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Parental Age, Inbreeding and Incubation Method Influence Extremely Low Hatching Success in the Ex-Situ Population of the Extinct in the Wild Sihek

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ABSTRACT

Low reproductive success rates can be a common problem for threatened species, impacting population viability and limiting recovery potential. Reproductive success can also be particularly low in populations that are managed ex-situ. This can pose a challenge for threatened species recovery programmes because high reproductive success rates are often required to provide offspring for wild releases while ensuring population viability. Understanding the underlying causes of low reproductive success rates in ex-situ populations of threatened species is therefore essential so that management programmes can optimise species' recovery potential. Here, we quantify rates of egg viability (i.e., indicating fertility and/or early embryo mortality) and total hatching success in the Extinct in the Wild sihek (Guam kingfisher, *Todiramphus cinnamominus*). Using Bayesian generalised linear mixed models, we investigate effects of parental age, parental inbreeding coefficient (f), egg f and incubation method on egg viability and hatching success of viable eggs. We find that the sihek population has extremely low egg viability rates (~48% ± 2.15%, $N = 304/635$) and total egg-hatching success rates (~30% ± 1.82% SE 190/635) compared to other threatened and non-threatened bird species, both ex-situ and in the wild. We find that increased paternal age and f are key drivers of decreased egg viability. In contrast, increased maternal age and use of artificial incubation are important contributors to decreased egg-hatching success. Our results are particularly pertinent given current active recovery planning for sihek, which may require increased offspring production for wild releases. Furthermore, our results suggest that, in closed ex-situ populations where f inevitably increases across generations such that at a given time point older aged individuals may have lower f, there is a need for breeding recommendations to quantitively and systematically balance genetic considerations with species' biological limitations such as reproductive senescence to meet recovery programme goals.

RESUMO

Takpapa' na chånsa na maolek mañågu un sesso na problema para esta manhassan na klasen gå'ga' siha, ya este siña umafekta i lina'la' mo'na i gurupu yan i chånsa na siña magoggue. Nina'mås takpapa' i chånsan maolek na mañågu para ayu na gurupon gå'ga' mapupulan taigue gi mismo lugåt-ñiha (ex-situ). Ha represesenta este un minappot para prugråmman siha put I fina'maolek i manhassan na klasen gå'ga' siha, sa' takhilo' na chånsa put maolek na mañågu sesso un nisisidåt kosaki guaha neni siha ni' siña masotta. I makomprende-ña håfa muna'taiguiguini este na takpapa' na chånsa put maolek na mañågu para i gurupon gå'ga' ni' manaigue gi mismo lugåt-ñiha gof prisisu kosaki i prugråman minaneha siña ma na'mås båli i chånsan i fina'maolek i gurupu. Guini mågi, in fa'numero i chånsan lina'la' chåda' (put hemplo kao hafañagu pat kao måtai taftaf i figan) yan i todu numeron mapulakes para i Taigue gi Halomtåno' na sihek (Todiramphus cinnamominus). Manu'usa ham "Bayesian generalized linear mixed models" kosaki siña in fanmanaligo put i idåt para i mañaina, "coefficient" put mañaina umaparientes (f), chåda' f yan i maneran "incubation" put i lina'la' chåda' yan i chånsan mapulakes put lå'la'la' na chåda' siha. In sedda' na guaha sen takpapa' na chånsan lina'la' mañåda' para i gurupon sihek (~48% ± 2.15%, N = 304/635) yan i kabåles na chånsa para mapulalakes (~30% ± 1.82% SE 190/635) anggen umakompara yan otro manhassan yan ti manhassan na paluma siha, kontodu ayu taigue gi halomtåno' yan gaige gi halomtåno'. In sedda' na i lumatakhilo' idåt put i mañaina yan f ayu muna'memenggua i chånsan i lina'la' mañåda'. Gi otro bånda, anggen mås åmko' i nana pat anggen mausa ti magåhet na "incubation" este siña umafekta ya muna'menggua i chånsa na maolek mapulakes i chada'. I hiniyong-måmi gof guaguan, ko'lo'lo'ña put i humåhanao ha' na plånu siha put i fina'maolek i sihek, sa' este siña ha nisisita mås neni siha para u masotta gi halomtåno'. Otro fino'-ta, i hiniyong-måmi, ha sugesta na makollat, taigue gi mismo lugåt-ñiha na gurupu nai f siempre para u mås takhilo' gi henerasion siha, gi un manera na gi un momenta i manla'åmko' buente manggaimåstakpapa' na f, guaha nisisdåt para rinekomenda put mamomoksai kosaki siña ma "quantitively" yan "systematically" na'acha'ungak kinonsidera "genetic" yan i chi-ña i klasen paluma put hemplon taiguihi put "reproductive senescence" I lumamemenos na chånsa na mañåñada' un paluma sa' lumå'amko', kosaki siña ha kumple i minalago'-ña i prugråma put i fina'maolek i paluma.

1 | Introduction

Low reproductive success rates are a common challenge in the conservation of threatened species, as they can impact population viability and hinder recovery efforts (Manlik et al. 2016; Marshall et al. 2023; McFarlane et al. 2018; Plard et al. 2020). Furthermore, ex situ-managed populations of threatened species can be associated with lower reproductive success than their wild counterparts (Bussolini et al. 2023; Marshall et al. 2023). Lower reproductive success may potentially impact the fulfilment of the conservation goals of these populations, including their ability to act as insurance against species' extinction and as a source for future releases (Farhadinia et al. 2020; McGowan et al. 2017). As anthropogenic pressures on the natural world increase, ex-situ management of threatened species is becoming increasingly necessary (Conde et al. 2013; Redford et al. 2012). Consequently, there is a pressing need to understand the causes of low reproductive success for threatened and/or ex-situ managed species so that effective mitigation strategies can be designed and species' recovery potential increased.

In birds, a low reproductive success rate can be due to egg-hatching failure, which may be due to failure of ova to be fertilised, or failure of fertilised ova to develop and survive to hatching (Hemmings, West, et al. 2012). Studies of egg-hatching success will ideally identify unfertilized ova through careful microscopic examination (Birkhead et al. 2008). However, these methods often require specialist techniques and equipment, and, because they are relatively recently developed, are not included in historical data of bird populations. Instead, studies often use detection of signs of development within ~1-week post-laying, through candling of eggs or visual inspection of egg contents (Birkhead et al. 2008). In these cases, eggs in which development is not detected encompass both eggs that failed due to infertility and eggs that suffered early embryo mortality (Assersohn, Brekke, et al. 2021; Hemmings, West, et al. 2012).

Hatching failure is more prevalent in threatened than non-threatened bird species, with ~79% of eggs hatching successfully in threatened species, versus ~85% across non-threatened species (Marshall et al. 2023). As threatened species often exist in small, closed populations, and as such are at high risk of inbreeding (Keller and Waller 2002), one potential cause of high hatching failure rates in these species may be inbreeding depression (Briskie and Mackintosh 2004; Crnokrak and Roff 1999; Heber and Briskie 2010; Hoeck et al. 2015), which can manifest as a high rate of embryo mortality in eggs produced from closely related breeding pairs (i.e., pairs with high pairwise kinship coefficient, *K*, equivalent to egg *f*; Assersohn, Marshall, et al. 2021; Crnokrak and Roff 1999; Hemmings, Slate, et al. 2012; Keller and Waller 2002; Wright 1977). The level of inbreeding of each individual parent (i.e., maternal and paternal individual inbreeding coefficients, *f*) can also be associated with decreased hatching success rates (Szulkin et al. 2007). For example, maternal inbreeding has been associated with reduced parental care, such as impaired incubation behaviour (Pooley et al. 2014), while paternal inbreeding has been associated with decreased sperm quality traits and thus increased rates of egg fertilisation failure (de Boer et al. 2018; Hemmings, West, et al. 2012; Opatová et al. 2016; Swinnerton et al. 2004). Identifying whether inbreeding depression is contributing to high hatching failure rates in threatened species is therefore important so that strategies to manage inbreeding levels, including through translocations between populations to increase gene flow (Heber et al. 2013; Miller et al. 2020) or careful management of breeding pairs in ex-situ populations (Foster et al. 2022; Russello and Jensen 2018), can be enacted.

Ex-situ managed threatened species may be particularly susceptible to low reproductive success, both from potential impacts of inbreeding and from breeding management techniques (Farquharson et al. 2018; Marshall et al. 2023). These populations are often founded from small numbers of individuals, representing an additional population bottleneck event, and may have little opportunities for genetic supplementation with wild individuals. Consequently, they are potentially liable to high rates of inbreeding and associated inbreeding depression (Witzenberger and Hochkirch 2011). Additionally, management techniques such as removal of clutches for artificial incubation (AI) are often used in ex-situ breeding programmes, with the aim of increasing the total number of eggs produced in each breeding season by encouraging re-laying (Jones 2004; Marshall et al. 2023; Wood and Collopy 1993). However, the relationship between hatching success and AI varies across species, with some studies finding a major decrease in hatching success when using AI (Burnham 1983; Smith et al. 2011), and others finding it to be a valuable conservation tool (Theule and Rimlinger 2023). Identifying underlying causes of hatching failure is particularly important for ex-situ managed threatened species, where achieving high reproductive success rates may be required to ensure the viability of small populations.

Egg-hatching rates can also be influenced by parental age (Alsobayel and Albadry 2012; Ricklefs et al. 2003). These relationships are expressed in a variety of forms across nature, including increasing (Croxall et al. 1992) or decreasing success with age (Rockwell et al. 1993), or an initial increase followed by a decline with age (Assersohn, Brekke, et al. 2021; Wilcoxen et al. 2011). One reproductive trait that can show a senescent decline is sperm quality, which can lead to decreased egg fertilisation rates with paternal age (Angelier et al. 2007; Rabier et al. 2021). Age effects may be particularly relevant for closed, ex-situ managed populations, where loss of genetic diversity and increases in inbreeding occur through time, meaning older individuals may tend to be more genetically valuable in breeding programmes (Faust et al. 2019; Marshall et al. 2023). Understanding the relationship between age and hatching success in ex-situ managed species is therefore important to identify if trade-offs exist between genetic value and age and therefore inform breeding recommendations.

Quantifying reproductive success rates and identifying factors influencing these rates is particularly important in Extinct in the Wild (EW) species because, by definition, these species are ex-situ managed and highly threatened (Bussolini et al. 2023; Marshall et al. 2023). Additionally, recovery programmes for EW species can require high reproductive success rates to support releases back to the wild while maintaining viable ex-situ insurance populations. One such EW species is the sihek (Guam kingfisher, *Todiramphus cinnamominus*), which is the focus of active recovery planning, including conservation translocations (US Fish and Wildlife 2023). However, recent research indicates that the ex-situ reproductive success rate needs to increase to support harvests for release (Trask et al. 2021).

Here, we quantify egg viability (i.e., eggs showing signs of development at one-week post-laying) and hatching success (i.e., viable eggs that completed incubation and hatched) rates in the sihek and test the effects of parental age, parental *f*, egg *f* and incubation method (parent/artificial) on egg viability and hatching success. Due to evidence of relatively high inbreeding load in the sihek population (Trask et al. 2021) compared to other ex-situ populations (Ryman and Laikre 1991; van Oosterhout et al. 2000) we hypothesised that parental *f* would strongly influence egg viability and hatching success in the sihek. By explicitly considering both egg viability and hatching success, we aimed to identify how different explanatory variables influence different components of reproductive success and therefore inform breeding strategies for sihek and other ex-situ populations of threatened species.

2 | Methods

2.1 | Study System

Sihek are endemic to the island of Guam but became extirpated from the wild in the 1980s after the accidental introduction of brown tree snakes (*Boiga irregularis*; Andersen et al. 2015; Birdlife 2016; Savidge 1987). Twenty nine sihek were brought into human care between 1984 and 1986, with the current population of ~133 birds (86 males, 46 females, 1 unknown sex) descended from only 16 wild-caught founders (10 males, 6 females; Newland and Ferrie 2024). Except for work by Baker (1951), Jenkins (1983) and Marshall (1949), little is known about sihek life history in the wild. However, in the ex-situ population, median age of first-producing hatchlings is age 3 for females and 4 for males, and maximum recorded age of producing hatchlings is 11 and 19 for females and males, respectively. Adult survival probability differs significantly between the sexes, resulting in a mean adult lifespan for females and males of 5.7 ± 0.23 SE and 7.1 ± 0.33 SE years, and maximum recorded lifespans of 15 and 23 years, respectively (Trask et al. 2024). Guidelines for sihek management are provided by the sihek husbandry manual (Bahner et al. 1998). Sihek are highly territorial and socially monogamous (Jenkins 1983), such that breeding pairs are housed in separate enclosures, and thus parentage of eggs is certain. Pairs are ideally housed out of sight and hearing range of each other, although space constraints prevent this in some cases. The sihek population is managed to retain maximal genetic diversity and prevent close inbreeding through careful selection of breeding pairs, by prioritising individuals with low mean kinship (i.e., the mean of the kinship coefficients between that individual and all living individuals in the population), and pairing to avoid producing offspring with high *f* relative to the rest of the population (Ballou and Lacy 1995). Breeding pair recommendations also consider husbandry, welfare and behavioural characteristics of each bird, as well as geographical location.

2.2 | Data Collection

In total, we compiled records of 982 eggs laid between 1985 and 2021 from 13 out of the total 26 institutions that hold or have held sihek. Eggs laid with no male present in the enclosure ($N = 128$) or with unknown development status (due to being broken, abandoned or missing data, $N = 219$) were removed from all analyses. Eggs with wild-caught parents ($N = 77$), and thus unknown parent age, and eggs with unknown lay date ($N = 60$), such that parent age at time of laying could not be determined, were removed from modelling analyses but retained when calculating rates of egg viability and hatching success. Further, four eggs were removed from modelling analyses due to being outliers from the dataset: two due to an extremely high f of 0.25 and two that were the only remaining records from a given institution after eggs that met other removal criteria were removed. Some eggs met multiple removal criteria, leaving a total sample size of 539 from 11 institutions for modelling analysis and 635 eggs from 11 institutions for calculation of egg viability and hatching success rates.

The Association of Zoos and Aquariums (AZA) Regional Guam Kingfisher Studbook (Newland 2022) was used to extract parental data and confirm hatching records provided by zoos. Pedigree data from the studbook were used to calculate each individual's f and each pair's K using PMx v1.6 (Lacy et al. 2012). Within the founding individuals of the ex-situ population, minisatellite DNA profiles have revealed likely full-sibling relationships between two pairs of founders (Haig et al. 1995). These individuals are therefore assigned as full-siblings in the species' studbook, and these relationships are accounted for in subsequent pedigree analyses. All other founders are assumed unrelated in the pedigree, and f of individuals in subsequent generations are relative to the founder population.

2.3 | Data Analysis

We first determined egg viability and hatching success rates. Egg viability rate was quantified as the proportion of eggs showing signs of development ~1 week after laying, as determined by candling following the sihek husbandry manual (Bahner et al. 1998). Hatching success rate was quantified as the proportion of viable eggs that completed incubation and successfully hatched (i.e., excluding eggs that did not survive to hatching for instance due to being broken during incubation or abandoned).

All analyses were conducted using R v4.4.1 (R Core Team 2024). We used Bayesian generalised linear mixed-effects models (GLMMs) in the package *brms* v2.21.0 (Bürkner 2017) to analyse how parent's age and f, egg's f and incubation method influenced egg viability and hatching success. We chose this Bayesian approach over similar frequentist methods because it allows for a greater understanding of the uncertainty of estimated model parameters (van de Schoot et al. 2021).

We coded egg viability and hatching success as binary variables in their respective models: visible egg development > 1 week was scored as '1' and no visible development as '0'; successful hatching was scored a '1' and no hatching a '0'. Parental ages were calculated as the number of years between the parents' hatching date and the egg's lay date. Maternal and paternal ages within our dataset ranged from 1 to 13 years (median = 4, IQR 3–6) and 1–23 years (median = 6, IQR 4–9), respectively. Maternal, paternal and egg f were continuous variables with the following ranges within our dataset: paternal f: 0–0.099 (mean = 0.464), maternal f 0–0.121 (mean = 0.514), egg f 0–0.137 (mean = 0.068). We scaled all continuous variables to have a mean of 0 and a standard deviation of 0.5. We then squared the maternal and paternal ages to create new variables that allowed us to test for both linear and non-linear age relationships.

We used R package *corrr* v0.4.4, (Kuhn et al. 2022) to test for collinearity across variables. This showed that maternal f and egg f were highly correlated ($r = 0.866$). All other variables had a correlation ≤ 0.751. Collinearity was likely due to the closed nature of the sihek ex-situ population, such that average f of individuals inevitably increases with time, with maternal f and egg f likely being particularly highly correlated because adult female sihek have shorter average lifespans than males, and thus shorter generation times (Trask et al. 2021, 2024). We therefore ran separate models containing maternal f and egg f (Table 1), and tested for model similarity using function r2 from package *performance* (Lüdecke et al. 2021). When investigating the effect of AI, we excluded eggs for which the incubation method was unreported or uncertain, and eggs that had been artificially incubated for only a short period of time before being placed back with parents. When investigating the effect of AI on hatching success, we removed eggs laid by females aged one due to small sample size ($N = 6$). Egg viability and hatching success analyses including incubation method had sample sizes of $N = 393$ and $N = 175$, respectively.

When selecting random effects for our mixed models, we followed Bolker et al. (2009). The sihek population has experienced changes in management strategies over time, which may be broadly categorised into four stages (Figure S1, Appendix S1), including periods of rapid increase where managers were actively growing the population, stable population size and managed decrease due to institutional capacity constraints. We therefore included a 'management stage' random effect in models, to account for any potential influences that changes in management strategy may have had on egg viability and hatching success. Management stages were used as opposed to a continuous 'time' variable because collinearity between time and individual's f in the population resulted in model convergence issues and thus unreliable model inference. As multiple eggs were produced by the same parents and from the same conservation breeding institutions, we included each parent's studbook ID and breeding location as random effects in our models, to encompass variation among individuals and locations and account for non-independence between observations (Bolker et al. 2009). As adult birds move between institutions over time, it was not appropriate to nest our random effects. Relationships between random effects and egg viability and hatching success rates can be seen in Figure S2. We ran models with 4 chains and a total of 15,000 iterations, including 7500 warm-up iterations and 7500 sampling iterations. All code is available at https://github.com/M-J-Mitchell/Sihek_Hatching_Success.

Posterior distributions were assessed by interpretation of their 'region of practical equivalence' (ROPE; Makowski, Ben-Shachar, Chen, et al. 2019). The ROPE represents the range of parameter estimates that are equivalent to a null hypothesis. The null can only be confidently rejected if the 95% highest density interval (HDI) falls entirely within the ROPE. Distributions to the left of ROPE indicate a negative relationship and those to the right indicate a positive one. Using the 'describe_posterior' function of package *bayestestR* v0.13.1 (Makowski, Ben-Shachar, and Lüdecke 2019), we calculated the 'probability of direction' (pd), 'practical significance' (ps) and 'percent intersection with ROPE' (PIR) for each effect. Pd measures the proportion of the posterior distribution that is of the same sign as the median

TABLE 1 | Summary of full models used to determine the effects of parental age, parental inbreeding coefficients (*f*), egg's *f* and incubation method ('AI') on egg viability and hatching success.

Model	Expression	Conditional R^2	Marginal R^2	LOOIC
Egg viability models				
1	Egg viability ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + egg *f*	0.412	0.241	537.0
2	Egg viability ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + maternal *f*	0.421	0.217	535.1
3	Egg viability ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + egg *f* + AI	0.482	0.300	364.0
4	Egg viability ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + maternal *f* + AI	0.486	0.284	361.7
Hatching success models				
5	Hatching success ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + egg *f*	0.246	0.194	320.7
6	Hatching success ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + maternal *f*	0.246	0.188	321.4
7	Hatching success ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + egg *f* + AI	0.303	0.280	215.9
8	Hatching success ~ paternal age + maternal age + paternal age^2 + maternal age^2 + paternal *f* + maternal *f* + AI	0.303	0.258	218.3

Note: Conditional R^2 values indicate variation explained by the whole model (i.e., including fixed and random effects). Marginal R^2 values indicate variation explained by the fixed effects only. Leave-One-Out Information Criterion (LOOIC) values evaluate model predictive ability.

and is the probability that the effect of a variable is positive or negative. Ps represents the proportion of the posterior distribution of the median sign outside the ROPE, in this case between −0.18 and 0.18 as recommended for logistic models (Digby et al. 2023; Kruschke and Liddell 2018). PIR represents the proportion of the posterior which overlaps the ROPE (Makowski, Ben-Shachar, Chen, et al. 2019). If PIR = 0%, the null hypothesis can be rejected; if PIR = 100%, the null hypothesis is accepted (Kruschke 2018). Together, these measures allow us to understand the importance of our effects and identify variation in the posterior outcomes, thus allowing us to determine whether our null hypotheses can be rejected.

Using the results of our ROPE analysis, we then created sub-models related to each 'full' model (Table 1) by removing any terms that had > 5% PIR (Table 2). We carried out model selection using cross-validation with the 'loo' function of the *loo* package v2.8.0 (Vehtari et al. 2023) for each full model and its sub-model, before using 'loo_compare' to determine which model was the better fit for our data. 'reloo' was set to 'TRUE' when conducting 'loo' commands to enable the models to refit if problematic observations were found. We used expected log predicted density (ELPD) and Leave-One-Out Information Criterion (LOOIC) to compare our full models to our sub-models and assess predictive ability. ELPD and LOOIC are commonly used model comparison statistics for Bayesian modelling and are analogous to AIC, such that they can appropriately account for different degrees of freedom among competing models (Gelman et al. 2014). All model comparisons between full and sub-models yielded ELPD differences of < 4, indicating the models were of similar predictive ability (McLatchie and Vehtari 2024; Sivula et al. 2023). Thus, we continued using the full models to avoid non-negligible overfitting and bias (McLatchie and Vehtari 2024). Sub-model results can be found in Table S9–S16.

3 | Results

3.1 | Egg Viability and Hatching Success Rates

From our dataset, we found ~48% ± 1.98% SE (304/635) of sihek eggs were viable, while only ~30% ± 1.82% SE (190/635) hatched. When considering only eggs that were viable, ~63% (190/304) hatched.

3.2 | Models of Egg Viability

Our model including egg *f* as an explanatory variable (Model 1, Table 1) found negative relationships between paternal *f* and egg viability (Figure 2a, Table 3, Table S1) and paternal age and egg viability, with more support for paternal age as a non-linear relationship (Figures 1 & 2a, Table 3, Table S1). The effect of maternal age is more uncertain, regardless of whether it is treated linearly or non-linearly (Figure 2a; Table 3, Table S1). We also found a positive relationship between egg *f* and egg viability (Figure 2a, Figure S3, Table 3, Table S1).

Our model including maternal *f* (Model 2, Table 1) found similar relationships between paternal age and egg viability (Figures 1 & 2b, Table 3, Table S2). The posterior distribution of paternal *f* moved to the right, now intersecting the ROPE (Figure 2b,

TABLE 2 | Summary of sub-models created by removing variables with > 5% PIR following the region of practical equivalence (ROPE) analysis of full models (Table 1), as part of our cross-validation model selection procedure.

Sub-model	Expression	Terms removed	ELPD difference from full model	LOOIC value	LOOIC difference from full model
Egg viability sub-models					
1	Egg viability ~ paternal age + paternal age^2 + paternal *f* + egg *f*	maternal age, maternal age^2	0.9	535.1	−1.9
2	Egg viability ~ paternal age + paternal age^2 + paternal *f*	maternal age, maternal age^2, maternal *f*	1.1	533.0	−2.1
3	Egg viability ~ paternal age + paternal age^2 + paternal *f* + egg *f*	maternal age, maternal age^2, AI	2.9	358.2	−5.8
4	Egg viability ~ paternal age + paternal age^2	maternal age, maternal age^2, maternal *f*, AI	3.4	345.9	−15.8
Hatching success sub-models					
5	Hatching success ~ maternal age + paternal age^2 + paternal *f*	maternal age^2, paternal age, egg *f*	2.1	316.5	−4.2
6	Hatching success ~ maternal age + paternal age^2 + paternal *f*	maternal age^2, paternal age, maternal *f*	2.4	316.5	−4.9
7	Hatching success ~ maternal age + maternal age^2 + egg *f* + AI	paternal age, paternal age^2, paternal *f*	2.7	210.5	−5.4
8	Hatching success ~ maternal age + maternal age^2 + paternal age^2 + AI	paternal age, maternal *f*, paternal *f*	2.1	214.1	−4.2

Note: Expected log predicted density (ELPD) and Leave-One-Out Information Criterion (LOOIC) values evaluate model predictive ability and allow for model comparison between sub-models and full models.

Table 3, Table S2). The direction and magnitude of the effect of maternal age and maternal *f* on egg viability cannot be confidently estimated, with the central portion of the HDI crossing the ROPE (Figure 2b, Table 3, Table S2; Kruschke 2018).

Models of egg viability including incubation method gave similar results to models without incubation method included, with a slightly greater indication of a linear effect of paternal age rather than non-linear. Incubation method itself had no effect on egg viability (Table 3, Tables S3 and S4, Figure S4).

3.3 | Models of Egg-Hatching Success

Our hatching success models gave similar results regardless of whether egg's *f* or maternal *f* was included (Models 5 & 6, Table 1). These models indicated some certainty that linear maternal age may be an important factor, although intersecting with ROPE while non-linear maternal age is likely less important (Figure 3a,b; Table 3, Tables S5 and S6). A non-linear effect of paternal age and paternal *f* (Figure 3a; Table 3, Table S5) may also have some importance, although both posterior distributions also intersect ROPE. A linear effect of paternal age, egg's *f* and maternal *f* all presented no certain relationship with hatching success (Figure 3a,b; Table 3, Tables S5 and S6).

Models using our reduced dataset with only egg records including incubation method gave similar results with either egg's *f* or maternal *f* included (Table 1). These models indicated a prominent negative effect of AI on hatching success, with no intersection of ROPE. In our model including egg's *f*, there was a prominent negative linear effect of maternal age on hatching success, which did not intercept ROPE (Figures 3c,d & 4; Table 3, Table S7), although this effect showed less certainty in our model including maternal *f* (Figures 3d & 4; Table 3, Table S8). Maternal age as a non-linear effect also showed a potential positive effect on hatching success, but with a small intersection of ROPE (Figures 3c,d & 4; Table 3, Tables S7 and S8). Our models also indicated a potential effect of paternal age when considered either as a linear or non-linear term, but with some uncertainty (Figure 3c,d; Table 3, Tables S7 and S8). We found no certain effect of either paternal, maternal, or egg's f on hatching success (Figure 3c,d; Table 3, Tables S7–S8).

4 | Discussion

The overall hatching success of eggs in the ex-situ sihek population is extremely low (~30%) in comparison to bird species generally (~83%) and other similarly threatened and ex-situ bird populations (~79%; Marshall et al. 2023). Egg viability rate

TABLE 3 | Model comparison table showing posterior statistics of each variable in models 1–8.

	Paternal age			Paternal age^2			Maternal age			Maternal age^2			Paternal *f*			Egg *f*			Maternal *f*			AI		
Model	PIR (%)	Ps	Pd (%)	PIR (%)	Ps	Pd (%)	PIR (%)	Ps (%)	Pd (%)	PIR (%)	Ps	Pd (%)	PIR (%)	Ps	Pd (%)	PIR (%)	Ps	Pd (%)	PIR (%)	Ps	Pd (%)	PIR (%)	Ps	Pd (%)
Egg viability models																								
1	0.02	0.97	98.4	**0**	**1.00**	**99.9**	23.4	0.53	64.8	13.9	0.75	82.0	**0**	**0.99**	**99.3**	**0**	**0.98**	**98.9**						
2	0.45	0.97	98.0	**0**	**1.00**	**99.8**	21.6	0.53	63.9	15.4	0.69	77.4	3.67	0.92	94.1				11.7	0.66	72.2			
3	**0**	**0.99**	**99.4**	**0**	**0.99**	**98.9**	18.2	0.53	61.4	11.3	0.59	64.5	1.93	0.94	95.5	1.67	0.95	95.3				27.1	0.48	61.5
4	**0**	**0.99**	**99.2**	0.007	0.97	98.0	16.3	0.60	68.1	11.4	0.48	53.4	5.76	0.79	82.3				7.22	0.73	76.3	26.3	0.49	62.3
Hatching success models																								
5	17.2	0.59	67.7	4.72	0.85	87.7	2.18	0.95	97.7	12.3	0.74	80.7	3.66	0.94	95.8	12.1	0.68	74.4						
6	15.8	0.62	69.7	3.34	0.90	92.1	1.77	0.96	97.8	10.4	0.80	85.4	2.18	0.95	97.1				15.1	0.66	73.8			
7	5.19	0.80	90.8	5.01	0.79	81.4	**0**	**0.98**	**98.7**	0.96	0.97	97.3	9.89	0.63	67.5	2.68	0.94	95.1				**0**	**0.99**	**99.7**
8	7.05	0.82	86.0	2.98	0.89	90.9	1.15	0.96	97.7	1.21	0.96	97.1	10.3	0.66	70.9				12.8	0.65	71.3	**0**	**1.00**	**99.9**

Note: PIR represents the percentage of the posterior distribution outside of the ROPE (Region of Practical Equivalence). Ps (probability of significance) represents the proportion of the posterior distribution of the median sign outside the ROPE. Pd (probability of direction) measures the proportion of the posterior distribution that is of the same sign as the median and is the probability that the effect of a variable is positive or negative. Bold text indicates effects with higher certainty due to the full posterior distribution falling outside of the ROPE.

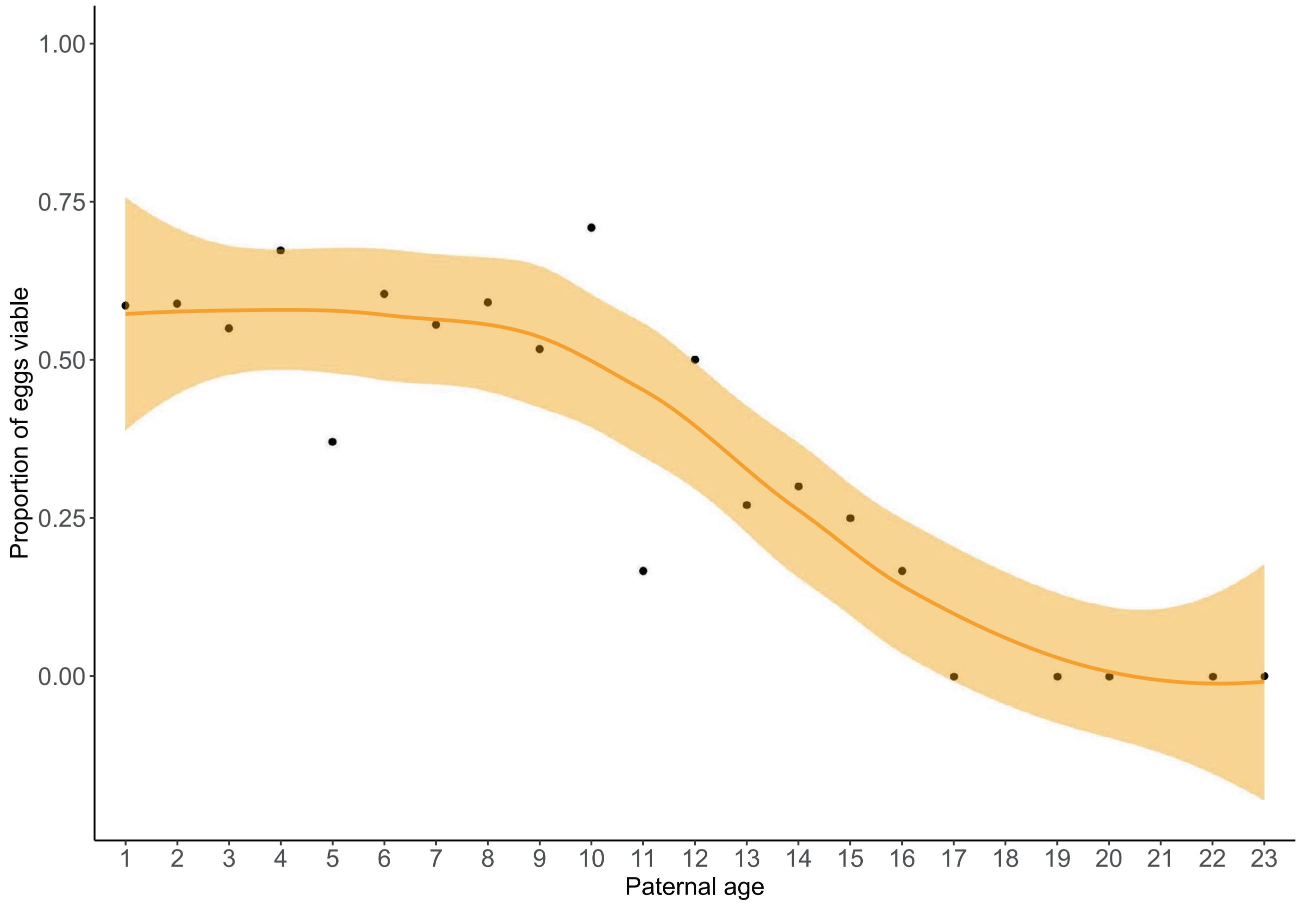

FIGURE 1 | The relationship between paternal age (x) and proportion of viable eggs per age class (y) in the full modelling dataset of 539 eggs. Each point represents the mean proportion of viable eggs produced in pairs with males aged between 1 years and 23 years. The line of best fit is calculated using a Locally Estimated Scatterplot Smoothing approach, with the shading representing 95% confidence intervals. The proportion of viable eggs produced from pairs with males of 8 years of age onwards decreases, with pairs containing males over the age of 17 not producing any viable eggs.

in sihek (~48%) is also lower than reported from other highly threatened species (e.g., ~64% in kakapo, *Strigops habroptilus*, and ~70%–80% in takahe, *Porphyrio hochstetteri*, Clout and Craig 1995), where reported egg 'infertility' is likely to reflect both infertility and early embryo mortality as in this study. These extremely low egg viability and hatching success rates limit sihek recovery potential and are particularly pertinent given the planned releases of sihek back to the wild, which may require increased production of hatchlings.

We find that paternal age has important influences on egg viability in sihek, with paternal age having little effect up to ~8 years of age, but with a sharp decrease in egg viability at older ages (Figure 1). In contrast, we detected little effect of maternal age on egg viability, potentially due to the differences in lifespan between the sexes in this population (Trask et al. 2024), such that females may die before effects of maternal age on egg viability can manifest (Figure 2). Decreased viability of eggs sired by older aged males could be due to a decreased ability to fertilise ova (Langen et al. 2017; Lifjeld et al. 2022; Lockyear et al. 2016; Pei et al. 2020; Rabier et al. 2021), potentially associated with decreases in sperm quality traits with age (Angelier et al. 2007; Rabier et al. 2021). Additionally, reduced sperm quality with age may result in increased early embryo mortality, as degraded DNA in the sperm head also impedes early embryo development (Sharma et al. 2015). Our results therefore indicate that paternal age could be an important factor that should be systematically included in breeding recommendations for sihek, as well as across other threatened species managed ex-situ.

We also find that the likelihood of egg viability decreases with increased paternal *f*, while maternal *f* has little effect. Increased paternal *f* could be associated with a decreased ability to fertilise ova in more inbred males, resulting in infertile eggs. Increased paternal *f* has been associated with a decreased fertility across numerous taxa due to mechanisms including a higher proportion of abnormal spermatozoa, lower sperm number, reduced sperm motility and reduced acrosome integrity (Huffmeyer et al. 2022; Langen et al. 2017; Lockyear et al. 2016; Opatová et al. 2016; Woodard et al. 1982; for review see Roldan and Gomendio 2009). Increased parental *f* may also lead to an increased rate of early embryo mortality if related to impaired parental incubation behaviour. This has been observed in zebra finch (*Taeniopygia guttata*, Pooley et al. 2014) in association with maternal *f*; as both sexes share incubation duties in sihek, paternal *f* effects on incubation could also potentially exist. These results support the importance of genetic considerations in breeding pair recommendations. However, in closed populations where *f* inevitably increases through time (Hedrick and Kalinowski 2000), at any given time point, older individuals are

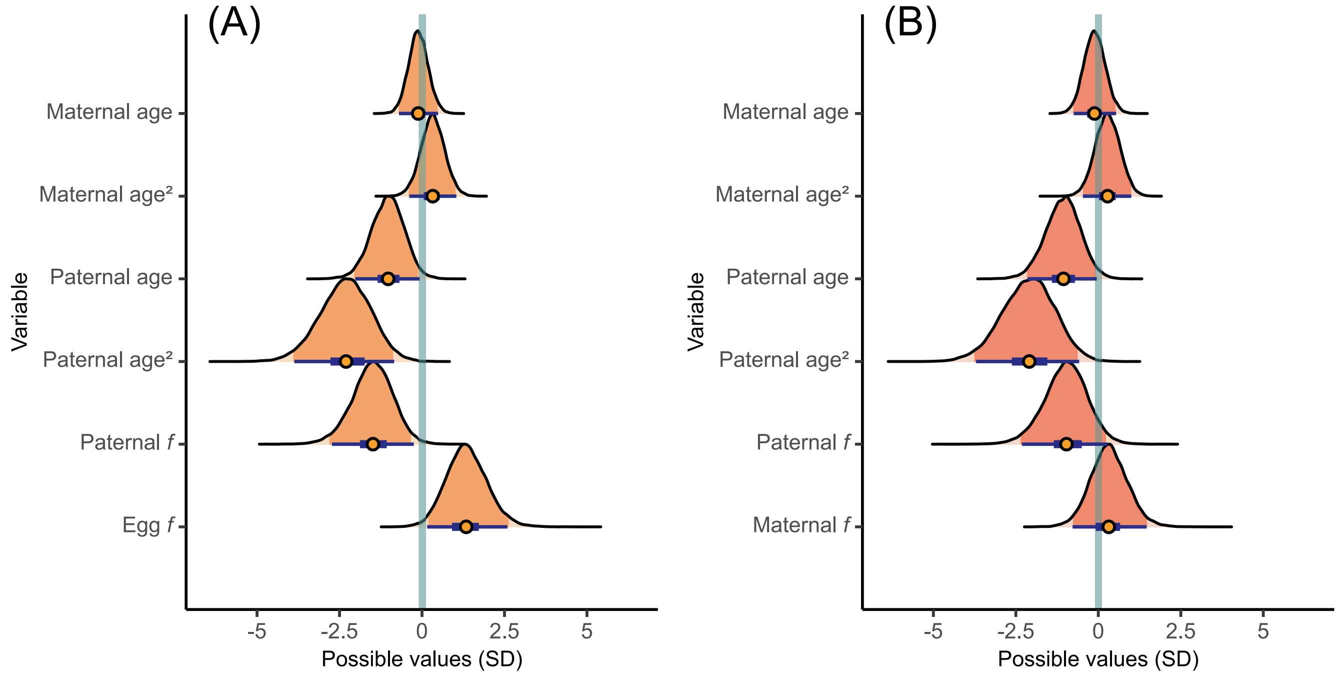

FIGURE 2 | Posterior distribution plots for egg viability models run (Models 1–2; $N = 539$, conditional R^2 0.412 and 0.421 respectively). (A) Model 1 includes both parental ages, paternal inbreeding coefficient (*f*) and egg *f*. (B) Model 2 includes both parental ages, paternal *f* and maternal *f*. The region of practical equivalence (ROPE, vertical stripe) represents the range of parameter estimates that are equivalent to the null hypothesis (no association between the variable and egg viability). The null can only be confidently rejected if the 95% highest density interval (HDI, the more darkly shaped central region of each distribution) falls entirely within the ROPE. Distributions to the left of ROPE indicate a negative relationship and those to the right indicate a positive one. Orange circles indicate posterior means and narrow and wide blue lines represent 50th and 95th percentiles, respectively.

likely to have lower *f* compared to younger individuals. With our results also suggesting decreasing egg viability with paternal age, breeding recommendations may need to trade off paternal age with *f*.

In contrast to expectation, we find that egg *f* (i.e., pair's *K*) may be positively associated with egg viability, although to a lesser degree when incubation method is considered (Figure 2, Figure S3–S4A). Increased egg *f* is expected to be associated with a decreased viability, due to the expression of large-effect lethal mutations in early development causing embryo mortality in more inbred eggs (Assersohn, Marshall, et al. 2021; Brown et al. 2019; Pei et al. 2020). Our positive relationship between egg *f* and viability could potentially be reflective of improvements in sihek husbandry techniques over time in the breeding programme, if increases in egg *f* over time are correlated with improvements in egg or breeding pair husbandry. By using a 'management stage' random effect (Figure S1), we attempted to control for broad-scale changes in management strategies that may influence egg viability, but this may not have captured finer-scale improvements in husbandry techniques through time.

In contrast to egg viability, maternal age and incubation method were important predictors of hatching success, with hatching success decreasing with increasing maternal age, potentially with a small increase at around 6 years of age. A similar general decrease in hatching success with maternal age has been observed in other birds (e.g., Catry et al. 2006; Morland et al. 2023; Rockwell et al. 1993). Further, the effect of maternal age on hatching success could be underestimated in our study, due to the higher mortality rates of adult females than males in the sihek population (Trask et al. 2024), thus potentially reducing statistical power to detect an effect of female age on hatching success.

Across our models, we were unable to determine the strength or direction of maternal *f* or egg *f* effects on hatching success. However, when including incubation method, there was a potential negative relationship between egg *f* and hatching success, potentially suggesting the expression of lethal alleles in more inbred embryos, as has been observed across birds (e.g., Hemmings, West, et al. 2012; Sittmann et al. 1966). The lack of certainty in our results regarding the effect of maternal *f* contrasts with previous findings of significant inbreeding depression in female sihek reproductive success (Trask et al. 2021), though in that study reproductive success was defined as hatchling production within a pair (i.e., encompassing number of eggs laid and number hatched) rather than the hatching success of each egg. Together, these results could suggest that maternal inbreeding depression may be acting more strongly on the number of eggs females produce rather than egg hatchability, although further data would be required to ascertain this. We found low certainty in any potential effects of our paternal variables on hatching success, indicating that further study may be required to determine if paternal age or *f* can affect egg hatchability.

Viable eggs that were artificially incubated had lower hatching success than parent-incubated eggs in concordance with that observed across other ex-situ managed bird species (Assersohn, Marshall, et al. 2021; Cook et al. 2005; Deeming 2002; Marshall

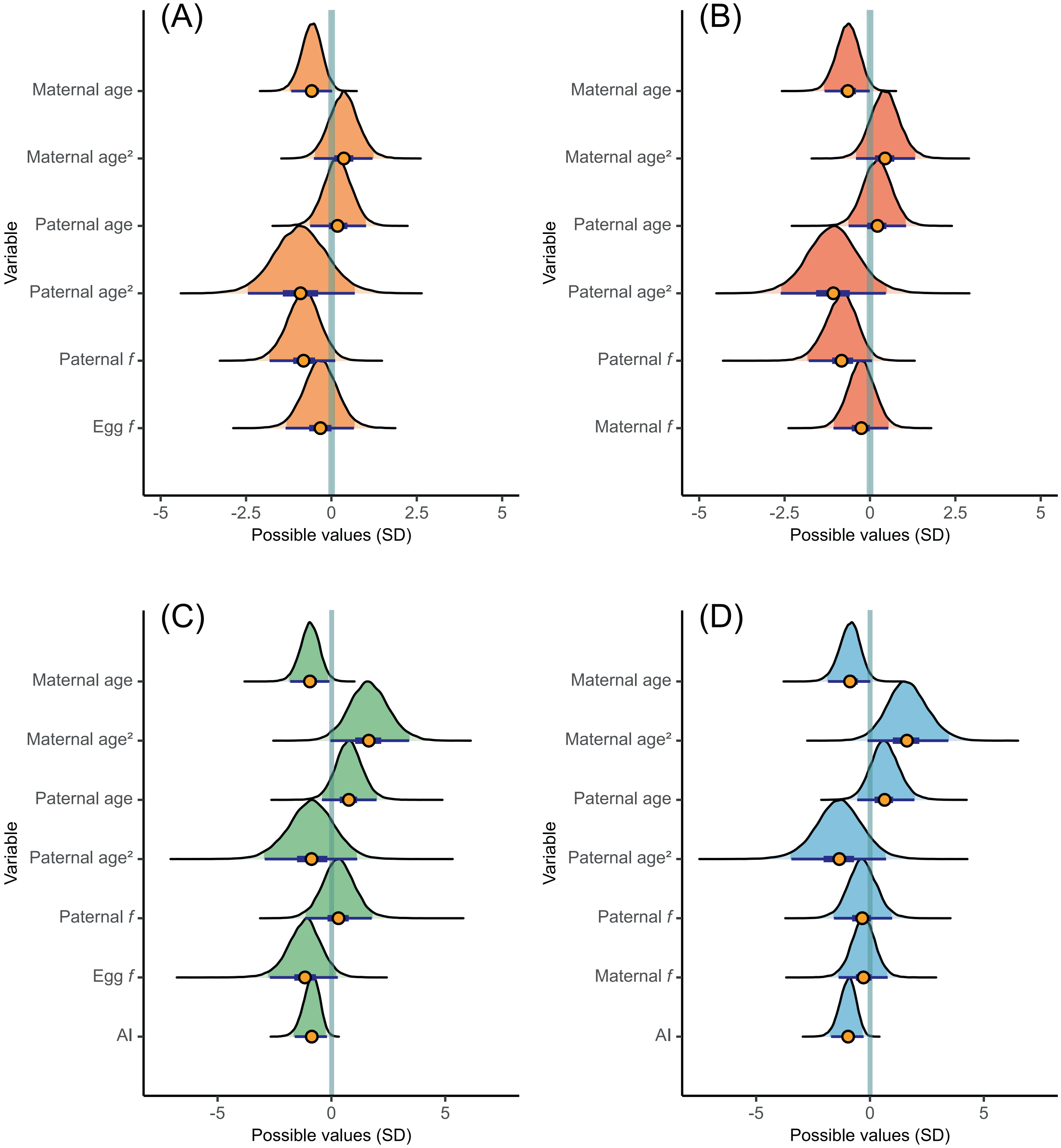

FIGURE 3 | Posterior distribution plots for all hatching success models run (Models 5–6; $N = 261$, conditional R^2 0.246 and 0.246 respectively, Models 7–8, $N = 175$, conditional R^2 0.303 and 0.303 respectively). (A) Model 5 includes both parental ages, paternal inbreeding coefficient (f) and egg f. (B) Model 6 includes both parental ages, paternal f and maternal f. (C) Model 7 includes both parental ages, paternal f, egg f and incubation method. (D) Model 8 includes both parental ages, paternal f, maternal f and incubation method. The region of practical equivalence (ROPE, vertical stripe) represents the range of parameter estimates that are equivalent to the null hypothesis (no association between the variable and hatching success). The null can only be confidently rejected if the 95% highest density interval (HDI, the more darkly shaped central region of each distribution) falls entirely within the ROPE. Distributions to the left of ROPE indicate a negative relationship and those to the right indicate a positive one. Orange circles indicate posterior means and narrow and wide blue lines represent 50th and 95th percentiles respectively.

et al. 2023). AI is often used to try to increase the total number of eggs, and thus hatchlings, produced by a pair, as removing eggs and artificially incubating them can encourage re-laying (Marshall et al. 2023). However, our results suggest AI could have limited efficacy in sihek, as any eggs that are artificially incubated often fail to hatch. In addition, high egg production rates have been linked to reproductive diseases in female birds (Abou-Zahr 2022; Rosen 2012) and reproductive disease is a

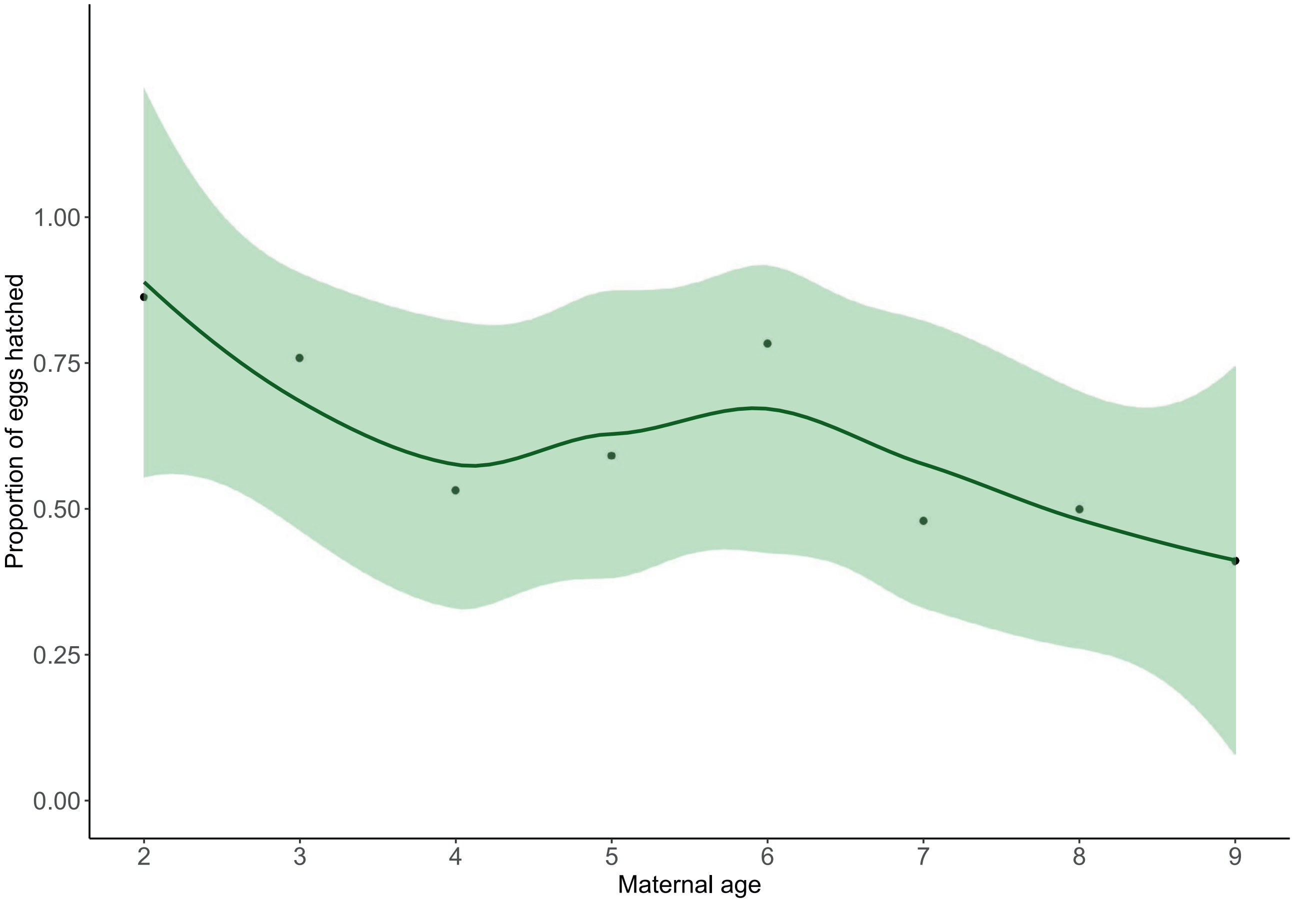

FIGURE 4 | The relationship between maternal age (x) and proportion of viable eggs that successfully hatched per age class (y) in the reduced incubation method dataset of 175 eggs. Each point represents the average proportion of eggs hatched across females at ages between 2 and 9 years. The line of best fit is calculated using a Locally Estimated Scatterplot Smoothing approach, with the shading representing 95% confidence intervals. Hatching success generally decreases with maternal age, with a slight increase at 6 years.

known cause of mortality in female sihek (Trask et al. 2024). These results suggest that allowing parents to incubate eggs where possible may aid improvements in hatching success rates, thus decreasing the total number of eggs that females are required to produce.

Overall, our results reveal extremely low egg viability and hatching success rates in the EW sihek compared to other endangered species and Coraciiformes (Ali et al. 2010; Clout and Craig 1995; Koenig 1982; Marshall et al. 2023; Naher et al. 2021; Palkar 2016). We find that increased paternal age and *f* drive low egg viability rates, while maternal age and incubation method influence hatching success of viable eggs. Ex-situ threatened species management programmes often use software such as PMx (Ballou et al. 2023) to quantitatively assess genetic suitability of different breeding pairs, to retain population genetic diversity and reduce inbreeding (Ballou et al. 1995). Our results suggest a need for a similar systematic framework that can quantitatively incorporate age considerations and balance these against genetic considerations to form holistic breeding management recommendations. This may be particularly important for EW species, as well as other highly threatened species, where high reproductive success rates may be required to ensure population viability and to provide offspring for releases to the wild. Furthermore, as the need for intensive conservation management strategies such as ex-situ breeding programmes is likely to increase into the future (Conde et al. 2013), identifying potential biological limitations to reproductive success, such as species-specific patterns of reproductive senescence, and how these may trade off with genetic considerations, is likely to become increasingly important to species recovery programmes.

Author Contributions

A.E.T. and J.G.E.: conceptualisation. A.E.T. and M.J.M.: data collection and curation. M.J.M., R.N.F., A.E.T.: data analysis. M.J.M.: writing – original draft. M.J.M., R.N.F., J.G.E., G.M.F., E.R., S.M., S.N. and A.E.T.: writing – review and editing.

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Data Availability Statement

All data and code are available at https://github.com/M-J Mitchell/Sihek_Hatching_Success.

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Supporting Information

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