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Research Article

Forty years of captive breeding in Przewalski's horse: pedigree-based insights into population growth, sex ratio, and inbreeding

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Long-term captive breeding programs play a critical role in the conservation and reintroduction of endangered species, yet they face persistent challenges related to demographic structure and genetic management. The Przewalski's horse *Equus przewalskii*, once extinct in the wild, represents a global model for conservation breeding supported by pedigree-based management. Here, we analyzed pedigree records from the Xinjiang Wild Horse Breeding Center (WHBC), the world's largest captive breeding facility for the species, covering the period from 1985 to 2023. Using demographic analyses and generalized linear models, we examined long-term trends in foaling output, first-year foal survival, sex ratio, maternal age at reproduction, founder contribution, and inbreeding. A total of 428 foals were born during the study period, of which 372 survived to at least one year of age. Foal survival was positively associated with maternal parity. In contrast, foal survival probability declined over time and was negatively associated with individual inbreeding coefficient, suggesting cumulative genetic and demographic constraints in this semi-closed population. Reproductive output was highly skewed among founders, with four males accounting for more than 90% of surviving descendants sired by founding males. Maternal reproductive age increased significantly over time, reflecting progressive aging of the breeding population. Offspring sex ratio was associated with maternal age, with mares in their prime reproductive years (5–14 years) producing a higher proportion of male offspring. Management-driven removal of older and younger females through release and transfer further influenced demographic structure and sex-ratio dynamics. Our results demonstrate that while pedigree-informed management has supported population persistence and large-scale reintroduction, emerging challenges – including demographic aging, skewed founder representation, and increasing inbreeding – pose risks to long-term sustainability. These findings highlight the need for introducing new genetic lineages

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and integrating pedigree data with molecular genetic tools to optimize future conservation breeding and reintroduction strategies for Przewalski's horse and other endangered ungulates.

Keywords: conservation breeding, foal survival, founder contribution, maternal age effects, pedigree analysis, reintroduction management

Introduction

As one of the flagship species of steppe ecosystems (Wakefield et al. 2002), the Przewalski's horse *Equus przewalskii* has become a global model for wildlife conservation, captive breeding, and species reintroduction (Armstrong and Seddon 2008, Kaczensky et al. 2016). Once extinct in the wild, the species' recovery has depended critically on the long-term success of ex situ breeding programs and the careful management of small founder populations.

A central tool supporting this conservation success is the International Studbook for Przewalski's horse, which systematically documents the lineage, demographic history, and movements of captive and reintroduced individuals worldwide (Mohr 1968, Boyd and Houpt 1994). Studbook records encompass critical information including birth dates, sex, parentage, transfers, and mortality, allowing conservation managers to monitor reproductive performance and genetic structure across generations (Zimmermann 2005). Coordinated breeding programs supported by these pedigree data have enabled substantial population growth since the mid-20th century and supported successful reintroductions beginning in the 1990s (Wakefield et al. 2002, Kaczensky et al. 2016). The first version of the studbook was published in 1959 (Mohr 1959, Ryder 1994). Back then, the captive population of Przewalski's horses in Europe was critically endangered due to war-related disruptions, and population numbers within the species' historical range remained uncertain (Volf 1994). In 1960, the International Studbook started to be maintained by Prague Zoo. It was also when the species was considered extinct in the wild (Bouman and Bouman 1994). Thus the studbook stands as a witness to the species' trajectory from near extinction to gradual recovery.

Pedigree-based approaches are especially valuable in captive or semi-closed populations, where restricted founder numbers and uneven reproductive success can rapidly lead to genetic drift and inbreeding. In polygynous ungulates such as horses, reproductive output is often highly skewed toward a small number of breeding males, both in free-ranging systems and under captive management (Zecherle et al. 2020, King et al. 2025). Studies of isolated feral horse populations have shown that demographic constraints and social structure can strongly shape reproductive skew and long-term viability (Spasskaya et al. 2022). In captive breeding programs, such skew may be further influenced by husbandry decisions, including controlled mating systems and breeder rotation, emphasizing the importance of studbook-informed reproductive planning. More broadly, pedigree data provide essential decision-making support for the conservation of endangered wildlife, by helping maintain genetic diversity and population health. For instance, studbook analyses have revealed elevated mortality in captive zebra populations (Tanton 2007), highlighted the long-term demographic risks of ex situ elephant management (Leimgruber et al. 2008), and demonstrated how integrated pedigree–genomic approaches can improve assessments of reproductive skew and conservation value in rhinoceros populations (Elsner-Gearing et al. 2024). In China, pedigree studies have also been applied to species such as the South China tiger (Chen et al. 2001) and the giant panda (Zhou et al. 2021), underscoring the broader relevance of pedigree-based management for threatened wildlife.

The Xinjiang Wild Horse Breeding Center (WHBC) represents one of the world's leading captive breeding facilities for Przewalski's horse. Between 1985 and 2005, WHBC imported 24 horses (14 males and 10 females) from European and American institutes, forming the founder basis of China's captive population (Chen et al. 2008). Since the first foal was born at the center in 1988, WHBC has successfully bred over 500 individuals across eight generations and has played a major role in reintroduction efforts within the Kalamaili Nature Reserve (KNR). Since 2001, more than 120 horses have been released into KNR, contributing to a free-ranging population exceeding 350 individuals by 2023 (Xia et al. 2014, Cao et al. 2025). Over the past four decades, WHBC has gradually shifted its breeding strategy from an early emphasis on rapid population growth toward a more integrated approach balancing demographic expansion with genetic quality. By maintaining detailed pedigree archives and collaborating with the International Studbook, WHBC has implemented genetically informed breeding management aimed at reducing inbreeding risk and optimizing founder representation. However, challenges remain, including demographic aging, limited introduction of new founder lineages, and renewed increases in inbreeding coefficients.

In this study, we analyzed pedigree records collected by WHBC between 1985 and 2023 to assess long-term reproductive dynamics within the captive population. Specifically, we examined trends in foaling numbers, foal survival to one year of age, sex ratios, maternal age at reproduction, founder contribution, and inbreeding coefficients. By linking demographic and genetic indicators over nearly four decades, this study provides insights into how captive breeding management strategies influence population viability, and offers practical guidance for the future conservation and reintroduction of Przewalski's horse and other endangered ungulates.

Material and methods

Study site and captive management at WHBC

The Xinjiang Wild Horse Breeding Center is located in Jimsar County, Changji Hui Autonomous Prefecture, Xinjiang Uygur Autonomous Region, China, along the southern edge of the Junggar Basin (Fig. 1). The facility lies approximately 60 km from the Kalamaili Mountains, where Przewalski's horses were first discovered in the 19th century (Bouman and Bouman 1994). Established in 1986, WHBC was the first national-level institution in China dedicated to the conservation, breeding, and reintroduction of *Equus przewalskii*.

Between 1985 and 2005, WHBC imported four batches totaling 24 Przewalski's horses (14 males and 10 females) from zoological institutions in Germany, the UK, and the USA (Chen et al. 2008). Of these, 17 successfully produced offspring at WHBC (Table 1). The first foal was born in 1988. Reintroduction efforts began in 2001, and by 2023, a total of 128 horses had been released into KNR, contributing to the establishment of five subpopulations (Supporting information). Additionally, many non-breeding, non-release individuals – mostly males – were relocated to Tianshan Safari Park in Urumqi, Xinjiang, where they established a semi-captive population.

Captive breeding at WHBC has been organized primarily using a harem-based management system. There were 15 enclosures, ranging from 0.2 to 0.7 ha in size. Horses in the breeding program were kept in nine larger enclosures (no. 3–11) and maintained in harem groups consisting of one adult stallion and multiple mares (Fig. 1). Each enclosure is equipped with access to water sources and supplementary forage, and animals are provided with regular feeding and veterinary monitoring throughout the year. Breeding groups are managed to reduce aggressive competition among males and to allow controlled assignment of reproductive pairs. Since the early 2000s, WHBC has increasingly adopted pedigree-informed breeding management. Every 5–7 years, individuals were periodically rotated in and out of the breeding

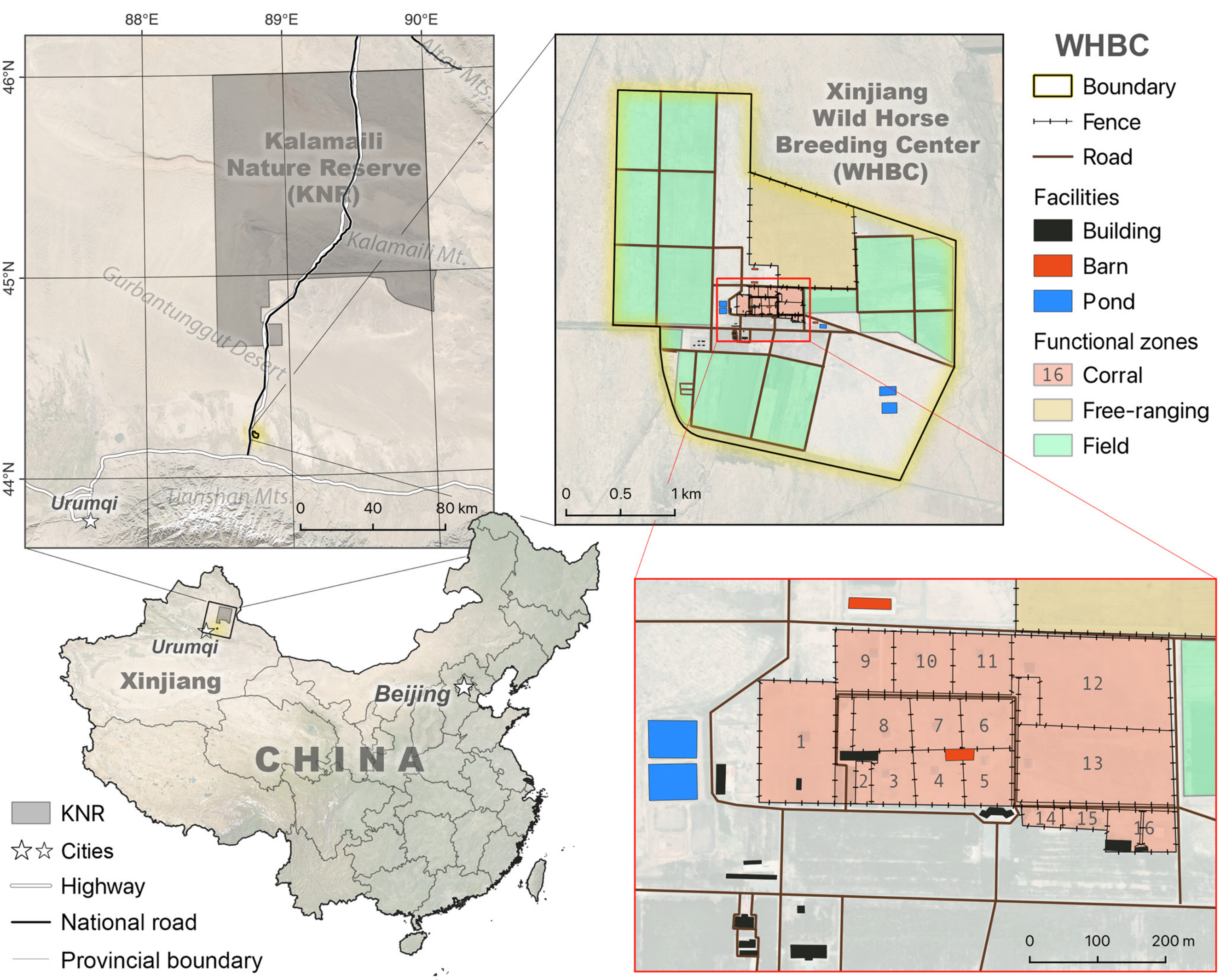

Figure 1. Location and layout of the Xinjiang Wild Horse Breeding Center (WHBC), China.

Table 1. Founding individuals of the Przewalski's horse *Equus przewalskii* population established at the Xinjiang Wild Horse Breeding Center (WHBC).

Batch	Introduction date	Source	Studbook no.	Nickname	Date of birth
1	1985-07-29	Berlin Zoo, Germany	1034♂	Bummi	1982-04-23
			1208♀	Bruni	1984-04-29
			1224♀	Bana	1984-05-13
2	1985-08-17	Marwell Zoo, UK	1202♀	Larmei	1984-04-17
			1283♂	Shan Yin	1984-09-04
			1284♂	Fei Xion	1984-09-06
		Midway Zoo, USA	1206♀	Donetska	1984-04-28
			1244♀	Valerie	1984-05-29
			1270♀	Maria	1984-07-13
3	1988-06-28	Munich Zoo, Germany	1187♂	Silit	1983-09-25
			1251♀	Roanne	1984-06-09
			1271♀	Roxelane	1984-07-19
			1289♂	Sikiang	1984-10-16
4	1991-11-02	San Diego Zoo Safari Park, USA	1662♂	Vaton	1988-01-16
5	2005-09-06	Cologne Zoo, Germany	3311♂	Amon	1999-06-10
			3310♂	Lando	1999-06-10
		Karlsruhe Zoo, Germany	3877♂	Rasaan	2003-06-05

program based on genetic relatedness according to the studbook. Individuals unsuited for breeding were housed in three larger enclosures (2–3 ha). In addition, an 80-ha free-ranging area was maintained on the outskirts of the facility, where non-breeding individuals selected for release were acclimatized prior to release.

Individuals released into the wild or transferred to other institutions were removed from the captive breeding pool. Wild-born descendants produced after release were not included in the pedigree dataset analyzed in this study.

Pedigree dataset and definitions

The Xinjiang Wild Horse Breeding Center has maintained detailed pedigree records for all individuals born at the facility as part of its long-term genetic management system (Supporting information). The pedigree includes each horse's birth date, sex, sire and dam identification numbers, mortality date, and records of transfers or releases. The founding individuals retain their original International Studbook numbers (Table 1), while all subsequent offspring were assigned internal WHBC identification codes. To ensure consistency in demographic analyses, we defined foal survival as survival to at least one year of age. Thus, 'surviving foals' refers specifically to foals surviving ≥ 1 year, whereas 'neonatal/juvenile mortality' refers to deaths occurring within the first year after birth. Data on mortality for individuals older than one year were not publicly accessible, and stillbirths were not systematically recorded in the historical dataset. Therefore these variables were not included in the present analyses.

Because breeding at WHBC occurs within controlled harem groups, paternity assignments were based on recorded breeding group composition and studbook documentation. Genetic testing was not routinely conducted during the earlier decades of the program, representing a limitation of the dataset. However, because only one mature stallion was typically present within each breeding unit, pedigree-based sire identification is considered reliable under the management conditions applied. The reproductive lifespan of an individual is defined as its length of time from the first successful reproduction to the last successful reproduction.

Statistical analyses

We imported the complete pedigree dataset into the R environment (ver. 4.2.2; www.r-project.org). For all individuals born between 1988 and 2023, we extracted information on individual ID, parental IDs, date of birth, sex, survival to one year of age, and maternal age at reproduction. Annual demographic metrics were calculated, including foaling numbers, first-year survival rates, sex ratios, mean maternal reproductive age, and inbreeding coefficient.

We used χ^2 tests to assess whether sex ratio differed: 1) between foals surviving ≥ 1 year and those dying within the first year; 2) among offspring produced by mares of different reproductive age categories; and 3) between primiparous and multiparous mares. To compare the mean reproductive lifespan between founders and non-founders, a one-way ANOVA was performed. In addition, individual inbreeding coefficients (F) were calculated as the probability that both parents of individual x share an identical ancestor. Coefficients were computed using the 'kinship2' package in R (www.r-project.org, Sinnwell et al. 2014), based on standard pedigree methods:

$$F_x = \sum \left(\frac{1}{2}\right)^{n_1+n_2+1} \left(1+F_A\right)$$

where n_1 and n_2 are the number of generations from each parent to their most recent common ancestor, and F_A is the inbreeding coefficient of that ancestor.

Foal survival probability was modeled using logistic regression with sex, year, maternal age, parity, and inbreeding coefficient as predictors (Supporting information). The generalized linear models (GLMs) were applied to improve interpretability and account for multiple predictors. Temporal trends in maternal reproductive age were also assessed using GLMs, with year as a continuous predictor. Model coefficients and standard errors are reported rather than relying solely on significance thresholds. All models were fitted in R using the 'lme4' package (www.r-project.org, Bates et al. 2014).

Founder reproductive contributions were quantified by counting the number of surviving descendants attributable to each founding individual. Differences in contribution among founders were tested using χ^2 methods. To visualize long-term trends, we performed locally weighted scatterplot smoothing (LOESS) using the 'ggplot2' package (Wickham 2016).

Results

Foaling output, first-year survival, and sex ratios

The WHBC pedigree records document a total of 428 foal births, between 1988 and 2023, from 33 sires and 107 dams. Of these, 372 foals survived to at least one year of age, while 56 died within their first year, corresponding to an overall first-year mortality rate of 13.1%. The overall sex ratio of all foals was 1.0:1.33 (♂:♀). Among foals surviving ≥ 1 year, the sex ratio was 1.0:1.28 (♂:♀), whereas foals dying within the first year showed a more female-biased ratio of 1.0:1.80. However, this difference was not statistically significant ($\chi^2 = 0.804$, $p = 0.370$; Table 2).

The annual number of foals surviving to one year increased rapidly during the early growth phase of the population, reaching a peak of 29 surviving foals in 2003 (Fig. 2A). As the captive population expanded, WHBC increasingly transferred individuals to other institutions or released them into the wild (Fig. 2B). By 2023, 79 Przewalski's horses had been transferred and 128 had been released to Kalamaili Nature Reserve. The sex ratio of released animals closely matched that of foals surviving ≥ 1 year within the captive population, whereas transferred individuals showed a male-biased sex ratio (Table 2). Coinciding with intensified releases and transfers, the number of surviving foals per year declined to fewer than 10 during much of the 2010s. A recent recovery was observed by 2023, with 18 foals surviving to one year, representing the highest annual number recorded in the past decade.

Table 2. Foal survival to one year of age and sex ratios of Przewalski's horses born at the Xinjiang Wild Horse Breeding Center from 1988 to 2023. [†] 'Died young' refers to foals that died within one year of birth. [††] Total = survived + died young. [†††] 'Released to wild' refers to captive-born individuals removed from the breeding population for reintroduction.

	Total	♂	♀	Sex ratio (♂:♀)
Survived	372	163	209	1.0:1.28
Died young[†]	56	20	35	1.0:1.80
(Total) [††]	428	183	244	1.0:1.33
Transferred	79	51	28	1.0:0.55
Released to wild[†††]	128	56	72	1.0:1.29

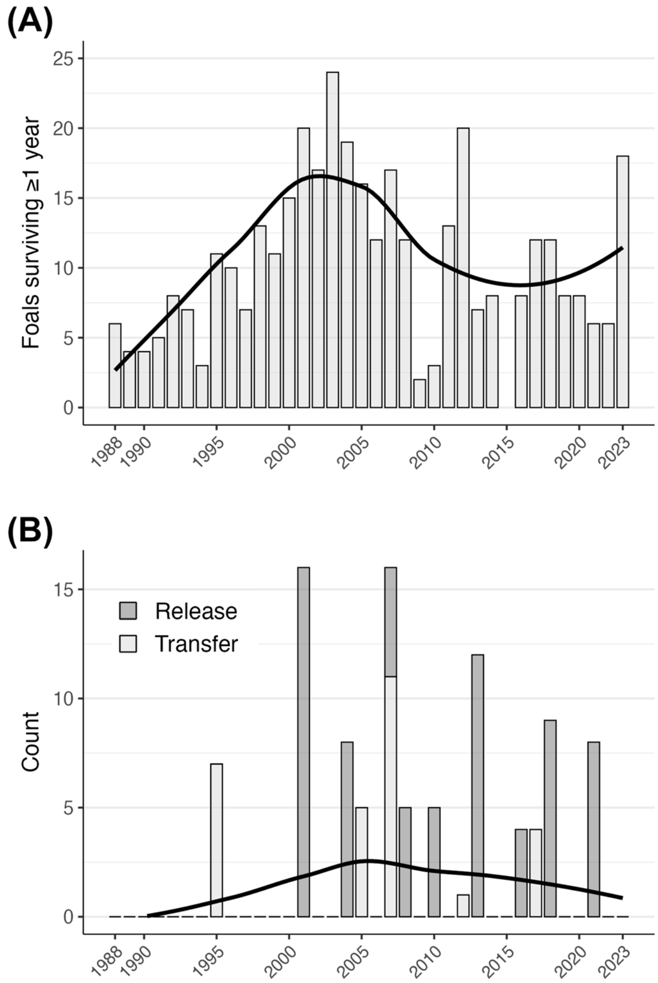

Figure 2. Annual numbers of foals surviving to one year of age and females released or transferred from the Wild Horse Breeding Center (WHBC) between 1988 and 2023. (A) Number of foals surviving to at least one year of age each year. Bars represent annual counts. (B) Number of females removed from the breeding center via release and transfer each year. Bars represent annual counts of individuals being released (dark) or transferred to other facilities (light). The black curves show the locally weighted scatterplot smoothing (LOESS)-smoothed trend.

Maternal age structure and reproductive performance

The mean reproductive age of mares at WHBC was 9.691 ± 4.103 years, with the majority of successful foaling events occurring between approximately 5 and 14 years of age, representing the prime reproductive period (Fig. 3A). The youngest recorded parturition occurred at 1.9 years of age, when mare *Z396* (born 21 July 2020) gave birth to *Z408* on 30 May 2022, 678 days after her own birth. The oldest reproductive age observed was 23 years; two founding mares (*1251* and *1208*) produced offspring at this age in 2007. Mean maternal reproductive age increased significantly over time ($\beta = 0.189 \pm 0.026$ SE, $z = 7.229$, $p < 0.001$), indicating progressive aging of the breeding population, particularly after 2015 (Fig. 3B).

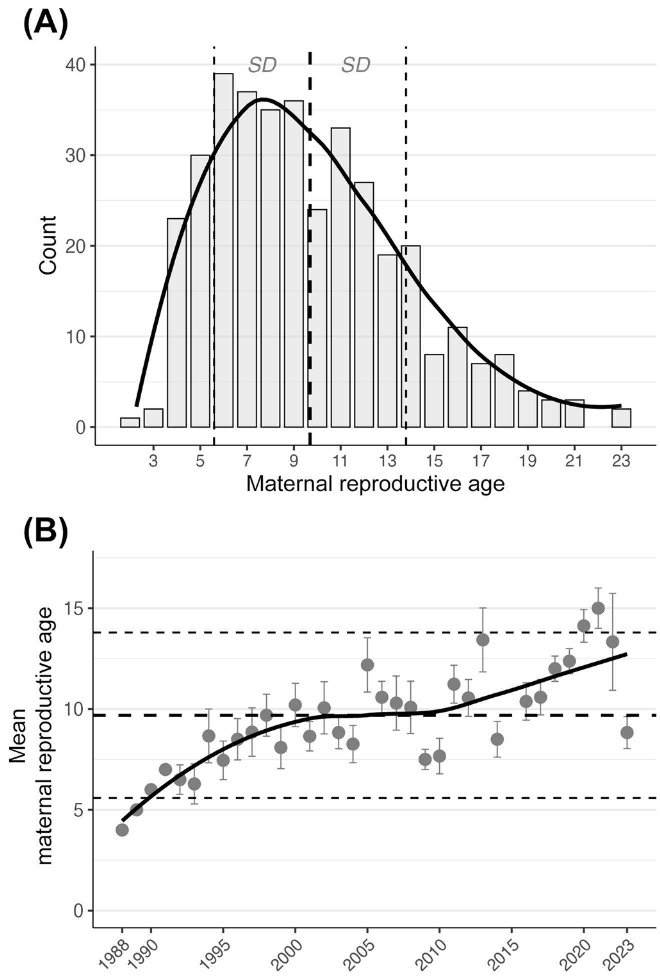

Figure 3. Maternal reproductive age patterns in captive breeding mares at the Wild Horse Breeding Center (1988–2023). (A) Distribution of maternal ages at foaling for all offspring surviving ≥ 1 year. The dashed line indicates the mean maternal reproductive age (9.69 years), with thin lines showing ± 1 SD. A locally weighted scatterplot smoothing (LOESS) curve (black curved line) is fitted to the distribution. (B) Annual mean maternal reproductive age over time. Points represent yearly means ± SD, and the black curve shows a LOESS-smoothed temporal trend.

Foal survival differed significantly between primiparous and multiparous mares. Foals born to first-time mothers exhibited substantially lower survival to one year compared with those born to mares that had reproduced previously (12.9% versus 28.8%; $\chi^2 = 8.536$, $p < 0.01$; Fig. 4A). Besides, maternal age also affected offspring sex ratio. Mares within the prime reproductive age (5–14 years) produced a higher proportion of male offspring compared with younger or older mares (1:1.14 versus 1:2.13; $\chi^2 = 4.5317$, $p < 0.05$; Fig. 4B).

These age-related reproductive patterns contributed to temporal fluctuations in offspring sex ratio. During the mid-development stage of the breeding program, when releases and transfers peaked, offspring production became increasingly male-biased (Fig. 5A). Females selected for release or

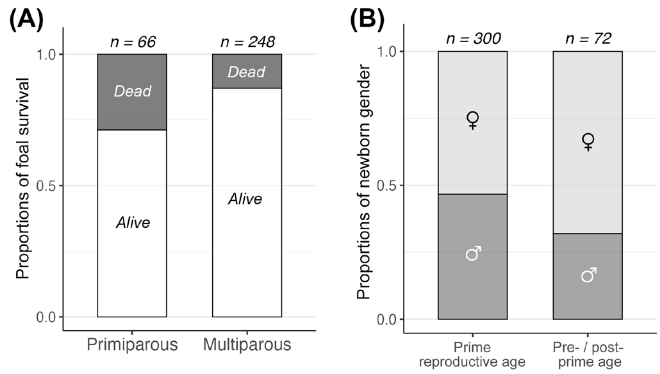

Figure 4. Effects of maternal parity and reproductive age on first-year foal survival and offspring sex ratio at the Wild Horse Breeding Center from 1988 to 2023. (A) First-year survival of foals born to primiparous and multiparous mares. Primiparous mares are females giving birth for the first time, whereas multiparous mares have produced two or more foals. Bars indicate the proportion of foals surviving to one year of age in each group. Survival differed significantly between mare categories ($\chi^2 = 8.536$, $p < 0.01$). (B) Influence of maternal reproductive age on offspring sex ratio. Mares within ± 1 SD of the mean reproductive age (5–14 years) were classified as being in prime reproductive age, whereas mares outside this range were classified as pre-/post-prime. Sex ratios differed significantly between age categories among foals surviving ≥1 year ($\chi^2 = 4.53$, $p < 0.05$).

transfer during this period were predominantly outside the prime reproductive age range (Fig. 5B), a demographic shift likely contributing to the observed sex-ratio bias.

Founder contribution, inbreeding, and foal survival

In the breeding program, the mean reproductive lifespan was 5.43 ± 4.52 years. Founders, by contrast, were delibratedly retained for longer breeding durations (9.31 ± 6.40 years) as a result of their genetic distinctiveness ($F_{1, 133} = 14.78$, $p < 0.001$). Moreover, founder reproductive contributions were highly uneven (Fig. 6A). Male founders exhibited significant disparities in their reproductive output ($\chi^2 = 116.44$, $p < 0.001$), whereas reproductive output among female founders did not show significant variation ($\chi^2 = 10.516$, $p = 0.161$). Stallions *3877*, *1662*, *1284*, and *3311* were the male founders retained longest in the breeding program (7–16 years). Together, they accounted for 94.1% of the surviving offspring descended from male founders, reflecting a strong reproductive skew driven by management preference within the captive breeding program.

The mean inbreeding coefficient was 0.193 ± 0.056 across the whole time period. Inbreeding levels increased rapidly during the early phase of population establishment, declined following the initiation of pedigree-informed breeding management and the introduction of new founders in 2005, and have shown a gradual upward trend again in more recent years (Fig. 6B). A total of 59 individuals (15.86%) exhibited inbreeding coefficients exceeding 0.25 (Supporting information), with 87.5% of these cases occurring before 2004.

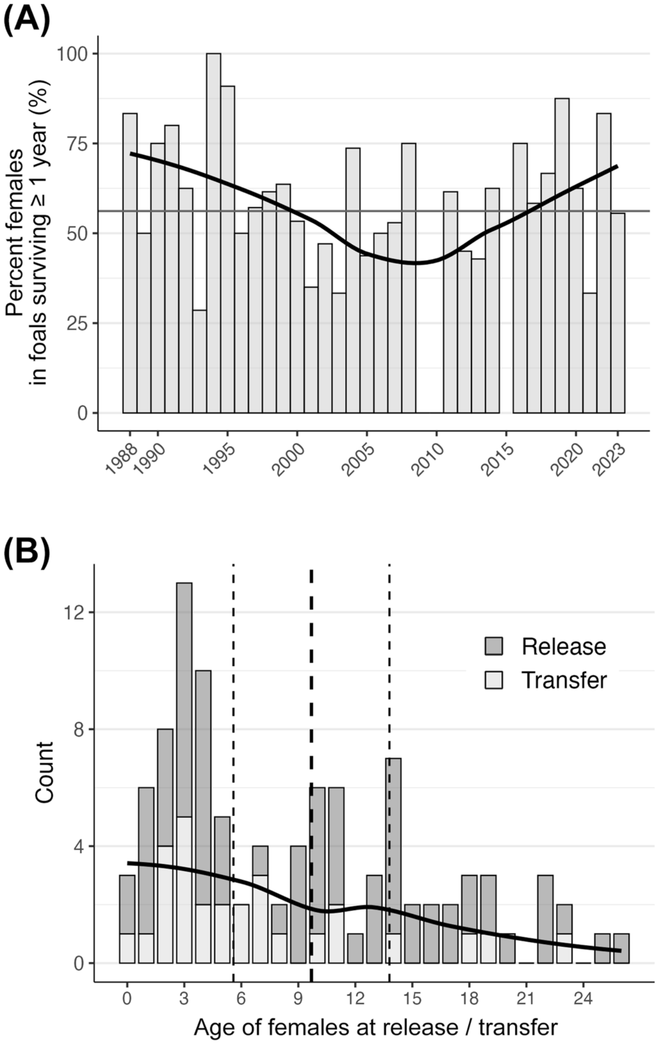

Figure 5. Annual offspring sex ratios and age structure of females removed from the breeding population through release or transfer at the Wild Horse Breeding Center (1988–2023). (A) Annual proportion of female foals among those surviving ≥ 1 year. The horizontal line indicates the overall mean proportion of female offspring across the study period. The black curve shows a locally weighted scatterplot smoothing (LOESS)-smoothed temporal trend. (B) Distribution of the age structure of females removed via release (dark) or transferred (light). The dashed line indicates the mean maternal reproductive age (9.69 years), with thin lines showing ± 1 SD. A LOESS curve (black curved line) is fitted to the age distribution.

Foal survival to one year was analyzed using logistic regression including birth year, maternal parity, and foal inbreeding coefficient (Table 3; Supporting information). Foal inbreeding coefficient was negatively associated with first-year survival (β = −4.65 ± 2.37 SE, z = −1.96, $p < 0.05$), indicating reduced survival probability among more inbred foals. Survival probability also showed, though marginal, a positive association with maternal parity and a negative one with birth year. Maternal age and foal sex were not retained in the best-supported model and showed no detectable effect on foal survival (Supporting information).

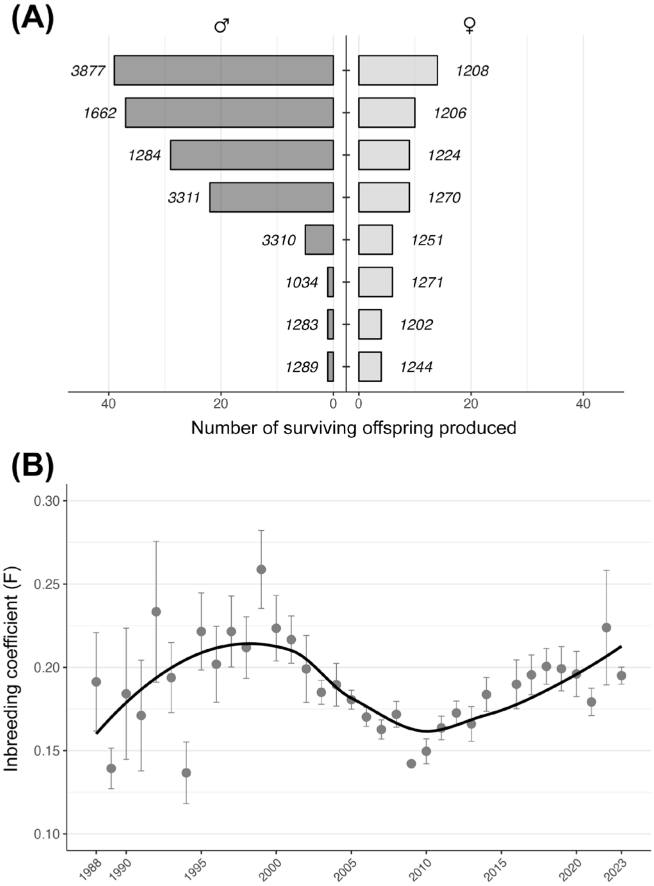

Figure 6. Founder reproductive contribution and temporal trends in mean inbreeding coefficient (F) at the Wild Horse Breeding Center beween 1988 and 2023. (A) Number of surviving descendants (≥ 1 year) produced by each founding individual. Male founders exhibited strong reproductive skew ($\chi^2 = 116.44$, $p < 0.001$), whereas contributions among female founders did not differ significantly ($\chi^2 = 10.52$, $p = 0.161$). Founder International Studbook numbers are shown. (B) Points represent yearly mean inbreeding coefficients ± SE for foals surviving ≥ 1 year. The black curve shows a locally weighted scatterplot smoothing (LOESS)-smoothed trend across the study period.

Discussion

Long-term population management and genetic structure

The Przewalski's horse population at the Xinjiang Wild Horse Breeding Center has experienced more than four decades of

Table 3. Generalized linear model results for first-year foal survival of Przewalski's horses at the Wild Horse Breeding Center. Foal survival was fitted using the logistic model, and the best model (Supporting information) was chosen with the lowest Akaike's information criterion (AIC) in the backward stepwise selection.

Covariates	β	SE	z	p
	−4.6487	2.3715	−1.960	< 0.05
	−0.3146	0.1687	−1.865	0.062
	0.6204	0.3328	1.864	0.062
	2.0633	0.6003	3.437	< 0.001

rapid demographic growth, contributing substantially to both national conservation breeding efforts and large-scale reintroduction programs in China. Our results demonstrate that the breeding strategy at WHBC has evolved substantially through distinct phases, shifting from an early focus on population expansion toward a more integrated emphasis on genetic management and long-term viability.

Pedigree-based breeding management has played a crucial role in limiting inbreeding in this closed captive population. During the earliest generations, WHBC faced the inherent constraints of a small founder base and limited opportunities for genetic exchange. Under such conditions, reproductive output was highly dependent on a few individuals, and the probability of close-kin matings increased rapidly. Similar patterns have been documented in other small or isolated ungulate populations, where reproductive skew and restricted founder representation can accelerate genetic drift and inbreeding accumulation (Saltz and Rubenstein 1995).

Following the initiation of systematic pedigree-informed management after 2001, mean inbreeding coefficient decreased substantially. This reduction coincided with several key interventions, including the rotation of breeders among breeding harems, the removal of individuals for reintroduction or transfer, and the introduction of three new founders in 2005. Together, these measures illustrate how demographic management and genetic planning can effectively decouple population growth from inbreeding risk in conservation breeding programs.

However, despite these achievements, our analyses also indicate that the benefits of these strategies have begun to diminish in recent years. Inbreeding coefficients have shown a gradual upward trend again, reflecting the absence of new founder introductions since 2005 and the increasing genetic relatedness within the remaining breeding pool. Although a full assessment of mortality causes across age classes was not possible due to mortality data restrictions, our survival analysis revealed that higher inbreeding coefficients were associated with reduced foal survival to one year of age, consistent with the expected negative fitness consequences of inbreeding in small or closed populations. This finding highlights the continued vulnerability of the population to inbreeding depression and underscores the urgent need for renewed international or inter-institutional exchange of genetic lineages to maintain long-term genetic diversity.

Reproductive skew and maternal demographic dynamics

Pedigree-informed management, while aimed at minimizing relatedness, resulted in intensive use of a small number of genetically distant founders. Consequently, founder contribution in the WHBC population became highly uneven, particularly among males. More than 90% of surviving descendants from the male founder cohort were sired by just four stallions, whereas the remaining ten contributed little or nothing to the gene pool. In free-ranging feral horse populations, reproductive success is often similarly skewed due to dominance hierarchies, female choice, and social structure (Spasskaya et al. 2022, Elsner-Gearing et al. 2024, King et al. 2025). In captive breeding systems, however, such skew may be further shaped by management practices, including controlled harem composition and selective retention of highly productive stallions.

Thus, the reproductive skew observed at WHBC should not be interpreted solely as a natural biological outcome, but rather as a combined product of equid social mating systems and institutional breeding decisions. Reducing reliance on a small number of paternal lineages remains an important management priority, as skewed founder representation can erode effective population size even when census numbers are high.

Maternal demographic structure also played a significant role in reproductive outcomes. Foal survival differed significantly between primiparous and multiparous mares, with foals born to first-time mothers exhibiting lower survival to one year. This pattern was also indicated – though marginally – by our survival models, and is consistent with reproductive experience effects documented in other equids and ungulates, where maternal age and parity influence neonatal viability (Cameron et al. 2000).

In addition, we observed a pronounced temporal increase in maternal reproductive age, indicating progressive aging of the breeding population. This trend likely reflects demographic constraints imposed by efforts to minimize inbreeding through repeated use of genetically distant individuals. Aging of the breeding pool may reduce long-term reproductive capacity and underscores the need for proactive demographic renewal through the retention of younger mares and the introduction of unrelated breeding stock.

Sex ratio variation and management implications

Maternal reproductive age was associated with offspring sex ratio among foals surviving to one year, with mares in their prime reproductive years (5–14) producing relatively more male offspring. This pattern aligns with the Trivers–Willard hypothesis, which predicts that females in better condition or with greater resource access may bias investment toward male offspring in polygynous species (Trivers and Willard 1973, Cameron et al. 1999). Similar age- or condition-dependent sex-ratio biases have been reported in other equids, including Asiatic wild asses (Saltz and Rubenstein 1995).

At WHBC, these sex-ratio patterns appear to have been further shaped by management-driven changes in age structure. During the early 2000s, many older or younger mares were removed from the breeding population through release into Kalamaili Nature Reserve or transfer to other institutions, leaving a breeding population dominated by prime-aged females. Such selective removal likely contributed to the prolonged male-biased offspring production observed during the mid-development stage of the program.

Although pedigree analyses provide powerful insights into demographic and genetic dynamics, molecular genetic studies have increasingly shown that pedigree-based estimates may underestimate or overlook cryptic relatedness. Genomic and microsatellite studies on reintroduced Przewalski's horse populations in China have revealed reduced genetic diversity and founder effects that align with the skewed lineage contributions identified here (Liu et al. 2014a, 2014b). Integrating pedigree records with molecular tools will therefore be essential for improving future breeding decisions, validating parentage, and optimizing genetic representation.

Management recommendations and future outlook

This long-term pedigree analysis provides several practical recommendations for improving the sustainability of the WHBC population.

1) Introduction of new founder lineages is urgently needed, as no new genetic stock has been incorporated since 2005 and inbreeding levels are rising again.
2) Breeding plans should prioritize underrepresented paternal lineages, reducing dependence on a small number of historically dominant stallions.
3) Demographic renewal should be promoted, including the retention of younger breeding mares to counteract population aging and maintain reproductive output.
4) Pedigree-based management should be expanded through molecular genetic integration, including genomic monitoring, parentage validation, and diversity assessments.
5) Captive–wild population management should be linked, with consideration given to incorporating naturally bred individuals from reintroduced herds into future conservation breeding frameworks.

Strengthening collaboration among international breeding centers, studbook institutions, and genomic research programs will be critical for ensuring the long-term genetic health and conservation value of captive Przewalski's horse populations.

Conclusions

The WHBC captive population has made a major contribution to the recovery and reintroduction of Przewalski's horse over the past four decades. Nonetheless, the population now faces emerging challenges, including demographic aging, skewed founder representation, and renewed inbreeding risk. Continued success will depend on the incorporation of new genetic lineages and the integration of pedigree and molecular approaches to guide sustainable long-term management.

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Data availability statement

Data are available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.31646548 (Cao et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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