in the first trait due to its higher value. Contrary to the direct genetic effect, the maternal genetic effect did not seem to importantly contribute to the prediction of these survival traits in the mhorr gazelle offspring. Therefore, the genetic variance of these offspring traits depends fundamentally on the direct genetic effect and the response

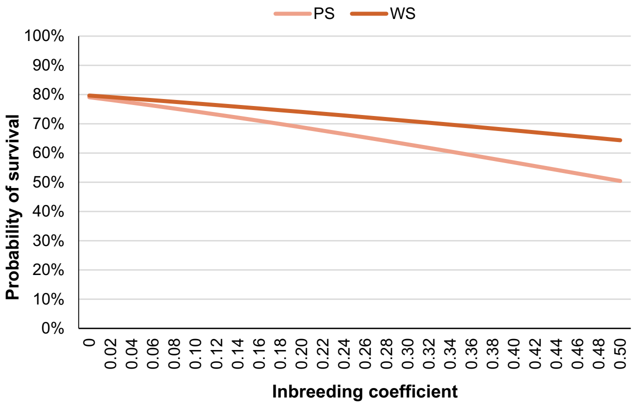

Fig. 2 Probability of perinatal (PS) and weaning (WS) survival according to the inbreeding coefficient of the calf and the inbreeding coefficient of the dam, respectively, in the mhorr gazelle captive population

to selection is not expected to improve significantly if it is based on the mother performance instead of on the genetic effect of the calf. Therefore, individuals with the highest probability of survival could be identified and chosen for reintroduction projects, increasing their chances of success and knowing that these animals will transmit half of their genetic value to their offspring. In the case of the WS, a proportion of the variance was also explained by a maternal permanent environmental effect, although it should be noted that the standard deviation of this estimate was high. The maternal permanent environmental effect does not respond to selection nor is it transferred between generations, but it can be useful to identify those mothers that provide the best environment to their calves, in terms of postnatal care and feeding (Wolf et al. 1998; Matika et al. 2003).

There was no significant genetic correlation between traits studied: a higher PS will not lead to a higher or lower WS, but rather the calf survival depends on different factors at different ages. Thus, the inbreeding level of the animal seems to affect its survival more in the first days of life, while the inbreeding coefficient of the dam has a greater effect on the period until weaning. The negative effect of inbreeding on offspring survival has been well studied in captive populations of wild ungulates (Ballou and Ralls 1982; Skotarczak et al. 2020). However, less attention has been paid to inbreeding depression in other fitness traits that may still arise later in life. If an inbred individual survives to adulthood, it may fail to breed, may produce poor-quality offspring (regardless of whether these offspring are themselves inbred) or may fail to raise its offspring (Margulis 1998). Therefore, behavioural or physiological deficits associated with maternal inbreeding appear to influence offspring survival to weaning in this captive population of mhorr gazelle.

We observed a higher mortality in the first week of life of calves born to primiparous females than those born to multiparous dams, so previous experience of mothers in rearing seems to play an essential role in the survival success of their calves (Lombard et al. 2007; Watts et al. 2009; Ibáñez et al. 2012). However, when the first 7 days of life are overcome in this species, the number of calving does not seem to significantly influence the offspring survival until weaning.

The lower PS we found in calves born in winter could be due to their greater difficulty in thermoregulation when temperatures are low. Newborn calves are prone to heat loss in cold environments due to their low body surface/mass ratio, poor insulation (thin skin and subcutaneous fat) and lack of heat produced by ruminal fermentation (Collier et al. 1982; Berman 2003), resulting in increased calf mortality because of thermal stress (Roland et al. 2016). Heat production of mammals begins to develop from the first week after birth and reaches full maturity during the first two months of life (Piccione et al. 2003), which can explain why no differences between seasons are found in the WS. Another explanation for this lack of differences could be that over the course of almost 6 months until weaning, calves can go through up to 3 different seasons of the year, making it difficult to determine the effect of each season on the WS.

Similarly to other gazelle species (Riesch et al. 2013; Ibáñez et al. 2014; Martin et al. 2023), female calves also showed a higher survivability in this study, both in the first 7 days of life as at the time of weaning. In polygynous species, mothers allocate more energy during maternal care to male offspring than female offspring (Macdonald et al. 2020), usually associated with the higher body mass of males. High energy demands on dams during gestation and lactation periods would lead to lower survival of male calves if the mothers are not able to cope with these energy requirements.

As previously described by Alados and Escós (1991) and Ibáñez et al. (2012), offspring survival in the mhorr gazelle also depends on the age of the mother. For the PS, calves born from long-lived dams are more likely to survive than calves from short-lived mothers. So, again, the experience accumulated by females with age increases their reproductive success in this critical period, as consequence of an improved quality of maternal care and a better ability to minimize high mortality risks facing newborn calves (Weladji et al. 2006). For the WS, the highest survival rates were associated with middle-aged females. Since lactation is the largest maternal energy expenditure in most mammals (Gittleman and Thompson 1988), females in physiological stages where their body mass is lower, such as growth or senescence, will require greater reproductive effort for dairy production. If younger and older females have a reduced ability to provide high quality milk to their calves during this demanding suckling period, the risk of juvenile

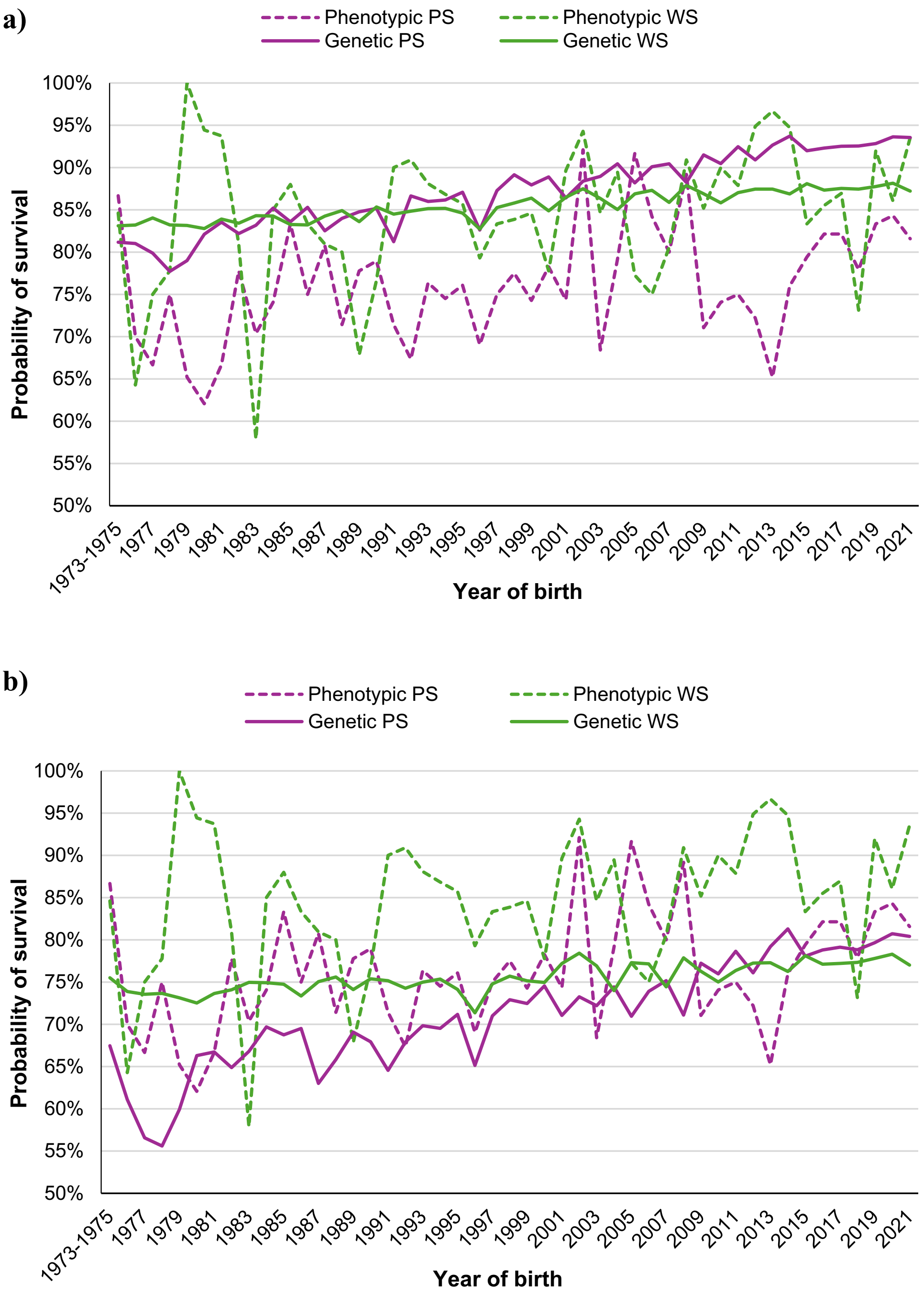

Fig. 3 Perinatal (PS) and weaning (WS) survival for the mhorr gazelle calves by year of birth according to the direct genetic effect (continuous line) and the phenotypic probability of survival (dashed line). The genetic trends have been calculated in two different ways: (**a**) without including any inbreeding coefficient across the years, and (**b**) including the mean inbreeding coefficient of the animal for the PS and the mean inbreeding coefficient of the dam for the WS

mortality will be higher (Ericsson et al. 2001). Although there is no data available on milk traits of this species that would allow precise conclusions to be drawn, variations in milk yield and composition related to mother age described in other ungulate species (Pérez-Barbería et al. 2022) would support this hypothesis.

Regarding the effect of birth location on PS and WS, we suggest it might be a consequence of the different housing conditions and management techniques between the institutions participating in the captive breeding program. Alternatively, it might be a consequence of different photoperiod in institutions distributed at different latitudes. The photoperiod experienced by females during pregnancy is relayed to young during gestation and lactation through the maternal hormone melatonin, which might influence offspring survival as it influences growth rate, fat deposition, pelage, and sexual maturation in other mammals (Lee and Gorman 2000).

In the study population the higher the inbreeding coefficient of the calf, the lower its probability of surviving to 7

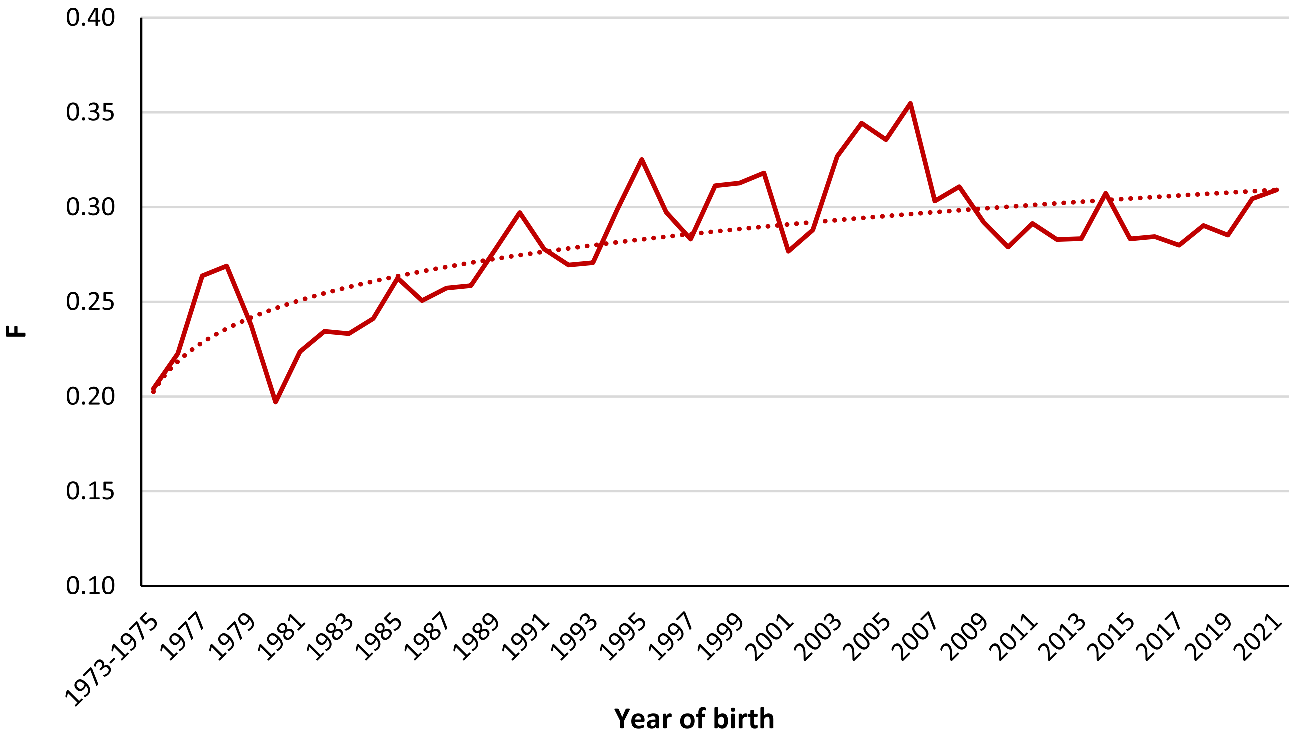

Fig. 4 Average individual inbreeding coefficient of the mhorr gazelle calves by year of birth (continuous line) and its trend line (dotted line)

days of life; and the higher the inbreeding coefficient of the mother, the lower the probability of survival of the calf to weaning. We also found that an increase in the direct genetic effect trends of the PS and the WS occurs. First results indicate inbreeding depression in this population (Fig. 2), according to Fisher's theory on natural selection (1930). But contrary to expectations, second finding indicates that the captive breeding program of mhorr gazelle seems to be effective in achieving some genetic improvement in the fitness traits, which indicates selection for juvenile survival over time, since only the individuals that survive and manage to reproduce are the ones that leave offspring in the next generation (Darwin and Wallace 1958). There are two non-exclusive explanations for this apparent inconsistency. First, in view of the small number of founders, our captive populations may be considered bottlenecked, and as such, may have purged, at least partly, deleterious alleles, thereby lessening the effects of inbreeding. Ibáñez et al. (2012) pointed out this possibility to happen studying only the captive population at "La Hoya" Experimental Field Station (the biggest one), and it was later demonstrated by López-Cortegano et al. (2021) using the inbreeding-purging model proposed by García-Dorado (2012). Second, in captive breeding programs for endangered species, managers make efforts to improve the living conditions of the animals, which may produce fitness rebound despite inbreeding increase over time (Kalinowski et al. 2000; Müller et al. 2011). Therefore, we cannot rule out the possibility that the observed increased trend in phenotypic variation in survival was due to the improvement of husbandry conditions with time.

The positive genetic trends of the calves over the years, together with the heritability values found in this study for the PS and the WS, evidence there is some evolutionary potential in this mhorr gazelle captive population and, therefore, its adaptive capacity against possible environmental changes, necessary requirement when populations are going to be restored in their natural habitat. Since heritability was greater for PS than for WS, selection appeared to have a higher effect on increasing the genetic capacity of this first trait. Given that this selection process has occurred, we can expect that the current population is more prepared to survive that the founder one. However, the effect of inbreeding depression in the population should not be neglected. It is necessary that the captive breeding program continues minimizing inbreeding when designing pairing strategies. Moreover, when managing the population, it is important to reach any level of inbreeding over a larger number of generations (Van Wyk et al. 2009). By doing this accumulation of inbreeding will happen more slowly, as is already happening in this captive population, allowing selection to operate and to remove the less adapted animals. It also will permit the genomic burden of putatively deleterious alleles to be purged from the population.

The phenotypic probability of survival by year of birth was very changeable, which may be due to different environmental effects, such as climatic factors, the appearance of diseases or the type of animal handling applied, among many others. Further studies on environmental non-genetic factors affecting the survival of mhorr gazelle offspring are necessary to complete the information obtained in this work and understand all aspects influencing these fitness traits of the species. Overall, the time difference that each trait encompasses (7 days in PS versus almost 6 months in WS) makes the results of heritability and systemic effects more evident in the first trait, since many more variables may not have been identified and included in the model during the period up to weaning.

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Data availability Pedigree information used in this study can be found on the website: http://www.eeza.csic.es/documentos/Studbook_2021_Nanger_dama_mhorr.pdf.

Declarations

Competing interests The authors declare no competing interests.

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