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Inbreeding Depression Across Multiple Life-History Traits in a Long-Lived Mammal

Léa Auclair[1] | Cécile Vanpé[2] | Guillaume Chapron[3] | Pierre-Yves Quenette[2] | Alexandre Robert[1]

[1]Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Centre D'écologie et Des Sciences de la Conservation (CESCO), Paris, France | [2]Office Français de la Biodiversité, Paris, France | [3]Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden

Correspondence: Léa Auclair (lea.auclair@mnhn.fr)

ABSTRACT

Inbreeding depression is widely recognised as a near-universal phenomenon of high conservation concern, particularly as wild populations continue to decline. However, most research to date has focused on early life stages, leaving later-life effects comparatively understudied, especially for wild populations of long-lived species. The Pyrenean brown bear (*Ursus arctos*), characterised by a small population, high levels of inbreeding and conflicts with human activities, embodies the conservation challenges faced by many large mammals. We analysed 27 years of monitoring data to quantify inbreeding depression across multiple life stages on survival, reproduction and dispersal. Our results reveal strong inbreeding depression effects, particularly in early life stages, including a reduction in litter size and in natal dispersal distance. In adults, more inbred mothers exhibit lower cub survival. The cumulative effect of inbreeding, as measured by lifetime breeding success, also shows a negative impact. These findings highlight the necessity of assessing inbreeding depression across the entire life cycle to accurately evaluate its threat to population dynamics and viability. Such comprehensive assessments will become increasingly essential for wild plant and animal populations constrained by habitat destruction, human–wildlife conflict and harvesting pressures.

1 | Introduction

Inbreeding depression—the reduction in individual fitness resulting from mating between close relatives—is a near-universal phenomenon observed across a wide range of species (Keller and Waller 2002). However, the magnitude of its effects can vary considerably both across species and populations (Hedrick and Kalinowski 2000), depending on factors such as the environment (Armbruster and Reed 2005; Fox and Reed 2011), the mating system, the demographic history and the architecture of the inbreeding load (Kyriazis et al. 2021; Dussex et al. 2023). For example, within a single species, populations that have experienced prolonged periods of large size followed by a recent bottleneck are particularly susceptible, as large populations may have high frequencies of deleterious recessive alleles responsible for inbreeding depression (Hedrick and Garcia-Dorado 2016).

The biological mechanism underpinning inbreeding depression involves the increased likelihood of homozygosity for deleterious alleles in inbred individuals, which can disrupt the functioning of key genes (Charlesworth and Willis 2009; Paige 2010). This phenomenon is expected to affect the whole genome of an organism and can potentially influence multiple life-history traits (Ayroles et al. 2009; Paige 2010). Indeed, inbreeding

depression can impact a broad array of functions, ranging from reproduction to survival, and can have stage- or age-specific effects (Margulis 1998; Szulkin et al. 2007; Huisman et al. 2016; Trask et al. 2021). Some studies suggested a higher sensitivity to inbreeding for early life stages, potentially due to the high selective pressures that occur during development (Charlesworth and Hughes 1996; Keller and Waller 2002; Armstrong et al. 2020). However, other studies argued that the negative effects of inbreeding might increase with age due to the accumulation of recessive or partially recessive mutations that are expressed late in life (Charlesworth and Hughes 1996; Keller et al. 2008; de Boer et al. 2018).

Understanding inbreeding depression is crucial for biodiversity conservation, especially for small and isolated populations, which are becoming increasingly common as the biodiversity crisis unfolds (Ceballos et al. 2017). Realistic levels of inbreeding have been shown to increase extinction risk, particularly in threatened populations (Frankham 2005; O'Grady et al. 2006; Trask et al. 2021). Despite the growing evidence of inbreeding depression in the literature, most studies focus on early life stages (Ralls et al. 1988; Ryan et al. 2002; Keller and Waller 2002; Hoeck et al. 2015), while comprehensive life-history-wide assessments, particularly for wild, long-lived, nonmodel species, remain scarce. Such studies require extensive, long-term datasets that are difficult to obtain, especially in endangered species, but are essential to capture the full impact of inbreeding depression. Incomplete life-history data can lead to underestimating the true impact of inbreeding depression and, by extension, the extinction risk faced by these populations (Trask et al. 2021).

The brown bear (*Ursus arctos*) population in the Pyrenees represents an ideal case study to investigate inbreeding depression across life-history traits. This population experienced a sharp decline throughout the 20th century and was nearly extinct in 1995, with five bears remaining in the population. Reinforcements of 11 bears from Slovenia (including four females in gestation while translocated) occurred between 1996 and 2018, leading to a demographic recovery of the population, which reached approximately 83 bears in 2023 (Quenette et al. 2001; Sentilles et al. 2024). However, not all translocated bears have reproduced, and one founder male monopolised most of the reproduction until 2017, leading to high inbreeding levels. Due to intensive demographic and genetic monitoring since the first reinforcements (Chapron et al. 2003; Vanpé et al. 2022), the population has a well-documented history of demographic changes, including a founder effect, making it particularly susceptible to inbreeding depression.

In this study, our aim is to measure the effect of inbreeding depression on different traits across the life history of bears in the Pyrenees. Understanding these dynamics in this population has direct implications for its conservation, as it is one of the most endangered brown bear populations in Europe that faces ongoing threats such as habitat fragmentation and conflicts with human activities, mainly related to depredation of sheep (Chapron et al. 2003; Kaczensky 2024). Habitat fragmentation can exacerbate genetic isolation, while human-induced pressures may further restrict population growth, increasing the risk of inbreeding.

2 | Material and Methods

2.1 | Model Species

In the Pyrenees, brown bears begin life in January–February, when one to three cubs are born in the den. After emerging from the den in spring, cubs are completely dependent on their mother until one year of age and generally stay with her for about two years. After that period, the subadults are weaned and leave their mother to establish their own home range. Natal dispersal generally occurs between two and four years old, with females being more philopatric than males (Zedrosser et al. 2007). They generally reach sexual maturity between three and six years of age, with males maturing slightly later than females (Sentilles et al. 2024). Adults begin seeking mates during the breeding season, which occurs from May to July. Females give birth to a litter every two to five years on average (Steyaert et al. 2012). Brown bears can live up to 20–30 years in the wild. Throughout their life, they hibernate each winter to conserve energy during the cold months when food is scarce (Penteriani and Melletti 2020). The conservation status of the brown bear is Least Concern on the international Red List of the IUCN (McLellan et al. 2016) and Critically Endangered on the national French Red List (UICN France et al. 2017).

2.2 | Study Population

In 2023, the Pyrenean brown bear population occurred at the border between France, Spain and Andorra, ranging over 7100 km². After reaching five bears in 1995, the population began to increase following the translocations of 11 bears from Slovenia between 1996 and 2018. Four of the females were pregnant during translocation, leading to the birth of five additional 'half founders' as cubs. Reproductive success varied among translocated bears: seven of the 11 Slovenian founders and three of the five half founders reproduced, with one Slovenian founder male and one female contributing respectively 48.8% and 21.8% of the genetic pool of the population in (Sentilles et al. 2024). In 2023, the Pyrenean brown bear population numbered 83 bears, including 82 coming from the sole Slovenian lineage and only one having a mixed origin (with a mother coming from the historical Pyrenean lineage that went extinct and a Slovenian founder as a father). This last individual (a 19-year-old male) had not reproduced as of 2023 (Sentilles et al. 2024).

2.3 | Monitoring of the Population

From 1996 (the year of the first reinforcement) to 2008, the population remained very small (less than 20 individuals per year) and was monitored through a combination of visual sightings, track identifications, hair and scat sample collection, camera trapping, sheep depredations and radiotelemetry. From 2008 to 2023, as the population grew, monitoring was organised in two main noninvasive standardised methods: Systematic Trail Surveys (walking transects equipped with hair traps and camera traps) and Opportunistic Monitoring (essentially visual observations, records of sheep depredation and scat searches

by scat detection dogs). In addition to systematic and opportunistic noninvasive monitoring, 14 bears (11 translocated ones, two orphan cubs and one bear captured as an adult) were temporarily equipped with VHF and/or GPS collars as well as ear tags from 1996 to 2020. Bear identity and sex were determined through genetic analyses of hair and scats, alongside visual data from camera traps whenever the individual could be identified through unique natural or artificial marks (Sentilles et al. 2021). For detailed methodology, we refer to Appendix 1 and to Vanpé et al. (2022).

2.4 | Pedigree Construction and Inbreeding Estimation

Using the genotypes of individuals based on 23 microsatellites, we built the pedigree of the population with CERVUS 3.07 software (Kalinowski et al. 2007), following the criterion of no genetic incompatibility between the cub and its two parents combined (Sentilles et al. 2021). The combined nonexclusion probabilities for identity and sib identity were 1.25×10^{-15} and 2.20×10^{-7} respectively. Field observations were also used to confirm the pedigree or to complete it in cases of multiple possible parents or lack of genetic samples. This combination of information resulted in a 96% complete pedigree, with missing links involving only cubs that died too young to be genotyped and therefore did not contribute to the next generations. When not all the cubs of a litter were genotyped (nine litters out of a total of 66), all cubs were assumed to have the same father as their genotyped siblings. Although multi-paternity exists, it was quite rare in the population: it was detected only once in the Pyrenean population and once in a pregnant female translocated out of a total of 57 fully genotyped litters.

Due to the long generation time of brown bears and to some recent reinforcements, the depth of the pedigree varied from zero to six generations known, with an average of 1.30 fully traced generations and 3.11 maximum generations traced. To compensate for the lack of depth of the pedigree, we used the molecular data available to estimate the relatedness of the founders and half founders captured in Slovenia (see Appendix 2 for more details). The molecular relatedness values (reported in Appendix 3) among individuals were incorporated into the analysis using the software PMx 1.6.5 (Lacy et al. 2012). Input relatedness transformed into kinship (division per two) by the software, combined with the pedigree data of the population, was then used to calculate the inbreeding coefficient (F_{ind}) for each individual, defined as the kinship coefficient between its parents. This correction to reduce the bias introduced by the founders' hypothesis (Rabier et al. 2022) gave very similar values of individual inbreeding coefficients as the estimates without the correction (Pearson's correlation coefficient = 0.98) due to low relatedness between founders that produced offspring together. Information on the inbreeding status of the only Pyrenean-lineage mother in this population was unavailable; however, it is presumed to be high due to the population's historical context. Depending on the type of analysis, this female was either excluded from the analyses, or her inbreeding coefficient was set at the population average. For the founders originating from Slovenia, an inbreeding coefficient of zero was assumed, reflecting the high genetic diversity of their large source population (Skrbinšek et al. 2012, 2019).

2.5 | Life History and Genetic Metrics

Three genetic metrics were used:

- F_{ind} designates the inbreeding coefficient of an individual estimated as explained above.

- F_{mother} designates the individual inbreeding coefficient of the mother of an individual estimated as explained above.

- F_t designates the average individual inbreeding coefficient (F_{ind}) of the cohort of the litters born in year t, with the two multi-paternal litters treated as four separate litters.

To measure the potential isolation of individuals, we estimated the home range of each individual per year using the locations of all samples associated with the individual each year and determining the centroid of these points. A circular buffer of $251\,km^2$ for females and $1440\,km^2$ for males was then created from this centroid to define the individual's home range based on an estimation made in the Pyrenees (Kervellec et al. 2023). If an individual was not detected in a given year but reappeared in later years, we estimated the missing year's centroid as the centroid of the available years, assuming that adult bears maintain relatively stable home ranges over time.

Using this home range, we defined two demographic metrics:

- Number of males was defined as the number of adult males with overlapping home range with the focal individual in a specific year.

- Number of potential reproductive partners was calculated as the yearly number of sexually mature individuals of the opposite sex with overlapping home range with the focal individual in a specific year.

We tested the effect of inbreeding depression on seven different life-history traits from different life stages (Figure 1):

- Litter size: The number of cubs in a litter was determined through direct observation or photography, as cubs typically remain close to their mother for the first two years. Litters not detected before cubs reached independence (two years old) were excluded due to uncertainty in cub count. Litter size therefore, reflected the number of cubs born minus early mortality occurring before the first detection. Data from 66 litters were analysed. Due to the absence of inbreeding information for the only Pyrenean-lineage mother, the value of F_{mother} of her litter was set at the mean of the rest of the litters (0.08).

- Cub survival: The cub survival was measured as the probability of a cub of the year to survive until one year old, estimated from capture-mark-recapture (CMR, see below). In CMR analyses, when using F_{ind} as a covariate, the missing values from the individuals with incomplete pedigree ($N = 14$) were replaced by the mean of the sample. When
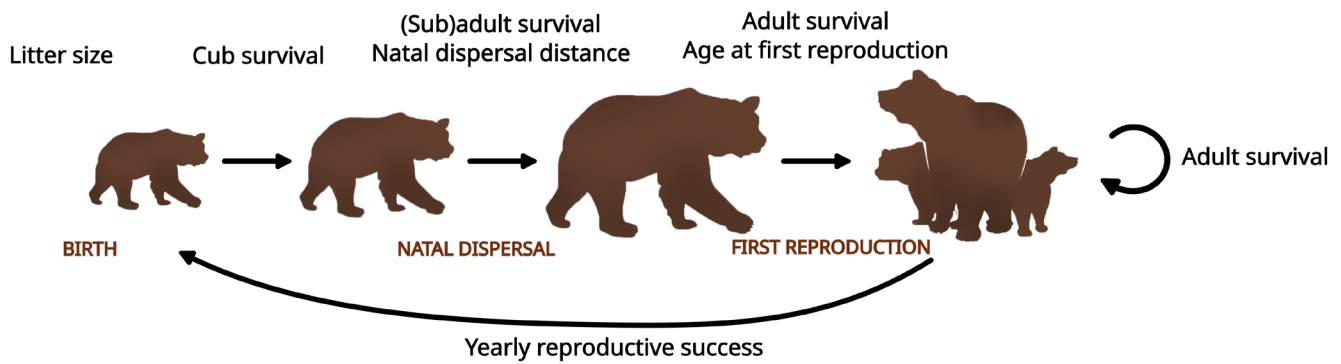
FIGURE 1 | Traits studied for inbreeding depression in the brown bear life history.

using F_{mother} as a covariate, only the cub with a Pyrenean-lineage mother for which we had no information on its pedigree was replaced by the mean of the sample. In total, our dataset included 132 bears detected as cubs.

- Subadult and adult survival: The subadult and adult survivals were measured as the probability of an individual older than one to survive from one year to another, estimated from CMR (see below). Our dataset included 104 individuals who survived until at least one year old.

- Distance of natal dispersal: All observed natal dispersal events in our population occurred before bears reached four years of age. After this age, except for one individual, bears typically maintained relatively stable home ranges. A total of 53 individuals born in the Pyrenees surviving to at least four years of age were considered. An orphan relocated by the technical team and a female with an unknown maternal home range were excluded, resulting in a final dataset of 51 individuals. The centroid of the natal home range was defined as the center of all maternal detections post 4 years old, while the centroid of the post-dispersal home range was calculated from all individual observations after reaching four years of age. For one male exhibiting multiple long-distance movements after 20 years in a relatively stable home range, only data prior to these movements were considered. The distance of natal dispersal was measured as the shortest distance on the WGS84 ellipsoid between natal and post-dispersal centroids (function distGeo in the geosphere package (Hijmans et al. 2024)).

- Age at first reproduction: The age at first reproduction of an individual was measured as the age corresponding to the year before first offspring was detected. The analysis was done on individuals born in the Pyrenees who survived to at least three years of age ($N = 62$ individuals).

- Yearly breeding success (YBS): YBS for both sexes was calculated as the number of offspring detected each year over an individual's reproductive period. This period was defined from the age of two for females and three for males until the last observed year of the individual's life. For mothers, the first year after they were observed with cubs was excluded from analysis if at least one cub remained alive after July of that year, as this would preclude new reproductive opportunities. A total of 66 bears were used for the analysis, which yields a sample size of 362 bears time years.

- Lifetime breeding success (LBS): LBS was measured as the total number of an individual's offspring that survived to at least one year old. The analysis included individuals who died before 2023 (with known LBS) and those born in or before 2017 who were still alive in 2023 (with known minimal LBS) using censored data. Founding members were excluded. To take into account cubs that may have died before being detected and the potential impact of F_{ind} on litter size, an adjusted dataset was created by adding individuals to known litters (excluding multi-paternal ones) to ensure each had three offspring. These added individuals had an LBS of zero. The analysis was conducted with ($N = 149$) and without ($N = 83$) these additional cubs for comparison.

2.6 | Statistical Analysis

In order to visualise the temporal change of inbreeding in the population, a linear model (lm function in R) was built between F_t and the birth year, with statistical decision based on the p value ($\alpha = 0.05$).

F_{ind} and F_{mother} were scaled in all analyses described below.

2.6.1 | Litter Size

The effect of F_{ind} on litter size was assessed using a generalised linear mixed-effects model (GLMM) with the glmmTMB package (Brooks 2024) in R, employing a Conway–Maxwell Poisson distribution that best fitted the data. An interaction term between F_{ind} and F_{mother} was also tested. The mother identity was included as a random factor, while the time in days between the first litter detection (used to count cubs) and the expected date of den departure (15th of March) was incorporated as a continuous covariate to account for potential bias due to cub mortality. The number of males in the home range of the mother in the year of birth, the age of the mother and her primiparity (whether it was her first litter) were included as fixed effects, the two former as quantitative and the latter as binary. The year of the litter was not included as a random effect due to convergence issues when both random effects were included (mother ID and litter year),

possibly due to the very low estimated variance components for both random effects: 6.86×10^{-11} for litter year and 1.14×10^{-10} for mother ID in the linear model. Models fitted with either one of the two random factors yielded the exact same estimates.

2.6.2 | Distance of Natal Dispersal

The effect of F_{ind} on natal dispersal distance was evaluated using a linear mixed-effects model (LMM) fitted with the lmer function from the lme4 package 1.1–35.1 (Bates 2024) in R. The natal dispersal distance (response variable) was log-transformed to meet model assumptions. Sex was included as a categorical variable, while maternal age (at birth) and individual litter size were scaled and included as continuous covariates. Random factors included maternal identity and the year of theoretical sexual maturity (three years old) of the focal individual. Given that post-dispersal centroids were calculated from a variable number of observations (minimum = 1, maximum = 3207 for one individual having GPS data, median = 29.5), weights were included in the regression using the logarithm of the number of observations plus one. When weights are applied in lmer, they modify the likelihood contribution of each observation in a way that observations with higher variance (less precision) should have less influence on the model, as described in (Bates 2024).

2.6.3 | Age at First Reproduction

The effect of F_{ind} on age at first reproduction for both sexes was assessed using a survival analysis with a Cox Proportional Hazards Model from the survival package (Therneau et al. 2024) in R, which handles censored data. This type of model simultaneously models the probability of an event occurring (the first reproduction of an individual) and the time required for this event to occur. The sex, F_{ind} and the number of potential reproductive partners at sexual maturity were included as fixed covariates, and the year of sexual maturity was included as a random effect.

2.6.4 | Yearly Breeding Success (YBS)

The impact of F_{ind} on YBS was tested using GLMMs (glmTMB package). Sex was included as a binary variable, while age, its quadratic effect and the number of potential reproductive partners were included as continuous covariates. The individual identity and the year were included as random factors.

The relationship between the life-history traits and inbreeding was first tested as a linear effect. If the coefficient of the effect was significantly different from 0 ($\alpha < 0.05$), a model with a quadratic effect was also built. The results of the quadratic model were presented only if the AICc of the quadratic model was better with a threshold of two AICc points (Burnham and Anderson 2002). Statistical decisions for the effects of explanatory variables were based on the p value. The validity of the assumptions of all models used was checked with the R package Dharma (Hartig and Lohse 2022). Collinearity between explanatory variables was checked by calculating Pearson correlations and variance inflation factors (VIFs) with the R package performance (Lüdecke 2025).

2.6.5 | Survival

We used Burnham models (Burnham and Burnham 1993) of CMR to study the impact of inbreeding on survival, as implemented in the Rmark package (Rakhimberdiev 2022). These models allow for the combination of dead recovery and live encounter data into a single analysis. The encounter event was considered a dead recovery when the body of the individual was found or when cubs were missing with their mother while less than one year old. The recapture session occurred during the monitoring season ranging from April to November, and the time step between them was a year.

The Burnham model is based on four parameters: (i) the survival probability (ϕ), which is the probability that an individual survives from one sampling occasion to the next; (ii) the recapture probability (P), which is the probability that a living marked individual present in the sampling area at a given sampling occasion is recaptured or resighted during that occasion; (iii) the recovery probability (r), which is the probability of being found dead and reported conditional on being dead (iv) and the fidelity parameter (Fid), which corresponds to the probability of remaining in the sampling area if alive between two recapture events. We considered that the ϕ, P, r and Fid parameters could potentially vary according to the following variables: time (t); sex (s) and age (a). The effect of t was considered either through discrete years or two groupings: before and after 2008 due to a reorganisation of the monitoring at that time, and before and after 2014 due to the use of dogs for scats detection. As sex was unknown only for some cubs, the sex effect was included only from one year of age and older.

To efficiently test a limited number of hypotheses on survival, we conducted our analysis using a two-step selection procedure (Grosbois et al. 2008). In step one, we tested the effects of t, s and a on ϕ, P, r and Fid to obtain a best, most parsimonious model without inbreeding effects. In the second step, we started with the best model obtained in step one and specifically examined the effect of inbreeding on survival. Inbreeding metrics were implemented as quantitative individual covariates.

In the first step, we started with a complex model: ϕ (s + a) P (t + s + a) r (a) Fid (constant) (model 11 in Appendix 4). We simplified the starting model by first selecting the best parameter structure for Fid, comparing the constant value estimated by the model with Fid fixed to one as all dead recoveries and live encounters were expected to occur in the same sampling area. We then simplified the model for r while keeping the best structure for Fid. Then we simplified the model for P while keeping the best structure for Fid and r. Finally, after adding an effect of t on ϕ, we simplified ϕ while keeping the best structure for Fid, r and P. The effects of sex and age through time were considered only as additive effects due to low sample size per year. All models tested in this step, and details about different age classes grouping are presented in Appendix 4. This step was performed, including all individuals ($N = 156$ individuals).

As a second step, we tested the best model from the previous step, the quadratic and linear effect of F_{ind} and F_{mother} as additive and nonadditive effects on cub survival (< 1 year old) and only the effect of F_{ind} on the survival of the other age class (≥ 1 year old).

Model selection was based on AICc, with a more complex model retained only when $\Delta AICc > 2$.

Prior to model selection, we assessed the goodness of fit (GOF) of the Cormack-Jolly-Seber model on live recaptures only of the data. We performed the four tests (3.SR, 3SM, 2CT, 2CL) of a GOF for the single-state model in the program U-CARE (Choquet et al. 2009). Only the test 3SR (for transience) indicated a significant departure from the assumptions, which was expected as cubs are known to have a lower survival than adults. In addition, the best model obtained at the end of the first step of the model included an age effect on survival. As the overall test in U-CARE, taking into account the age structure ($3SM + 2CT + 2CL$), indicated no deviation from the homogeneity assumption, we did not apply overdispersion correction in subsequent model selection.

2.6.6 | Lifetime Breeding Success (LBS)

To study LBS, censored data were employed due to the long lifespan of the species, leaving many individuals still alive at the time of analysis and therefore leading to incomplete observations. The Bayesian framework implemented in the brms package (Bürkner 2024) in R provided a robust approach to assess the effect of inbreeding on LBS with censored data. LBS was modelled as a censored count using a negative binomial distribution, fitting the best to the data, with F_{ind} as the predictor and maternal identity and birth year as random factors. The model was run with four Markov chains, each consisting of 3000 iterations and a 900-iteration warmup phase, yielding a total of 8400 posterior samples after convergence diagnostics. A noninformative prior (flat prior) was used for the effect of F_{ind}, and the adapt delta control parameter was set to 0.97 to enhance sampling efficiency and convergence. Posterior distributions were analysed to estimate the effects of inbreeding on LBS. We calculated the proportion of the posterior density below zero to estimate the probability that F_{ind} had a negative effect.

2.7 | Lethal Equivalents

We calculated a number of haploid lethal equivalents (B) to estimate the inbreeding load for life-history traits that exhibited evidence of inbreeding depression. Dispersal distance was the only trait not directly related to fitness; therefore, we did not calculate lethal equivalents for this parameter. Following Nietlisbach et al. (2019), we calculated an unbiased estimate of lethal equivalents as the negative slope of a regression of the logarithm of a trait on the inbreeding coefficient. All of our models were GLMs with a log link, which provides an unbiased estimate of inbreeding load, except for CMR models that are based on a logit link. We specifically used the log link on MARK (White and Burnham 1999) on the model including the effects of inbreeding to estimate lethal equivalents. We calculated lethal equivalents with unscaled F_{ind} and F_{mother}.
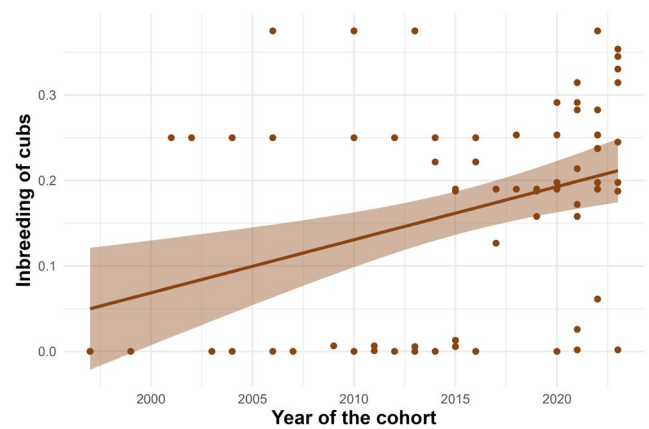

FIGURE 2 | Variation of inbreeding coefficient of cubs as a function of time. Dots represent F_t (the average individual inbreeding coefficient of the litters born in each year). The line represents the linear regression between F_t and year of the cohort. The shaded area represents the 95% confidence interval of the prediction.

3 | Results

Over the 1996–2023 period, the average individual inbreeding coefficient F_t among the Pyrenean brown bear litters ranged from 0 to 0.375 and showed a significant increasing trend over time, with an annual rate of increase estimated at 0.0060 ± 0.0018 (mean $\pm$ SE; p value < 0.001) (Figure 2).

3.1 | Litter Size

Across 66 observed litters in the population, 23 consisted of one cub, 33 had two cubs and 10 included three, resulting in an average litter size of 1.80. The model incorporating a quadratic effect of F_{ind} had a lower AICc than the linear model ($\Delta AICc = 10.80$), and both provided strong evidence of a negative impact of F_{ind} on litter size (Appendices 5 and 6, Table 1) ($p \leq 0.01$). In the quadratic model, low inbreeding values (0–0.15) showed minimal effect on litter size; however, beyond this range, a significant decline was observed (Figure 3A). For instance, a litter with an inbreeding coefficient of 0.15 is expected to average 2.37 cubs, while a coefficient of 0.30 corresponds to an average of 1.56 cubs. The model with an interaction between F_{ind} and F_{mother} brought no evidence of a negative effect of the maternal inbreeding but moderate evidence that the highest F_{mother} is, the stronger the negative impact of F_{ind} ($\beta_{Find:Fmother} = -0.09$, SE $= 0.04$, $p = 0.05$, Appendix 7). Additionally, we found moderate evidence that primiparity was associated with a reduction in litter size; primiparous females had, on average, 26% smaller litters than multiparous females (p value $= 0.02$, Appendices 5–7). Using F_{ind} as a predictor, the linear model estimated the number of lethal equivalents at 0.93 for litter size.

3.2 | Dispersal

Among 51 bears born in the Pyrenees and reaching at least four years of age, the maximum observed dispersal distance was approximately 113 km (recorded in a male), with an average dispersal of 25 km and a standard deviation of 26 km. The weighted

TABLE 1 | Effects of individual (F_{ind}) and maternal (F_{mother}) inbreeding coefficients on life-history parameters.

Life-history traits	F_{ind}						F_{mother}				Statistical model
	B	β	SE	p/ΔAICc/AUC	N	Lethal equivalents	β	SE	p/ΔAICc/AUC	N	
Cub traits											
Litter size	0.93	−0.11	0.04	p=0.01	66	—	4.14×10^{-3}	0.04	p=0.93	66	GLMM with a Conway–Maxwell Poisson (log link)
Cub survival	—	−0.34	0.22	ΔAICc=0.40	132	1.10	−0.39	0.18	ΔAICc=2.66	132	CMR Burnham model with (logit link)
Sub-adult trait											
Distance of natal dispersal	—	−0.26	0.11	p=0.03	51	—	—	—	—	—	LMM with a log transformation of the response variable
Adult traits											
Adult survival	—	0.03	0.18	ΔAICc=−2.00	104	—	—	—	—	—	CMR Burnham model (logit link)
Age at first reproduction	—	0.07	0.17	p=0.68	62	—	—	—	—	—	Cox Proportional Hazards Model (log link)
Yearly breeding success	—	−0.21	0.16	p=0.20	362 bears X years	—	—	—	—	—	GLMM with a negative binomial (log link)
Life time traits											
Lifetime breeding success	16.98	−2.05	1.38	AUC=0.95	149	—	—	—	—	—	Bayesian generalised linear multilevel model with a negative binomial (log link)

Note: B represents the number of haploid lethal equivalents, β the estimated regression coefficient of the predictors, SE the standard error of β, p/ΔAICc/AUC the statistical metrics reported as p: p value, ΔAICc: change in Akaike Information Criterion corrected for small sample size, AUC: area under the curve and N the sample size. Lethal equivalents were measured using nonscaled variables with a log link. F_{ind} and F_{mother} were scaled in all other models.
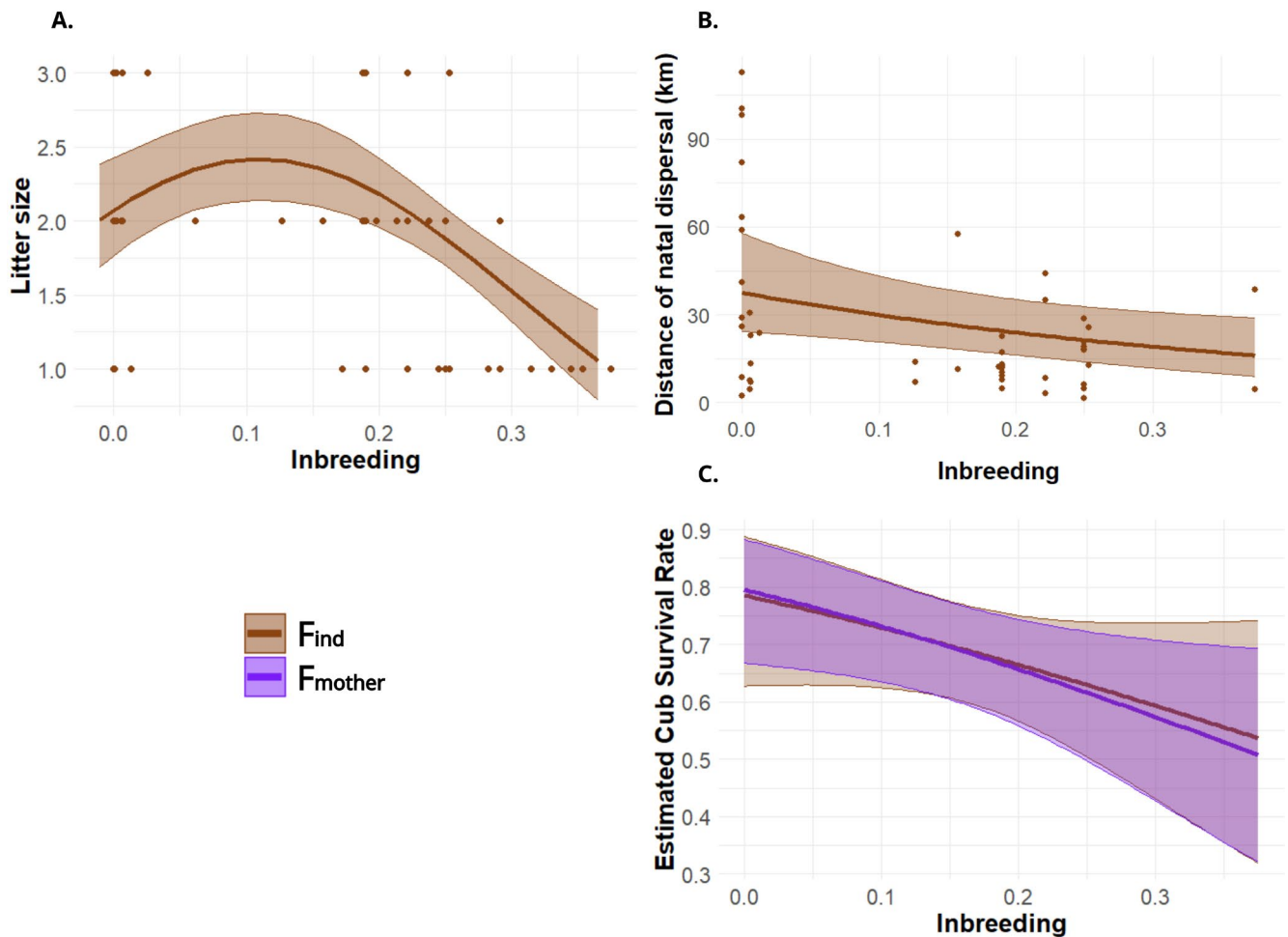
FIGURE 3 | Effects of individual (F_{ind}) and maternal (F_{mother}) inbreeding on litter size (A), natal dispersal distance (B) and cub survival probability (C). The lines indicate the fitted values, shaded areas indicate the 95% confidence interval from the model-averaged estimates and the dots represent observed values. In panel B, the predictions are made for males.

linear inbreeding model and the quadratic model had comparable AICc values (ΔAICc = 1.75). The linear model provided moderate evidence of a negative association between inbreeding and dispersal distance (p value = 0.03) (Table 1, Appendix 8). Specifically, individuals with an inbreeding coefficient of 0.30 were predicted to disperse 51.6% shorter distances than noninbred individuals (Figure 3B). The model without the weights gave similar results. The model also provided strong evidence that males dispersed significantly farther than females—approximately three times as far ($p < 0.001$) (Appendix 8).

3.3 | Age at First Reproduction

Of the 62 bears included in the age at first reproduction analysis, 41 reproduced with an average age at first reproduction of 4.22 years old, a standard deviation of 1.97, the earliest reproduction occurring at two for females and three for males and the latest at 13 years of age. Five died before reproducing (censored), and 14 were still alive without having reproduced as of 2023. No evidence was found to support an effect of individual inbreeding on the rate of achieving reproductive maturity or the age at first reproduction ($p = 0.68$) (Table 1, Appendix 9). However, the model indicated strong evidence that males had a lower

annual probability of reaching reproductive maturity compared to females, leading to a later average age at first reproduction ($p < 0.001$) (Appendix 9).

3.4 | Yearly Breeding Success (YBS)

On average, bears produced 0.64 cubs per year during their breeding years, with a maximum of eight for one male and three for females. There was no evidence to suggest that inbreeding affected YBS ($p = 0.20$) (Table 1, Appendix 10). However, there was a significant positive association between YBS and the local number of potential reproductive partners ($p < 0.001$), age ($p = 0.05$) and a negative one for being a male ($p < 0.01$) (Appendix 10). Notably, there was substantial individual variability in YBS, reflected in the random effect standard deviation of 0.66.

3.5 | Survival Analyses

The best-fitting model resulting from the first step of model selection included: a fixed fidelity of one, a recapture probability depending on sex at 0.87 [95% CI: 0.82, 0.90] for females and 0.93

TABLE 2 | Capture-mark-recapture model selection: Effect of individual (F_{ind}) and maternal (F_{mother}) inbreeding coefficients on survival.

Model	ϕ	npar	ΔAICc	Weight	Deviance
1	a1: F_{mother} + a	7	0	0.28	849.96
2	a1: $(F_{ind} + F_{mother} + F_{ind}: F_{mother})$) + a	9	0.46	0.22	846.32
3	a1: F_{mother} quadratic + a	8	1.05	0.17	848.97
4	a1: F_{ind} + a	7	2.26	0.09	852.23
5	a	6	2.66	0.07	602.55
6	a1: F_{ind} quadratic + a	8	3.82	0.04	851.74
7	a + F_{ind}	7	3.99	0.04	853.95
8	a + F_{ind} + a: F_{ind}	8	4.27	0.03	852.19
9	a2: F_{ind} + a	7	4.66	0.03	854.63
10	a + F_{ind} quadratic	8	5.74	0.02	853.65
11	a + F_{ind} quadratic + a: F_{ind} quadratic	10	7.86	0.01	851.67

Note: The AICc of the best model (model 1) is 864.12. For all the models, P depends on sex, r depends on 2 age classes (cubs < 1 and adults >= 1 year old) and F is fixed to 1. Age class (a) refers to a grouping of two levels according to the age of bears: the cub age class (a1, < 1 year old) and adult age class (a2, >= 1 year old): represents an interaction between two variables.

[0.89, 0.96] for males and age-class-specific variations in both recovery and survival rates (Model 1 in Appendix 4). The age classes retained were cubs under one year old and sub-adults/adults over one year. Results indicated higher recovery rates for cubs under one year (estimated at 0.59 [0.42, 0.73]) compared to older individuals (0.26 [0.14, 0.43]). Survival probabilities were higher for sub-adults/adults (0.95 [0.92, 0.96]) compared to cubs (0.69 [0.60, 0.77]).

In the second step, testing the impact of inbreeding showed moderate evidence of a negative effect of F_{mother} on cub survival. Both the linear and quadratic models incorporating F_{mother} effects had lower ΔAICc values than the reference model (Models 1 and 3 in Table 2), with the linear model being superior (ΔAICc = 2.66, Model 1 vs. reference Model 5 in Table 2). A 0.10 increase in F_{mother} was associated with a 6% reduction in the odds of cub survival, translating to an approximate 9% decrease of survival probability (β F_{mother} = −0.39, SE = 0.18) (Figure 3C). The number of lethal equivalents under the log link model was estimated at 1.10. We observed a weak negative but nonsignificant association between F_{ind} and cub survival (Model 4 in Table 2).

No evidence was found for an inbreeding effect on adult survival (Model 7–11 vs. reference Model 5 in Table 2).

3.6 | Lifetime Breeding Success (LBS)

The Bayesian analysis of LBS in relation to F_{ind} revealed weak evidence of a negative association. The estimated effect of F_{ind} (scaled) was −2.05, equalling 16.29 lethal equivalents with 94.78% of the posterior density laying below 0 for the dataset including the added cubs (Appendices 11 and 12). However, the 95% credible interval for the effect estimate ranged from −5.04 to 0.43 (Appendix 12), reflecting substantial uncertainty about its negative effects. This uncertainty increased using only the raw data (without the added cubs), as the effect estimate was

−2.01 (−16.99 for lethal equivalents), ranging from −5.70 to 1.07, with 90.76% of the posterior density laying below 0 (Appendices 11 and 13).

4 | Discussion

Our study demonstrates clear evidence of inbreeding depression in a wild, threatened population of long-lived mammals, the Pyrenean brown bear. Individual inbreeding coefficients are negatively associated with three life-history traits and with lifetime breeding success.

The most statistically supported negative effect of inbreeding was observed on litter size, which is in line with the idea that inbreeding depression compromises developmental survival and/or first-month survival. The negative impact of inbreeding on litter size has been observed in various animal species (Margulis 1998; Rabon and Waddell 2010; Gooley et al. 2020), notably in brown bears in captivity (Laikre et al. 1996). Our estimate of lethal equivalents for litter size (0.97) is close but lower than the one from Laikre et al. (1996) estimated at 1.60. Inbreeding depression may partially explain the low average litter size (1.80) observed in the Pyrenean population compared to other large populations (i.e., 2.7 for Frković et al. (2001), 2.23 for Hensel et al. (1969) and 2.24 for Sellers and Aumiller (1994)). These values are very close to the values expected in our study population for low inbreeding levels (an average litter size of approximately 2.25 is expected for F_{ind} > 0.15, Figure 3A).

Our analysis suggests that the correlation between inbreeding and litter size is better described by a quadratic model than a linear one, suggesting that inbreeding decreases litter size only for moderate to strong inbreeding. Although this result is consistent with the hypothesis of an accelerated decline in fitness as the number of mutations increases (Willis 1993; Koelewijn 1998; Sharp and Agrawal 2016), the sample size does not allow us to interpret further the shape of this relationship. Another

interesting point is the significant interaction between F_{mother} and F_{ind} showing that maternal and individual inbreeding have more than an additive negative effect. This supports the idea that individual and parental inbreeding should be studied in the same model for species with parental care (Margulis 1998; Hoeck et al. 2015; Bérénos et al. 2016; Huisman et al. 2016).

Our data also show signs of inbreeding depression in later life stages in the Pyrenean brown bear population. Indeed, non-inbred subadults seem to disperse further than inbred ones. Whereas the reduction of inbreeding between close relatives by dispersal has been documented in several species of mammals and birds (Szulkin et al. 2013; Li and Kokko 2019), few studies have reported a negative effect of inbreeding on dispersal distance (but see Szulkin and Sheldon 2008). This negative correlation could be explained by a lower body condition due to inbreeding depression that would impede the dispersal, known to be energetically expensive. The impact of body condition on dispersal pattern, including dispersal distance has been demonstrated by numerous studies (Barbraud et al. 2003; Debeffe et al. 2012; Goossens et al. 2020). These findings challenge the fitness-associated dispersal (FAD) hypothesis by Hadany et al. (2004), assuming that more homozygous individuals, presumed to have lower fitness and being less competitive, are more prone to disperse. This tendency arises due to their limited ability to secure resources or mates or their displacement by more competitive individuals during agonistic interactions (Matthysen 2005; Shafer et al. 2011). However, this hypothesis still lacks empirical evidence (Vanpé et al. 2015); but see (Vanpé et al. 2016) among poor quality individuals using immune gene diversity. Another potential explanation for our results is the heritability of natal dispersal patterns: over few generations, individuals that disperse less are more likely to reproduce with close relatives, resulting in inbred offspring that inherit the tendency for short dispersal distances (Hansson et al. 2003). However, the review by Saastamoinen et al. (2018) indicates that while variation in dispersal can result from additive genetic variation, in many cases, a significant portion of the phenotypic variation is attributed to environmental factors. In addition, cubs born to more inbred females exhibit lower survival rates compared to those of noninbred females. Similar results have been found in other species with maternal care, such as the red deer *Cervus elaphus* (Huisman et al. 2016) and in a mouse species (Margulis 1998) but remain scarce.

These signs of inbreeding depression on subadult/adult stages align with previous studies that have similarly documented the impact of inbreeding depression on various life-history traits, including during adulthood, such as yearly breeding success or adult longevity (Margulis 1998; Szulkin et al. 2007; Huisman et al. 2016; Trask et al. 2021; Rabier et al. 2021). Nevertheless, our results on litter size are consistent with previous studies, which have also shown the impact of stronger inbreeding depression on early life-history traits possibly because individuals that survive to reproduce are fewer and less inbred than juveniles, making it harder to detect inbreeding depression among adults (Charlesworth and Hughes 1996; Keller and Waller 2002; Hoeck et al. 2015; Armstrong et al. 2020). Several studies have shown that genomic methods, being more powerful, could specify these effects and detect new ones in adults that often require more statistical power (Kalinowski and Hedrick 1999; Kardos et al. 2016; Huisman et al. 2016).

Our findings contribute to the growing body of literature emphasising the need to assess the cumulative effects of inbreeding across life stages. Although the confidence interval of the estimate of lifetime breeding success is very large and overlaps zero, its posterior density indicates there is more than a 90% chance that inbreeding has a negative impact on lifetime breeding success. The lethal equivalents estimated for the lifetime breeding success of individuals (B = 16.98) are substantially higher than the ones for individual fitness traits that do not exceed two (Table 1). Similarly, Nietlisbach et al. (2019) reported lethal equivalents estimates for different traits ranging from 0 to 24.6 with a median of 2.3, confirming that weak effects of inbreeding on specific life-history traits accumulate over life stages. Our estimate (B = 16.98) of lethal equivalents appears consistent but on the higher end compared to values reported in other species, such as B = 4.6 for lifetime reproductive success in kangaroo rats (Willoughby et al. 2019) and B = 8.43 from birth to hatchling production in song sparrows (Trask et al. 2021).

However, these estimates of lethal equivalents should be interpreted carefully, as one major limit of our case study is the low depth of the pedigree. The low resolution of pedigree-based inbreeding coefficients has multiple consequences. First, it leads to a compression of estimates toward zero and limits the variance among individuals, with inflated counts of individuals with an inbreeding coefficient of zero or discrete values such as 0.25, and very few in the intermediate range (Kardos et al. 2016). Second, the estimated values of inbreeding coefficients are very likely underestimated. This can lead to an overestimation of lethal equivalents (Nietlisbach et al. 2019). Moreover, if founders are related, inbreeding estimates can be further biased. While we attempted to mitigate this issue by incorporating pairwise relatedness among founders based on microsatellite data, this correction cannot fully compensate for the lack of pedigree depth. However, the relatively low estimated relatedness based on microsatellites suggests that this last bias is limited (i.e., inbreeding may be underestimated overall, but the differences between individuals are broadly unbiased). In addition, the significance of some of the inbreeding effects (on natal dispersal distance and survival of cubs) is weak and would require further evidence. This is primarily due to the relatively small sample size inherent to studying such critically endangered populations, as well as various limitations that obscure the signals of inbreeding depression. Pedigree data do not capture realised inbreeding, making it more difficult to detect inbreeding depression (Kardos et al. 2016; Nietlisbach et al. 2019; Caballero et al. 2021). Limitations also exist in the fitness data. Specifically, in our data, cubs that died very young may not have been detected or genetically sampled and therefore not included in our analyses. Furthermore, even with a dataset covering 27 years, the study of parameters such as age at first reproduction and lifetime breeding success in a long-lived species is necessarily based on censored data, which may result in less precise estimates. Despite these limitations, the evidence of inbreeding depression on multiple life stages in close alignment with theoretical expectations suggests the presence of a high inbreeding load in the Pyrenean brown bear linked to the recent bottleneck of the population.

The implications of our findings extend to both the specific population studied and broader conservation efforts. Like many large carnivore populations (Sillero-Zubiri and Laurenson 2001; Chapron 2014; Carter and Linnell 2016), conflicts with human activities—primarily due to livestock depredation—undermine social acceptance and remain a major barrier to conservation (Woodroffe et al. 2005; Treves and Bruskotter 2014). Additionally, anthropised landscapes reduce connectivity for species often requiring vast ranges (Ripple 2014). For instance, anthropised landscapes have been shown to impede bear movements within their home range across Europe (Hertel et al. 2025), including the Pyrenean population through the effect of roads (Kervellec et al. 2023). In the long term, while recent demographic trends of the Pyrenean brown bear are encouraging, these conditions will probably not allow the population to reach a sufficient size and connectivity to reduce inbreeding. Our data indicate that inbreeding depression affects several demographic parameters, with potentially important consequences for population growth rate and the risk of entering a positive feedback loop between demography and inbreeding (Blomqvist et al. 2010). Also, negative effects of increasing inbreeding could, according to our analyses, reduce dispersal distances and thus accelerate the increase in local inbreeding (Szulkin and Sheldon 2008). Continued monitoring and further analyses, such as population viability analyses, are needed to better understand the impact of inbreeding depression on the long-term viability of the population and to inform adaptive management strategies.

Author Contributions

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Conflicts of Interest Statement

The authors declare no conflicts interest.

Data Availability Statement

The scripts and data are available at this Dryad link: https://doi.org/10.5061/dryad.w9ghx3g1s.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1.**