Evaluate and simulate the reproduction and survival of a reintroduced population in an endangered bird species Crested ibis (*Nipponia nippon*)

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Keywords: Population monitoring; Mortality rate; Reproductive success; Matrix population model; Reintroduction; Crested ibis (*Nipponia nippon*); Endangered species

Abstract

1. Reintroduction programs are critical for restoring endangered species, yet their success hinges on a detailed understanding of stage-specific demographic rates and the factors limiting population growth. The scientific evaluation of reintroduction programs, particularly assessments and management recommendations informed by full life-cycle monitoring, remains limited. The Crested ibis (*Nipponia nippon*), once nearly extinct, has been the focus of intensive conservation efforts, including reintroduction into its historical range. Here, we systematically evaluate the success of a Crested ibis reintroduction population by integrating long-term field monitoring with population dynamic modeling.

2. We conducted a systematic, multi-year (2023-2025) demographic study of a reintroduced Crested ibis population in Dongzhai National Nature Reserve, China. From 2013 to 2023, a total of 133 captive Crested ibises were released in seven batches within the nature reserve. By 2025, the number of the wild population had exceeded 500. Based on the combination of field monitoring (n = 176 pairs) and GPS telemetry (n = 74 GPS tags, the longest living time lasting 4 years), we quantified reproductive output and mortality rates across six life stages: nest building, incubation, offspring provisioning, fledgling (< 1 year), subadult (1-2 years), and adult (> 2 years).

3. The results show that the average clutch size of this population is 3.24 &[plusmn] 0.08, and each pair of parent birds can rear 1.31 &[plusmn] 0.12 nestlings to fledging each year. And we found that high mortality during the incubation (32.5%, n = 425 eggs), offspring provisioning (34.1%, n = 287 chicks), and fledgling stages (38.6%, n = 63 birds). Key causes included unfertilized eggs, predation, food shortage, and human disturbance. While in the nest building (9.1%, n = 176 pairs), subadult (9.8%, n = 28 birds) and adult stage (21.3%, n = 15 birds), the mortality rate was relatively low. Stage-structured matrix model showed a positive population growth of this reintroduced population (growth rate λ = 1.053), with the population expected to increase 13-fold over 50 years (6858 individuals). Sensitivity analysis indicated that adult survival had the strongest influence on population growth. Correspondingly, we predict that by

2075, its distribution range will expand 13-fold in tandem with population growth, exceeding 51,000 square kilometers and covering several surrounding cities.

4. Our full life-cycle monitoring, evaluation and simulation confirms this reintroduced population is a successful establishment and a self-sustaining population. This addressed research discrepancy of scientific and systematic assessment of population reintroduction in endangered species. Moreover, we proposed key conservation practices and targeted strategies for improving population growth and maintenance: predator control, supplemental feeding, rescue of weak chicks, reducing human disturbance via public engagement, and implementing genetic management to avoid inbreeding. Our framework provides a practical model of enhancing reintroduction success and species recovery for other endangered species.

Keywords: Population monitoring; Mortality rate; Reproductive success; Matrix population model; Reintroduction; Crested ibis (*Nipponia nippon*); Endangered species

1. Introduction

Global biodiversity is facing unprecedented threats from climate change, habitat loss, and human disturbance (Krauss et al., 2010; Urban, 2015; Pyšek et al., 2020). According to the IUCN, more than 48,600 species are currently at risk of extinction, representing approximately 28% of all assessed species. Effective conservation actions are urgently needed to slow down or reverse this declining trend. Currently, multiple conservation programs at various levels are initiated. Among these ambitious conservation initiatives, species-oriented conservation, particularly for rare and endangered species, is of great significance (IUCN 2025). This is because the necessity and significance of protecting such species lie not only in their critically endangered status, which calls for immediate attention and protection, but also in their ecological and symbolic roles. Importantly, these species often function as flagship or umbrella species, promoting the broader protection of biodiversity and habitats within their ecosystems (Zacharias & Roff, 2001; Qian et al., 2020; Lambeck et al., 1997). In this aspect, drawing lessons from well-known and typical successful species-oriented examples is essential and insightful for improving conservation efficiency and providing valuable experience and guidance for the conservation of other endangered species.

For endangered species that experienced a serious bottleneck with a small population, reintroduction is an intentional movement and release of a species into its historical range from which it has disappeared, with the goal of establishing a self-sustaining wild population (IUCN/SSC 2013). Reintroduction is an important and necessary step in restoring the historical distribution of species. As an important component of modern wildlife conservation, reintroduction complements in-situ conservation efforts by facilitating the recovery of species that have been extirpated or severely depleted in the wild (Armstrong & Seddon, 2008). Well-documented successes illustrate that reintroduction can be effective when combined with habitat management, predator/poaching control, and long-term monitoring. The successful rescue of the Arabian oryx (*Oryx leucoryx*) exemplifies the power of coordinated conservation. After being declared extinct in the wild in 1972, a captive-breeding and reintroduction program, initiated in the 1980s and supported by habitat restoration and anti-poaching measures, has enabled its wild population to exceed 1,000 individuals. Its recovery has not only led to its downlisting in IUCN but, as a flagship species, has also spurred the recovery of associated desert flora and fauna (Spalton et al., 1999; Mallon et al., 2023). Similarly, the recovery of the black-footed ferret (*Mustela nigripes*) underscores the necessity of holistic habitat management. This species is near extinction due to sylvatic plague and its impacts on its prairie dog (*Cynomys spp*.) prey base; its recovery relied on vaccinating against plague, restoring prairie dog towns, and using pre-release conditioning. The subsequent growth of the wild population to over 300 demonstrates the efficacy of restoring predator populations by first securing their prey base (Biggins et al., 2011; Salkeld, 2017). In contrast, the reintroduction of the California condor (*Gymnogyps californianus*) faced a critical challenge. Although a captive-breeding and release program increased the population from 22 individuals in 1985 to nearly 400 by 2010, with approximately half free-flying (Walters et al., 2010), this numerical success masks a deeper vulnerability. The species' persistence remains entirely dependent on intensive, ongoing management, as lead poisoning continues to pose a severe threat. Without a decisive reduction in lead exposure, the condor remains highly likely to face re-extinction in the wild (Finkelstein et al., 2012). The abovementioned cases collectively affirm the significance of reintroduction as a necessary step in restoring the historical distribution of species. Furthermore, identifying and

mitigating the core ecological and anthropogenic threats is fundamental to achieving sustainable reintroduction outcomes and ensuring the long-term viability of restored species.

The Crested ibis is a medium-sized wading bird with red facial skin and legs, and predominantly white plumage with cinnamon tones on the tail, abdomen, and flight feathers. It was historically widespread across Northeast Asia, including China, Korea, Japan, and eastern Russia (BirdLife-International, 2001). However, its population declined sharply during the 20th century due to habitat destruction and increasing human activity (e.g., illegal hunting and overuse of fertilizers and pesticides) (Ding, 2004). It was once thought to have gone extinct in the 1960s; thus, it was listed as an endangered species (Anderson, 1984; IUCN, 2025). Fortunately, a remnant wild population consisting of seven individuals—including two breeding pairs and three offspring from one of the pairs—was rediscovered in Yangxian County, Shaanxi Province, China (Liu, 1981). Since then, tremendous efforts have been made to protect this rare and endangered species. Today, the global population of the Crested ibis is estimated at over 10,000 individuals (Zheng et al., 2025). In China, apart from other counties in Shaanxi Province, the Crested ibis has also been reintroduced to several parts of its historical range, including Dongzhai in Henan Province (Cai et al., 2024), Deqing in Zhejiang Province (Qiu et al., 2023), and Beidaihe in Hebei Province (Xie et al., 2020), where wild releases have also been carried out. In addition, South Korea (Lee et al., 2024) and Japan (Mochizuki et al., 2015) have both established populations through the introduction of breeding stock from China. The recovery of the Crested ibis has been achieved through decades of persistent efforts in situ conservation and reintroduction programs. Learning from successful experiences and summarizing practical approaches from this case can enhance conservation efficiency and provide valuable references for other endangered species. To date, studies have been conducted on the Crested ibis covering aspects such as morphology and physiology (Sun et al., 2019), reproductive ecology (Ye et al., 2017), captive breeding (Okahisa et al., 2022), habitat evaluation (Li et al., 2002), and genomic characteristics (Feng et al., 2019). Given that reintroduction plays a significant role in the conservation and recovery of this species, research focusing on reintroduction populations, especially details on the process of successful establishment since reintroduction, is both theoretically and practically essential. Previous research on this species regarding its population size and distributional changes has been limited to its founder population (Wang et al., 2017; Wang et

al., 2021). In contrast, studies addressing reproduction and survival, especially detailed reproductive success and mortality monitoring from the start of breeding (egg stage) to independent sexual maturity in adults, as well as the corresponding practical conservation measures in both original and reintroduced wild populations, remain scarce. Nevertheless, such information is crucial for implementing more targeted conservation measures and evaluating the long-term viability of this species.

In this study, we comprehensively assessed the survival and population viability of a reintroduced population of Crested ibis. Specifically, we used field monitoring data collected over three consecutive years and GPS tracking data spanning five years. We first investigated the rates of reproductive failure, stage-dependent mortality (i.e., the rates during nest building stage, egg incubation stage, offspring provision stage, fledgling stage (< 1 year), sub-adult stage (1-2 years), adult stage (> 2 years)), and their main causing reasons. We then suggested concrete conservation practices at each stage to increase the breeding or survival success of this species. Second, based on those reproductive parameters and mortality rates, we simulated the population dynamics over the next 50 years to determine whether a self-sustaining population was established. Finally, we predict the distribution range of this reintroduced population in the future. The findings of this study will provide an important basis for evaluating the effectiveness of reintroduction efforts, which could serve as a reference for the conservation of other reintroduced populations of this species and other endangered species.

2. Method

2.1 Study species and the study site

The Crested ibis is a long-lived monogamous bird species. It typically reaches sexual maturity at 2-4 years of age, with the maximum reproductive age up to 15 years (Yu et al., 2007). The breeding season usually lasts from late February to late June. Nest building, incubation, and chick-rearing are jointly undertaken by both parents (Zhai et al., 2001). They usually build nests in tall arbors such as Masson pine (*Pinus massoniana*) and Chinese wingnuts(*Pterocarya stenoptera*). The average height of the nest-building trees is 16.1 meters, and the height of the nest is 12.6 meters (Zhu et al., 2023).

Crested ibises generally lay one clutch per year, with each clutch containing 2-4 eggs (Shi et al., 1999). The incubation period is approximately 28 days, and the chick-rearing period typically ranges from 40 to 45 days. After fledging, juvenile birds continue to follow their parents for a period to learn survival skills, such as foraging (Ding, 2004).

Dongzhai National Nature Reserve (31°58' N, 114°17' E) is located at the northern foothills of the Dabie Mountains, straddling the border of Henan and Hubei provinces within Luoshan County, Henan Province. The reserve (46,800 hectares) is primarily designated to protect rare forest-dwelling avian species and their associated habitats (Zhu et al., 2023). This nature reserve, with a transitional zone between the northern subtropics and the warm-temperate region, is characterized by a warm, humid climate and well-preserved forest ecosystems and farm landscapes (rice paddies, which are essential for the Crested ibis). It was once a historical distribution area of the Crested ibis (Liu et al., 2008). As one of the pioneering sites for Crested ibis reintroduction, 17 Crested ibises were introduced to Dongzhai National Nature Reserve in 2007, initiating the captive breeding program. Wild release efforts commenced in 2013, and by the last release event in 2023, a total of 133 individuals had been released into the wild across seven separate cohorts (Huang et al., 2024). The extensive forest cover, combined with paddy wetlands within the reserve, provides ideal habitat conditions for wild Crested ibis populations. This population has been continuously increasing. It is estimated that the wild population has exceeded 500. From 2023 to 2025, we continuously monitored the Crested ibis in the Dongzhai Nature Reserve and surrounding distribution areas, covering approximately 73,000 hectares.

2.2 Reproductive monitoring

Regular monitoring of breeding began since the first cohort of birds was released, including some newborn individuals equipped with satellite transmitters started in 2021 (n = 12). However, systematic and intensive monitoring has been carried out since 2023. From February to June (breeding season) each year between 2023 and 2025, continuous observations and recordings were made on all breeding attempts of paired Crested ibises identified in the study area. Monitored parameters included nest site location, egg-laying date, clutch size, number of hatched eggs, and

number of fledged chicks. Routine nest checks were performed at intervals of 1–3 days to confirm the survival status of eggs or nestlings and to identify any causes of mortality. When nestlings were approximately 25–30 days old, all individuals were fitted with leg bands for individual identification, and a subset was fitted with satellite-tracking devices (GPS tags) for ongoing monitoring. The devices were supplied by Hunan Global Messenger Technology Co., Ltd. (Changsha, China) and had the model number HQBG3621L.

2.3 Failure/mortality and its main causing factors survey

Specifically, we conducted a comprehensive investigation of stage-specific failure and mortality (rates) in this reintroduced population, identified the primary causes of these failures, and proposed corresponding management measures to enhance population viability as follows.

a) attempt failures at the nest-building stage

In the early breeding season, we search for and confirm potential nesting sites or nests under construction using information such as Crested ibis calls, signs of their activity, and environmental suitability. Next, we conduct continuous monitoring of these sites or nests. Because adults are particularly sensitive to disturbance during nest construction, observations were made every 3–5 days from a distance using binoculars. A nesting attempt was classified as failed when no nesting activity was detected on three consecutive visits (e.g., no additional nest material, absence of adults in the nesting area, or no new droppings beneath the nest). We have monitored 176 nesting attempts over three years (45 in 2023, 64 in 2024, and 67 in 2025).

b) hatching failures at the incubation stage

The incubation period was defined as beginning on the day when an adult was first observed sitting on the nest for an extended duration. Monitoring was conducted every 2-3 days, then increased to daily or every other day near the expected hatching date (the incubation period lasts approximately 28-30 days) to accurately determine hatching time. To avoid flushing incubating birds, we recorded the behavior of adults and any evidence of damaged eggs below the nest from a distance using binoculars. Hatching failures were classified into five categories (causing factors) based on the

condition of the adults, incubation duration, and egg characteristics: 1) early egg loss, 2) unfertilized or rotten eggs, 3) egg predation, 4) nest desertion, and 5) extreme weather events (e.g., strong winds). The classification details and criteria are summarized in Table S1. At this stage, we monitored a total of 160 nests, including 41 in 2023, 58 in 2024, and 61 in 2025.

c) mortality at the offspring provision stage

During the offspring-provision period (including the offspring brood), nests were inspected every 1 to 2 days to obtain timely information on nestling status. For any dead chicks, the cause of death was inferred from field observations and necropsy examinations. Mortality causes were categorized into six groups: 1) nest predation; 2) food shortage; 3) food poisoning associated with the use of fertilizers or pesticides in foraging areas; 4) extreme weather events (e.g., sudden temperature drops or heavy rainfall); 5) gastrointestinal parasitism, and 6) other unknown causes. The classification details and criteria are summarized in Table S2. At this stage, we monitored a total of 123 nests, including 32 in 2023, 47 in 2024, and 44 in 2025.

d) mortality at the fledgling stage (< 1 year)

Crested ibises typically reach sexual maturity at two years after fledging. We classified individuals (after fledging) of this population into three life stages: fledglings (<1 year), subadults (1-2 years), and adults (≥2 years) (Ding, 2004). From 2021 to 2025, 74 fully feathered fledglings were fitted with GPS tags (12 fledglings in 2021, 18 fledglings in 2023, 18 fledglings in 2024, and 26 fledglings in 2025). The GPS tags record and transmit data at least once per hour, including position, temperature, acceleration, and other relevant metrics. By integrating telemetry data with field observations, we accurately determined the timing of mortality events, enabling us to estimate mortality rates for each life stage. A total of 63 transmitter-fitted nestlings successfully fledged, excluding those that died prior to fledging or experienced transmitter failure. These individuals (11 in 2021, 12 in 2023, 17 in 2024, and 23 in 2025) were monitored through the fledglings stage, yielding 457 bird-months of data by September 2025. Within this period, 22 fledglings died, primarily attributed to two causes: predation (by snakes and mammals) and starvation.

e) mortality at the sub-adult stage (1- 2 years)

Excluding individuals with equipment failures and those less than 1 year old, a total of 28 transmitter-fitted individuals were included in the monitoring of the sub-adult stage. Those were 7 in 2021, 10 in 2023, and 11 in 2024. The cumulative monitoring was 234 bird-months. Among them, two sub-adults died, and the cause of death was predation.

f) mortality at the adult stage (> 2 years)

A total of 15 individuals entered the adult monitoring stage. Among them, seven were in 2021 and 8 were in 2023. The cumulative monitoring reached 152 bird-months, and three individuals died. To maximize the use of monitoring data at each stage (e.g., individuals with monitoring periods shorter than a full year due to equipment failures or transmitter attachment batches), we set the survival interval to 1 month. We used Known-fate models in Program MARK (White & Burnham, 1999) to estimate the monthly survival rate, and then calculated the corresponding annual survival and mortality rates. A detailed description of the methods and results is provided in the appendix.

2.4 Population growth simulation

We estimated the stochastic population growth rate by simulation using a stage-based matrix (Caswell, 2001). The population was modeled with an annual post-breeding census and a 1:1 sex ratio. All adults were assumed to first reproduce at age year three and thereafter breed annually. We defined the demographic matrix as:

$$A_i = \begin{bmatrix} 0 & 0 & \frac{1}{2} f_i S_i^{ad} \\ S_i^{fle} & 0 & 0 \\ 0 & S_i^{sub} & S_i^{ad} \end{bmatrix},$$

and the population size at time i+1 equals: $N_{i+1} = A_i \cdot N_i$.

Each column of the demographic matrix manifests one age class. The elements of the first row represent the reproductive output produced by each age class for the next year's population. The number of female offspring produced by each female adult that survives to breed in the next year equals to $\frac{1}{2} f_i S_i^{ad}$. Parameter f_i s the average number of fledglings produced by each female adult

in year i; S_i^{ad} is the adult survival rate of year i. Survival coefficients over age classes are presented along the sub-diagonal of the matrix. S_i^{fle} is the first year (fledglings) survival rate during year i, $S_i^{sub}$is the second year survival rate during year i.

According to the results of the autumn synchronized population survey at nocturnal roost-sites of Crested ibis in 2025 by the Nature Reserve Administration, the number of wild Crested ibis in Dongzhai is conservatively estimated to have exceeded 500.

Therefore, in the matrix model, we assumed an initial population size of 500 with a stable stage structure. We simulated a 50-year population dynamic using empirical parameters for reproduction and mortality across life stages. Temporal variability was added to reproductive output during each discrete time step. Specifically, we stochastically varied clutch size and the failure rates of the nest-building, incubation, and offspring-provision stages by drawing them from the lower and upper 95% confidence intervals (CIs), respectively. To estimate the average number of fledglings produced per female (f_i), we computed the product of clutch size and the success rates of these three sequential reproductive stages (success rate = 1 − failure rate). Similarly, the same treatment was applied to the mortality rates of the three stages after fledging. We ran 1000 stochastic simulations to estimate the mean population trajectory and its 95% confidence interval. Multiply the quantity obtained from the simulation by 2 to get the total population quantity for each stage. We assessed the sensitivity and elasticity of the asymptotic growth rate using the population-matrix projection model with eigenvectors (Caswell, 2001). We also constructed a classic Leslie matrix based on the assumptions that the minimum reproductive age is 3 years, the maximum reproductive age is 15 years, and the maximum lifespan is 17 years. Then, we calculated the proportion of each age group in the stable age structure and drew an age pyramid diagram.

2.5 Future distribution simulation

Based on projected population sizes, we simulated changes in the population's distribution range over the next 50 years. The specific methodology is outlined as follows: 1) Using all breeding nest sites monitored in 2025, a minimum convex polygon was constructed to represent the current

population distribution, with a total area of 3,700 km². 2) Assuming the population maintains a stable age structure, the proportion of individuals in each life stage was calculated via the demographic matrix in section 2.4. This allowed us to infer that the initial 2025 population of 500 individuals included 139 breeding pairs, yielding an average habitat requirement of 26.62 km² per breeding pair (calculated as the ratio of total distribution area to the number of breeding pairs). 3) The number of breeding pairs was extracted from population projection data at 10-year intervals between 2025 and 2075. Combined with the standard of 26.62 km² of breeding area per pair, the distribution range of the Crested ibis over the next 50 years was ultimately calculated. Each range was converted to an equivalent-area circle, centered on the geometric center of the current distribution, for map visualization.

3. Result

3.1 Failures/mortality in each stage of the life history

Over three consecutive breeding seasons from 2023 to 2025, a total of 176 breeding attempts were monitored, among which 16 attempts failed (9.1%, Table 1 & Figure 1). For some nests (n = 32), due to their significant distance from the research base, the observation frequency was relatively low, making it impossible to determine the fate of the eggs in these nests fully. To avoid potential biases, we excluded those observations from the statistics during the incubation and offspring provision stages. Among the remaining 144 breeding attempts, 131 nest-building attempts were successful (attempt failure rate: 9.0%). These nests produced a total of 425 eggs, from which 287 chicks hatched. Eventually, 189 of these chicks fledged (Table 1). The mean clutch size was 3.24 ± 0.08 (Mean ± SE; the same hereinafter), and on average, each pair of breeders produced 1.31 ± 0.12 offspring when the breeding season finished (Table 1). The detailed reproductive performance parameters, along with failures or mortality at each stage, are summarized in Table 1 and Figure 1.

We found that incubation, offspring provisioning, and fledging are the three stages during which broods experienced the highest mortality rates (hatching failure, nestling failure and fledgling mortality, Table 1). Specifically, the mortality rate at the fledgling stage is the highest (< 1 year), at

38.6% (Table 1). Moreover, most individual mortalities during this stage occurred in the first half of the year (see Figure S1), likely due to the vulnerability of inexperienced fledglings to predation or starvation. Mortality at the offspring-provision stage is the second-highest, at 34.1% (Table 1). The main causes of mortality at this stage are predation and food shortage. Among the nestlings that died during this stage, the proportions of deaths attributable to these two factors are 39.1% and 32.6% respectively (individual level, Figure 1). During incubation, hatching failure also has a relatively high rate of 32.5%. The most common cause for this is unfertilized or rotten eggs, accounting for 60.9% of all cases (egg level, Figure 1). Nest desertion was another major cause of hatching failure (egg level, 17.4%), most often occurring in early incubation. Details of failure/mortality for these six stages, along with the corresponding causes and proposed conservation practices, are shown in Figure 1.

Table 1: Summary of breeding parameters and vital rates for the Crested ibis in Dongzhai during 2023–2025 (Mean ± SE). *Year-productivity: the average number of fledged chicks produced per breeding pair per year.

Year	2023	2024	2025	Overall
Number of attempts	45	64	67	176
Number of nests	41	58	61	160
Number of eggs	115	163	147	425
Number of chicks	68	117	102	287
Number of fledglings	34	91	64	189
Clutch size	3.108±0.121	3.327±0.159	3.267±0.132	3.244±0.082
Year-productivity*	0.829±0.167	1.655±0.23	1.333±0.198	1.313±0.122
Nest building failure rate	0.089±0.044	0.094±0.037	0.090±0.036	0.091±0.022
Hatching failure rate	0.409±0.045	0.282±0.035	0.306±0.038	0.325±0.023
Nestling failure rate	0.500±0.059	0.222±0.038	0.373±0.047	0.341±0.028
Fledgling mortality rate	\	\	\	0.386±0.040
Subadult mortality rate	\	\	\	0.098±0.019
Adult mortality rate	\	\	\	0.213±0.031

Stage	Cause	Sample size (nest level)	Failure pro. (nest level)	Total failure rate (nest level)	Sample size (egg/ind level)	Failure pro. (egg/ind level)	Total failure rate (egg/ind level)	Conservation practices
Nest building (n = 176 pairs)	Incomplete nest building	16	\	9.1%	\	\	\	1) Provide nest materials. 2) Nest behavior training in the captive
Incubation (n = 425 eggs)	Unfertilized or rotten eggs	11	40.7%		84	60.9%		1) Parental birds management
	Nest desertion	12	44.4%		24	17.4%		1) Decrease human disturbance. 2) Maintain/increase ideal nest habitat.
	Early - incubation fall	0	0.0%	20.6%	18	13.0%	32.5%	1) Install protective facilities beneath the nest to prevent falling eggs
	Egg predation	2	7.4%		8	5.8%		1) Install protective facilities to prevent predators such as ravens
	Abnormal meteorological events	2	7.4%		4	2.9%		1) Provide protective facilities for high-risk nests
Offspring provision (n = 287 chicks)	Nest Predation	12	42.9%		36	39.1%		1) Install protective facilities to prevent predators such as snakes
	Starvation	3	10.7%		30	32.6%		1) Provide appropriate food supplementation
	Poisoning	4	14.3%	26.9%	12	13.0%	34.1%	1) Increase public awareness of environmental protection. 2) Green and organic agriculture
	Abnormal meteorological events	3	10.7%		7	7.6%		1) Provide protective facilities for high-risk nests
	Parasitic infection	0	0.0%		1	1.1%		1) Implement veterinary medicine
	Unknown reasons	6	21.4%		6	6.5%		1) New monitoring technologies
Fledging (< 1 year) (n = 63 birds)	Predation/starvation/ poisoning/unknown	\	\	\	22	\	38.6%	1) Provide appropriate food supplementation. 2) Increase public awareness of environmental protection. 3) Green and organic agriculture. 4) New monitoring technologies
Sub-adult (1~2years) (n = 28 birds)	Predation/starvation/ poisoning/unknown	\	\	\	2	\	9.8%	1) Provide appropriate food supplementation. 2) Increase public awareness of environmental protection. 3) Green and organic agriculture. 4) New monitoring technologies
Adult (> 2 years) (n = 15 birds)	Predation/starvation/ poisoning/unknown	\	\	\	3	\	21.3%	1) Provide appropriate food supplementation. 2) Increase public awareness of environmental protection. 3) Green and organic agriculture. 4) New monitoring technologies

Figure 1. Mortality rate of the Crested ibis at each life history stage and targeted conservation strategy. Sample size: Number of nests or eggs that failed due to various causes. Failure pro.: Contribution ratio of each cause to the total number of failures in the current stage. Total failure rate: Overall failure rate in the current stage.

3.2 Population growth trend

Based on the results of the population matrix projection model, the population's asymptotic growth rate (λ) stood at 1.053 (95% CI: [0.970, 1.148]), the intrinsic rate of increase (r) was 0.052 (95% CI: [0.042, 0.062], Figure 2c), and the age structure of the population exhibited a positive pyramid-shaped pattern (Figure 2d). This indicates that, under current environmental conditions, the studied population has the potential for continuous growth, with the overall population in a healthy, positive development phase (Figure 2). The population size is expected to reach 1,400 (95%CI: [1052, 1926]) in 20 years. In 50 years, it will increase by 13-fold to reach 6,858 (95%CI: [4122, 10607]) (Figure 2a), including 3,838 adults (95%CI: [2333, 5889]) (Figure 2b). The sensitivity and elasticity analysis of the demographic model showed that the asymptotic growth rate was most sensitive to changes in adult survival (Table S5).

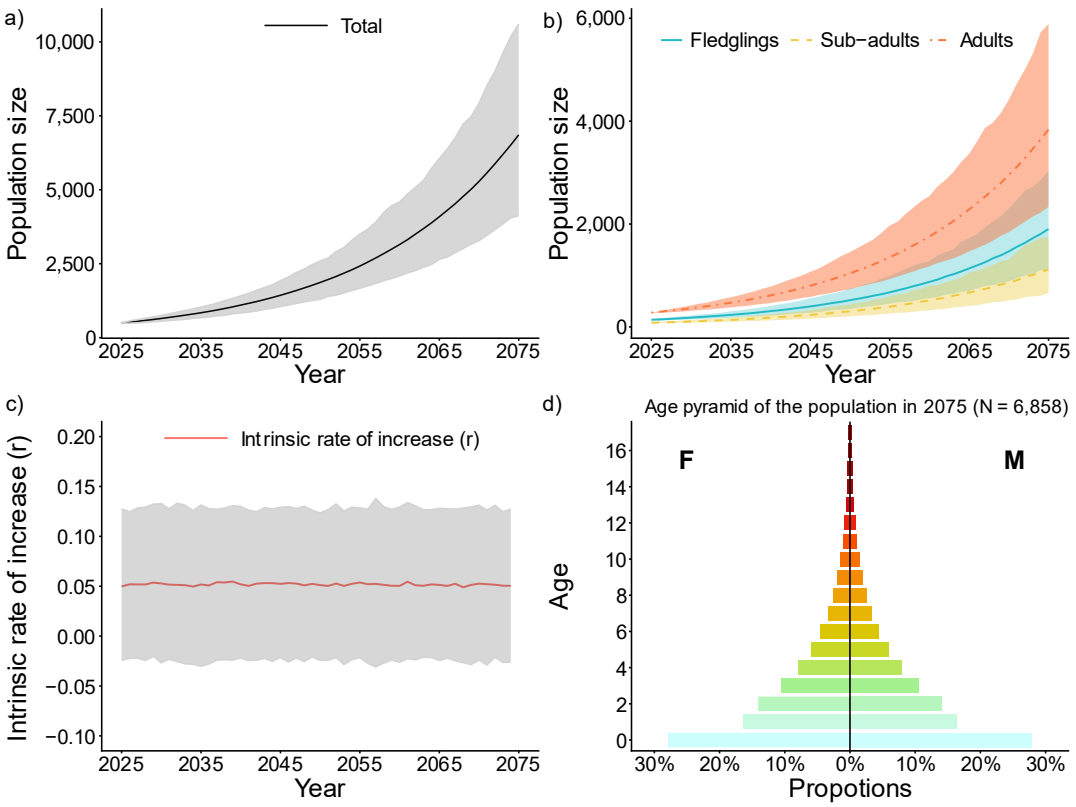

Figure 2. Simulation results of the population growth trend over the next 50 years. a) and b) showing the total population size and the sizes of different age categories (i.e., fledglings, sub-adults, and adults) over the next 50 years. c) the intrinsic rate of increase (r) and 95%CI of the population over the next 50 years. d) the population age-structure pyramid after 50 years in 2075.

3.3 Expansion of the distribution area

The area of the minimum convex polygon constructed using all the breeding nest areas in 2025 is 3,700 km², with an average occupied area of 26.62 km² per breeding pair. Based on the predictions regarding the number of breeding pairs and the expansion of the distribution range, by 2075, the radius of the distribution range of this population will increase to 3.7 times its current length. Correspondingly, the area will expand to 13.8 times the current size, reaching 51,058 km², covering the surrounding Zhumadian City, Huanggang City, Wuhan City, Xiaogan City, and Suizhou City, all located around Xinyang City (Table 2, Figure 3).

Table 2: The number of adults, corresponding range size, and 95% confidence interval over the next 50 years.

Year	Number of adults	Range size (km^2)
2025	278	3700
2035	471 [380, 578]	6282 [5058, 7693]
2045	802 [582, 1070]	10675 [7747, 14242]
2055	1355 [930, 1970]	18049 [12378, 26221]
2065	2283 [1470, 3364]	30401 [19566, 44776]
2075	3837 [2334, 5889]	51058 [31066, 78371]

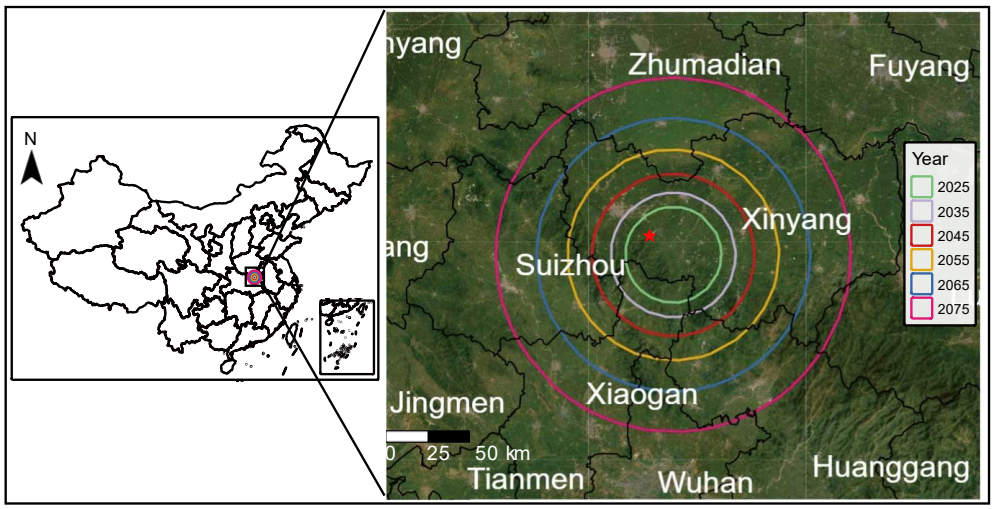

Figure 3. Prediction of the distribution expansion of the Crested ibis population in Dongzhai in the next 50 years. The red pentagram indicates the location of the conservation station. Six concentric circles (differentiated by color, from innermost to outermost) denote the projected distribution ranges for 2025–2075 at 10-year intervals.

4. Discussion

In this study, combined GPS telemetry data with intensive monitoring, we systematically assessed the reproduction and survival of a reintroduced Crested ibis population over three consecutive breeding seasons (2023–2025). Our study provides a detailed summary of key demographic traits across the full life cycle of this species (i.e., from nest attempting and egg-laying to fledging and adulthood). Correspondingly, we identified the main factors threatening this reintroduced population and proposed pinpointed conservation practices at different stages. Furthermore, we simulated the population growth and distribution expansion in the next 50 years of this population. The results of this study provide a comprehensive picture of a successful reintroduction population. Previous studies on the Crested ibis have typically focused on one specific life stage or failed to clarify stage-specific stressors, lacking a panoramic and systematic perspective (Wang et al., 2017; Okahisa et al., 2022). Importantly, we established a research framework for reintroduction conservation initiatives in endangered species that integrates detailed monitoring, concrete conservation practices, population growth and expansion prediction, and management recommendations. This framework not only offers practical methodologies and decision support for other Crested ibis reintroduction programs but also strengthens global conservation and population recovery efforts for this flagship species. By identifying critical intervention points and refining management strategies, our work marks the significance of linking theory and practice in endangered species reintroduction.

Key parameters of reproduction and survival, and their main causes

The reintroduced Crested ibis population in the Dongzhai National Nature Reserve had a mean clutch size of 3.24 ± 0.08 (SE) eggs and a mean productivity of 1.31 ± 0.12 (SE) fledglings per nest per year (Table 1). Compared with the previous results from Tuohetahong et al. (2025), this productivity was lower than that of the founder population in Yangxian (1.87 ± 0.46) and another reintroduced population in Ningshan (1.76 ± 0.42). The fledgling mortality rate (0.386 ± 0.040) and the adult mortality rate (0.213 ± 0.031) were both higher than those of the Yangxian population (0.380 ± 0.095; 0.190 ± 0.040), yet lower than those of the reintroduced population in Ningshan (0.486 ± 0.038; 0.314 ± 0.034). Additionally, the subadults' mortality rate (0.098 ± 0.019) was

significantly lower than that of the Yangxian population (0.270 ± 0.051) and the Ningshan population (0.218 ± 0.023). Besides this, no other studies have shown the panoramic and detailed stage-specific parameters (i.e., six stages across reproduction and life-history) of reproduction and survival in this species. In this respect, our investigation into the causes of reproductive failure at each stage yielded valuable insights.

The nest-building stage exhibited the lowest failure rate (9.10%) among all stages. We hypothesize that failures primarily result from the parents' inexperience with nest construction and external disturbances. As the founder populations are often artificially bred and raised in cages or with artificial nests, they lack exposure to natural nest-building processes. Therefore, we recommend that future wild-training programs incorporate training using natural nest materials and pre-constructed natural nests to improve early post-release success. Previous research for this species overlooked this stage as many begin monitoring at incubation. However, this rate is likely an underestimate due to “survivorship bias”, as early failures may have gone thus undetected. Meanwhile, some breeders may try multiple potential nesting sites and eventually pick the ideal one. Because some adult birds in this population have not yet been ringed, we are unable to identify breeders with multiple potential nest attempts. Nevertheless, recording breeding pairs trying to select multiple potential nest sites at the beginning and finally setting their ‘ideal’ nest site is very interesting. In doing so, we can evaluate the habitat quality for nest in this species (i.e., final nest site *vs*. abandoned nest sites before). In the future, as bird ringing scales up, we expect to be able to more accurately determine the failure rate at this stage and deepen our understanding of the Crested ibis habitat and nest-site selection.

The hatching failure rate of this reintroduced population (32.5%) is higher than that of the Ningshan (28%) and Yangxian (19.8%) populations (Shen, 2018; Yu et al., 2006). This is mainly due to the relatively high rate of infertile or rotten eggs and nest desertion rate in this population. For threatened birds, inbreeding depression is a well-documented major driver of hatching failure (Assersohn et al., 2021), and this failure rate increases with the severity of population bottlenecks (Briskie & Mackintosh, 2004). Consistent with these findings, our previous research demonstrated a negative correlation between hatching success and the inbreeding coefficient in this population (Zheng et al., 2025). Therefore, scientific pedigree management is essential for selecting specific

breeding pairs for the reintroduction founder population to mitigate inbreeding. The high nest desertion rate warrants attention, accounting for 44.4% of nest failures and 17.4% of egg losses. While external disturbances are recognized as a primary cause, identifying the specific factors in the field is challenging, as nest desertion is often conflated with egg predation. Based on prior studies and our field observations, opportunistic egg predators such as the Collared crow (*Corvus dauuricus*) or the Eurasian jay (*Garrulus glandarius*) may harass Crested ibises and ultimately induce nest desertion (Jiang et al., 2023). Collared crows are common and sympatric with the Crested ibises in our study area. The two species were even observed nesting in the same tree. It is worth noting, however, that this issue has two sides—our field observations indicate that Crested ibises sometimes benefit from the anti-predator behavior of Collared crows, which drive raptors away from their shared nesting areas. This suggests a more complex interspecific relationship than previously assumed and warrants further research. Furthermore, human interference is another reason for nest desertion. We recorded three cases of nest desertion caused by humans—two during the Qingming Festival, when visitors entered the area for ancestral worship with firecrackers, and one during the peak of tea-picking activities. These incidents underscore the need for enhanced public conservation awareness and targeted measures to mitigate human-induced disturbances.

Predation, starvation, and pollution from excessive fertilizer and pesticide use were the primary threats across all post-hatching life stages. Snakes and raptors were the dominant predators, with the King Rat Snake (*Elaphe carinata*) being the most frequently recorded nest predator. This finding is consistent with observations from the Yangxian wild population and the Ningshan reintroduced population (Yu, 2006; Jiang, 2022). Although experimental measures such as wrapping nest trees with plastic film were used to deter snakes, these were only partially effective. Given the serious threat snakes pose to nestlings, it is necessary to enhance current protective measures by implementing additional measures. Food shortage was a primary cause of mortality in Crested ibises during both the nestling and post-fledging periods. The Crested ibis is a typical asynchronously hatching species, with earlier-hatched chicks generally holding a competitive advantage. Consequently, later-hatched chicks are more likely to perish when food is limited (Ding, 2004). In reintroduction programs, providing supplemental feeding may improve breeding success (Yu et al., 2006). In combination with our results in this study, we recommend providing food supplements

during years of natural scarcity. For nests with many siblings, artificially fostering, especially for later-hatched chicks, might be a good option. These interventions are crucial for enhancing reproductive output, particularly in small populations. Twelve chicks (13.04%) and two breeding adults (in 2023 and 2025) died from poisoning associated with fertilizer and pesticide use in nearby foraging areas. While modern agriculture heavily relies on agrochemicals, the promotion of organic rice cultivation in Yangxian has provided an effective example of reconciling agricultural production with habitat safety for the ibis (Wang et al., 2021).

The threat of extreme climate to eggs and nestlings warrants significant attention. Beyond the direct impacts we observed (i.e., nests destroyed by strong winds and nestlings succumbing to severe cold and precipitation), the pathways and mechanisms by which climate affects avian reproduction are complex and often confounded with other factors. For instance, persistent heat and drought have been linked to rapid declines in nest survival for Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) (Grisham et al., 2016). Against the backdrop of global climate change, future research must clarify the specific impact pathways of extreme weather on Crested ibis reproduction and quantify their magnitude.

Despite systematically investigating key stages affecting population viability, this study has some limitations. We could not assess the impact of inbreeding depression on mortality across these stages. Extensive research has established that inbreeding increases the homozygosity of recessive deleterious alleles, leading to abnormal embryonic development and reduced fecundity, survival, and recruitment (Taylor et al., 2017; Brekke et al., 2010; Ahlinder et al., 2021; Hoeck et al., 2015). Furthermore, individual-based models for Crested ibis population reinforcement indicate that inbreeding poses a significant extinction risk for bottlenecked populations, a critical consideration for reintroduction efforts (Zheng et al., 2025). This limitation stems from data constraints: 1) genetic samples were not collected from all individuals released initially, making pedigree reconstruction impossible; 2) the fact that Crested ibises nest high in tall trees makes capturing parents for genetic sampling prohibitively challenging; 3) a lack of systematic historical banding data of newborn individuals prevents the identification of inbreeding events. Given the essential impact of inbreeding on reproduction and survival, future research should prioritize quantifying its effects on key life-

history parameters in the wild. Fortunately, remedial actions are underway to address the aforementioned constraints. Since 2023, we have systematically collected genetic samples and applied unique bands to all accessible nestlings. The first of these banded individuals began successfully reproducing in 2025, paving the way for a complete field-based pedigree database to address this knowledge gap. Additionally, the subadults' mortality rate (1-2 years, 0.098 ± 0.019) was lower than that of the other two populations. Moreover, it is also lower than the adult mortality rate in this population, which is uncommon. Generally, it is believed that as survival experience increases, the adult mortality rate will be lower than that during the subadult stage. Regarding this result, we cannot rule out the possibility of sampling error. In the future, we need to further confirm these mortality estimates by increasing the sample size.

Population growth simulation

Our model projections indicate a sustained growth potential ($\lambda = 1.053$) for this reintroduced Crested ibis population, forecasting an approximately 13-fold increase over the next 50 years. Sensitivity analysis revealed that adult survival exerts the strongest influence on the population growth rate, a finding consistent with other long-lived birds, such as the White Stork (*Ciconia ciconia*) and the California Condor, whose populations are also highly dependent on adult survival (Schaub et al., 2004; Walters et al., 2010). This is because adults have long reproductive lifespans, directly determining the number of breeding pairs annually. Concurrently, their relatively low annual productivity (averaging 1.31 fledglings per pair) prevents rapid compensation for adult mortality. Therefore, safeguarding adult survival is the paramount strategy for sustaining population growth.

Several limitations inherent in our stage-structured matrix model should be noted. First, although the model assumed a 1:1 sex ratio, the adult sex ratio may deviate due to ecological processes like the female-biased dispersal (Hu, 2016), potentially leading to differential mortality between the sexes—a hypothesis that awaits further testing. Second, the assumption of a stable age structure in 2025 may not hold, as the population has been founded through multiple releases of young birds (2-4 years old) since 2007, likely leading us to underestimate short-term reproductive output. Future models should incorporate realistic initial age structures based on banding-resighting data. Finally, the model did not account for potential future stressors, such as local habitat saturation (although

individuals could freely move or dispersal in this area), disease outbreaks, or climate extremes. Thus, while current projections are optimistic, more detailed monitoring data are essential to re-evaluate population viability and enhance the robustness of our predictions and the relevance of management recommendations.

Distribution expansion

Our model projects that the Crested ibis population in Dongzhai will expand to a distribution range of 51,058 km² by 2075, encompassing multiple cities around Xinyang (the released city). This projection, however, relies on simplified assumptions of concentric expansion and an average home range of 26.62 km² per breeding pair. In reality, range expansion is shaped by more complex processes, primarily long-distance dispersal and metapopulation dynamics.

Subadults are key dispersal agents, with some undertaking long-distance movements of tens to hundreds of kilometers to colonize new habitats. Such "jump dispersal" creates isolated distribution points rather than continuous expansion. For instance, our field monitoring records document several Crested ibises dispersing nearly 70 km from the natal site, where they successfully settled and reproduced. Tuohetahong et al. (2025) reported that a captive-bred Crested ibis released in the Yellow River Delta of Shandong completed a long-distance migration, flying 260 km over 11 hours. Beyond accelerating range expansion, this process alleviates density-dependent pressures in the core area, freeing up capacity for further population growth. As the range expands, the core Dongzhai population may form a metapopulation network with satellite populations established through reintroduction or dispersal. Genetic exchange and demographic rescue effects through this network would enhance overall stability—a process not captured by our current model. If suitable habitat patches exist, the actual expansion rate may thus exceed predictions.

In the future, the complexity and difficulty of population management will also increase accordingly. Conservation efforts need to focus not only on the survival of individuals and the assessment of the suitability of new habitats, but also on coordinated cross-regional conservation. Establishing process-based habitat conservation goals within the species expansion range (Runge et al., 2014), identifying important ecological corridors, enhancing connectivity among populations, and

promoting the formation of a metapopulation network play an important role in reducing the extinction risk of endangered species populations (Haines et al., 2006; Yang et al., 2016).

Reintroduction evaluation

Against the backdrop of severe global biodiversity loss, the reintroduction of endangered species has emerged as a pivotal tool for species restoration. The success of these reintroductions extends beyond ensuring the persistence of the target species. As the flagship species, they can generate a significant "umbrella effect", thereby profoundly influencing the conservation of entire ecosystems (Crespo-Gascón et al., 2019; Mekonnen et al., 2024). However, evaluating the success of reintroduction programs should not be limited to assessing the short-term survival of released individuals. Seddon (1999) posited that a successful reintroduction should sequentially achieve three progressive objectives: the survival of released individuals, the successful reproduction and rearing of offspring, and the long-term self-sustainability of the population. Robert et al. (2015) argued that reliable evaluations of ultimate success demand that populations have entered their regulatory phase. A population is regarded as self-sustaining if its long-term growth rate is positive and the probability of its persistence remains high, even in the face of environmental or demographic stochasticity (Schaub et al., 2004, 2009).

Although multiple populations have been established through reintroductions for many endangered species, the assessment of most programs remains confined to short-term monitoring, lacking systematic analysis of population dynamics and long-term projections. This gap hinders an accurate determination of their true self-sustaining status. In this respect, our study focusing on a reintroduced population of an endangered species might address this gap. By integrating long-term monitoring of vital life-history parameters with population-matrix modeling and spatial-distribution simulations, we provide a comprehensive assessment of its growth trajectory and expansion potential. Our results indicate that the population has clear potential to progress towards a self-sustaining state. Therefore, our study provides a validated assessment protocol and generalizable conservation strategy for the Crested ibis reintroduction program. The methodology also serves as a valuable reference for reintroducing other endangered species globally, thereby optimizing resource allocation and enhancing the scientific rigor and effectiveness of conservation practices.

5. Conclusion

This study provides a comprehensive, full life-cycle assessment of a reintroduced Crested ibis population with intensive field monitoring with predictive modeling. Through multi-year tracking across six key life stages, we pinpointed stage-specific bottlenecks, with high mortality during incubation and offspring provisioning, and during the fledgling stage, driven primarily by predation, food scarcity, and human disturbance. These findings informed targeted interventions, including predator control, supplemental feeding, and public engagement. A stage-structured matrix model projected a positive growth rate ($\lambda = 1.053$), indicating a potential 13-fold population increase over 50 years. Concurrently, the species' distribution is forecast to expand to over 51,000 km² by 2075. This work establishes a transferable framework for evaluating reintroduction success, linking empirical demography with spatial projections. Our approach not only supports the Crested ibis's ongoing recovery but also provides a validated model for strengthening the scientific basis and efficacy of global conservation for endangered species.

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