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ORIGINAL ARTICLE

Why do parents produce small broods of offspring that have lower body mass, survival, and lifetime reproductive success? A case study in a long-lived bird

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Abstract

Numerous studies have examined the correlation between offspring quantity and quality, and many have found that the most common brood size is often smaller than broods with the highest offspring quality or production. However, the reasons why these small broods with lower offspring quality are produced are still poorly explained. Using data spanning 29 years, we investigated the effects of brood size on nestlings' body mass and the lifetime fitness for those offspring as adults (as proxies of offspring quality) in the Crested Ibis (*Nipponia nippon*). We also examined the temporal variation of brood size. We found that overall offspring quality increases with brood size and that individuals from broods of three had the highest quality, as quantified by larger body mass, higher adult survival, and lifetime reproductive success. Furthermore, the brood size of an individual pair significantly varied across years, and the proportion of broods containing two offspring increased while broods of three decreased after 2000 when the population dispersed to low-quality habitat. These findings indicate that spatiotemporal variation in resources may impact variation in brood size and subsequent fitness consequences, and that small broods are more common in resource-poor years or low-quality habitats. In contrast, parents with access to high-quality resources produce larger broods of nestlings that achieve higher body mass and subsequently experience higher adult survival and lifetime fitness. This study highlights how variation in life history traits can be influenced by resource condition and provides an insight into particular habitats that need conservation for Crested Ibis.

Significance statement

Although life history theory predicts a trade-off between offspring quantity and quality, and that fewer, high-quality offspring are expected to be more common to prolong one's own survival prospect in long-lived species, birds, mammals, and humans often show a positive correlation for these traits. Why do parents produce small broods with lower offspring quality? Here, we found that offspring quality—such as nestlings' body mass, survival, and the lifetime reproductive success of offspring as adults—increased overall with brood size, up to broods of three of Crested Ibis. Brood size varied across years; in particular, pairs appear to produce smaller broods of nestlings that have lower body mass and lifetime fitness in resource-poor years or lower-quality habitats. This long-term study helps to advance our understanding of the fitness consequences and ecological mechanisms that impact offspring quantity and quality in long-lived animals.

Keywords Brood size · Offspring quality · Fitness consequences · Crested Ibis · *Nipponia nippon*

Introduction

Examining the correlations between life history traits is fundamental to our understanding of species ecological and evolutionary processes (Lack 1947; Stearns 1992). One of the most frequently examined correlations has been the quantity and quality of offspring in species that produce litters or clutches (e.g., mammals: Emery Thompson et al.

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2016; birds: Leach et al. 2019; reptiles: Hao et al. 2021). Many studies have experimentally determined a negative relationship between offspring quantity and quality, indicating a trade-off between the number of offspring produced and the quality of offspring. For example, nestlings in reduced broods have higher body mass than those in control and enlarged broods (Lessells 1986; Jacobsen et al. 1995; Roulin et al. 1999; Rytkönen and Orell 2001; Parejo and Danchin 2006). Other studies, however, have failed to find evidence for a trade-off, suggesting that offspring quality continues to increase with the number of offspring (Lepage et al. 1998; Loonen et al. 1999; Lengyel 2007) or fitness maximization reportedly occurs at intermediate levels of offspring number (Mulder 2000). In birds, the modal clutch size is often smaller than the brood size with the highest offspring quality or fledgling success (Lepage et al. 1998; Leach et al. 2017). For instance, Leach et al. (2019) demonstrated that the most common clutch size is relatively smaller than the most productive brood size in Black Brent Geese (*Branta bernicla nigricans*). The reason why parents produce these small clutch size or broods (the most common brood size is always less than or equal to the most common clutch size in the natural population) of nestlings with lower quality and how the variation in nestlings' quality among brood sizes may affect the lifetime fitness of offspring—such as survival and reproduction of offspring as adults—are still not well explained (Leach et al. 2017; Sedinger et al. 2017). Understanding the effects of brood size on offspring quality and their fitness consequences, and identifying which factors are responsible for these relationships, can provide important insights into the ecological relevance of reproductive behavior and for formulating conservation management strategies of endangered species.

A negative correlation between offspring quantity and quality (including the process of decline when offspring number up to a given size) could be explained by the fundamental trade-offs determined by life history theory (Lack 1947; Smith and Fretwell 1974; Stearns 1992; Lepage et al. 1998; Roff et al. 2006). For instance, since resources are not unlimited, and that higher allocation to current reproductive effort may decrease the residual reproductive value (Williams 1966), parents can produce fewer, high-quality offspring to prolong survival prospects and to maximize their fitness (Martin 1996; Drent and Daan 1980; Sæther 1988; McNamara et al. 2008; Boyce et al. 2015; Emery Thompson et al. 2016). This may be especially relevant for long-lived animals with a relatively slower life history, as they are expected to prioritize their future reproductive value even if it reduces their current offspring quantity. Thus, small broods are expected to be the most common size. However, it is commonly observed that offspring quality tends to increase with brood size, and nestlings from small broods have lower quality (Lack 1967; Pettifor 1993; Lepage et al. 1998), even in some altricial bird species (the quantity-quality trade-off is generally expected to be more obvious in altricial birds due to the heavy parental care and hard competition for foods within a brood). In such circumstances, clearly, the quantity-quality trade-off cannot explain why parents may produce these small broods.

There are at least three possible hypotheses to explain this behavior. First, the "incubation limitation" hypothesis proposes that brood size is limited by the incubation capacity of the parent (Lack 1947; Sandercock 1997). Tests with clutch size manipulations have often supported this hypothesis: incubating additional eggs led to a prolonged hatching duration, resulting in reduced egg success, growth rate, and survival of the nestlings (Delehanty and Oring 1993; Larsen et al. 2003; Lengyel et al. 2009; Leach et al. 2017). Consequently, parents often produce smaller broods than the maximum number of nestlings that they can rear, but this hypothesis seems still less likely to explain the lower quality of nestlings from small broods in the wild population. Second, it is possible that resources constrain offspring number and quality, as the availability of resources extracted from the environment determines the amount of energy to pairs to be invested in fitness-related traits, such as survival and reproduction (van Noordwijk and de Jong 1986), such that only pairs with access to more resources (high-quality habitats) would produce larger broods of nestlings and raise offspring with higher quality (Smith and Moore 2005; Kowalczyk et al. 2014; Rushing et al. 2016; Sepp et al. 2017). For instance, Meyrier et al. (2017) found that the number of fledglings per pair decreased with the distance to good-quality foraging grounds in Western Jackdaw (*Corvus monedula*). In Black Brent, the availability of high-quality food resources directly influences the growth of goslings (Herzog 2002). Finally, parental pairs of low quality may result in consistently producing small broods of nestlings with low quality (Hamel et al. 2009; Nicolai and Sedinger 2012). We explore this last two hypotheses in the current paper by investigating whether there is significant variation across years or whether individual pairs tend to consistently produce broods of a given size.

The vast majority of existing studies have examined the relationship between offspring number and quality with clutch/brood size manipulation experiments (e.g., Lepage et al. 1998; Pettifor et al. 2001), which are a useful and integral way to show trade-offs among life history traits. However, as Charmantier et al. (2006) pointed out, these experiments often underestimate the cost of reproduction, such as the individual differences in energy cost of egg laying or egg incubation. Marvelde et al. (2012) found that daily energy expenditure during the egg-laying period is positively correlated with female body mass and this energy expenditure of parents may be closely related to offspring number and quality. Hence, the results of brood size manipulation experiments may not fully explain smaller or larger broods in the natural population, and this raises the question: how strong is the trade-off and under what circumstances do we expect to see it in natural broods without conducting experimental manipulations?

Individual fitness is equivalent to an individual's lifetime reproductive output. In long-lived species, the conditions experienced during growth could affect the short- and long-term fitness of individuals (long-lasting effects, Haywood and Perrins 1992; Madsen and Shine 2000; Harrison et al. 2011; Alberts 2019; Moore and Martin 2019). Studies with experimental manipulations have previously documented the variation in nestlings' quality (Lepage et al. 1998; Pichorim and Monteiro-Filho 2008), pre-fledging survival (Lengyel 2007; Sedinger et al. 2017), and short-term survival after fledging (e.g., 3 months: Pettifor 1993; first autumn and winter: Loonen et al. 1999; first year: Millon et al. 2011; Nicolai and Sedinger 2012; Bosman et al. 2016) among brood sizes. While the limitation of such studies is mainly due to the difficulty of monitoring individual reproductive parameters during an entire lifespan, little attention has been given to how brood size affects the survival of offspring as adults, as well as important components of lifetime fitness, such as the age of first reproduction, breeding lifespan, and annual and lifetime reproductive success (Sedinger et al. 2017). Consequently, our full understanding of the effects of the correlation between brood size and nestlings' quality on the subsequent survival and reproduction of offspring in long-lived birds is meager.

Crested Ibis (*Nipponia nippon*) is an endangered bird species, and as part of protective actions, banding from 1987 and long-term monitoring have allowed for the continuous identification of brood size, individual age, lifespan, and reproductive success. This system provides a unique opportunity to study lifetime fitness consequences of offspring from different brood sizes and test relevant hypotheses in a long-lived species. Crested Ibis have 1–4 nestlings and a long rearing period with 40–45 days. With regard to such a species, we sought to examine how the number of offspring may affect the quality of nestlings, their survival, and their reproduction as adults. We also examined the circumstances in which we could see quantity-quality trade-off in this natural broods. In this study, we first investigated the relationship between brood size and nestlings' body mass, as a proxy of offspring quality before fledging. Using a long-term dataset spanning 29 years, we then examined the variation in annual survival of offspring who have reached reproductive maturity (hereafter termed the "adult survival") and their lifetime reproductive performance including the age of first reproduction, breeding lifespan, and annual and lifetime reproductive success. Due to the long-lasting effects, we predicted that the adult survival and their lifetime reproductive performance would shift with brood size in a pattern that is consistent with the variation in nestlings' body mass. Furthermore, we predicted that if offspring quality does decrease with brood size, this would indicate a quantity-quality trade-off. Alternatively, if offspring quality increases with brood size, this could indicate natural variation in habitat or parental quality: those high-quality pairs or pairs with access to good resources might be able to raise large, high-quality broods, whereas others might be restricted to producing small, poor-quality broods. To test this prediction, we investigated whether the brood size of a given pair varied from year to year. If there was variation in the population, we explored the particular factors (e.g., year, habitat type) that contributed to the production of small broods with low-quality offspring in the Crested Ibis.

Materials and methods

Study area and species

Our study area was in Shaanxi Hanzhong Crested Ibis National Nature Reserve (33°05′– 33°45′ N; 107°25′–107°82′ E), located at Yang County, Shaanxi Province, central China. This area includes the Hanzhong plains and the southern slopes of the Qingling Mountains. Notably, there are different tillage methods and land use between mountains and plains during winter and spring, which could result in shifting food resource diversity and richness (Xu et al. 2022). Presently, the wild Crested Ibis population is mainly distributed in the low elevation mountain and plain areas. The Crested Ibis was once widely distributed in Northeast Asia, but the populations rapidly declined in the early twentieth century to the point at which they were even evaluated as extinct in the wild (Ding 2004). In 1981, seven wild birds (two couples and three juveniles) were rediscovered in a remote mountain village in Shaanxi Province, China (Liu 1981). Under diligent and continuous conservation efforts, the wild population size has been recuperated to more than 4500 individuals by 2020; the breeding range has dispersed from the original area (mountains) to new habitat of plains since 2000 (Wang et al. 2014, 2020; Ye et al. 2022); and the threatened level was downgraded from critically endangered (CR) to endangered (EN) in 2001 (BirdLife International 2001).

The Crested Ibis is a monogamous bird, which breeds from February to June, nests in tall trees (such as *Ulmus pumila*, *Pinus* spp.), and shows strong nest site fidelity (Ding 2004, 2010; Song et al. 2019; Huang et al. 2022). Female birds usually produce one clutch of one to four eggs, which are incubated by both males and females during the approximately 28-day laying and incubation period (Ding 2004). Crested Ibis is an asynchronous hatching and altricial bird with a 40–45 days brood-rearing period, during which time both parents undertake brood-rearing duties. Long-term records have shown that an individual can survive to 18 years old and breed successfully in the wild.

Marking and life history traits data

In each breeding season from 1981 onwards, all previously used nests were checked to record whether they were reused or abandoned. Likewise, newly discovered nests were recorded through surveys by nature reserve staff and through reports by local people. Because of these ongoing efforts, most of the Crested Ibis' nests have been located, and the nesting trees are protected during the breeding season. All nests were monitored every 5 days until the nestlings were observed. About 30–35 days after hatching and around a week before fledging, nests were re-checked, and brood size was determined by counting the nestlings. From 1987 to 1999, nestlings were captured and banded with color combination rings, and since 2000, nestlings were marked with a 3-cm-tall plastic colored tarsus band engraved with a unique alphanumeric code that can be easily identified in the field (Ding 2004, 2010). During the marking process, the length of the tarsus, bill, wing, and other body measurements were measured with a tape measure (± 1 mm), and body mass was measured on an electronic scale (± 5 g). From 2011, one dorsal feather of all banding nestlings was sampled for sex identification with molecular assay (He et al. 2013).

Throughout each breeding season, a telescope (Zeiss Diascope 65 T*FL) was used to read the band color and codes from their nests in order to identify parents and obtain their life history traits. Based on the high nest site fidelity (Song et al. 2019), an individual's age of first reproduction was determined as the age at which a bird without a previous breeding history was observed breeding in a new nest. If the nest was not reused and the bird was never found breeding again in the following years, the number of years in which the bird was observed nesting was recorded as the breeding lifespan. The years in which parents successfully fledge at least one nestling were determined to be reproductive success years. The lifetime reproductive success of an individual was represented by the total number of nestlings (surviving to 35 days) produced in its breeding lifespan. It was not possible to record data blind because our study involved focal animals in the field.

Variation in nestlings' quality

Since all body measurements of nestlings were not measured every year during the marking process, we selected for body mass for analysis based on the integrity of the data available. Data collected on 537 nestlings from 289 broods were used as proxies of nestlings' quality. To control for the effect of sex on body mass in analyses, we included the sex of these nestlings (307 males, 230 females) in the analysis.

Apparent survival analysis of offspring as adults

Due to the low re-discover rate of marked Crested Ibis, and because the calculated individual lifespan obtained from marking and re-discover surveys is lower than the breeding lifespan observed from the nest, the possibility of nest reuse was used to evaluate the adult survival rate of each individual more accurately. From 2003 to 2004, 172 nestlings with confirmed brood size were captured and marked. After 2 years, when most of these birds had approached early adulthood and started breeding, we carried out re-discover surveys for 53 individuals between 2006 and 2015. Thus, we established an encounter histories dataset containing 10 occasions with 1-year intervals. We used this dataset to evaluate the effects of natal brood size on the survival of offspring as adults in the following life.

To estimate adult survival, we used the Cormack–Jolly–Seber model in the program MARK (White and Burnham 1999) implemented via RMark (Laake 2013) to explore the effects of natal brood size on apparent survival (φ) and re-encountering probabilities (P) for wild Crested Ibis. We evaluated the goodness-of-fit (GOF) of the global model [$\varphi(BS^*t)p(BS^*t)$] with a "median c-hat" approach in the program MARK. After correcting for over-dispersion by adjusting $c\text{-hat} = 1.26$, model selection was conducted based on $QAIC_C$ (converted Akaike's information criteria corrected for small sample size) score. We selected the best-supported model structures with the lowest $QAIC_C$ score ($\Delta QAIC_C < 2.0$, Burnham and Anderson 2002) for survival. Finally, we averaged our estimates over the models in the candidate model set to avoid model selection uncertainty (White and Burnham 1999).

Effects of brood size on lifetime reproductive performance

From 1990 to 2018, long-term monitoring of nests and observation of marked parents allowed us to collect data on the age of first reproduction for 90 individuals and breeding lifespan, reproductive failure years, and lifetime reproductive success for 71 out of 90 individuals. Here, we did not distinguish sex because Crested Ibis is a monogamous bird with high fidelity to their mates and both parents undertake brood-rearing responsibilities throughout the breeding season (Ding 2004). Because of these life history characteristics, we calculated other traits such as reproductive success per year in the entire breeding lifespan and the number of young fledging per successful year. We used these parameters to describe the lifetime reproductive performance of Crested Ibis and to evaluate the effect of natal brood size on lifetime fitness consequences. We also tested the relationship among the age of first reproduction, breeding lifespan, and lifetime reproductive success using data from 71 individuals.

Statistical analyses

We determined whether the body traits of nestlings varied as a function of brood size in Crested Ibis by fitting a generalized linear mixed effect model (GLMM) with normal error structure; brood size and individual sex were included as a fixed effect. Since not all nestlings were marked and measured at the same age (35 days) in field work, for those individuals whose age is uncertain, we estimated the day age of nestlings using the following equation (logistic model of Crested Ibis's growth rate) (Zeng et al. 2017):

$$W = 1373.23/\left(1 + e^{2.863-0.22x}\right),$$

where W is the body mass (g) and x is the day age. We included individual day age (range from 15 to 40 days, $n = 537$ young) as a fixed effect. Because our previous study found that hatching order significantly affects the growth rate of Ibises (Song et al. 2019), the model also included hatching order as fixed effects to control for hatching order difference. Brood ID and year were included as random effects to control for repeated measures and environmental condition, respectively. We performed the model to 537 body mass of nestlings in 289 broods.

Survival and reproduction are two aspects of individual fitness. We first used the encounter histories of 2-year-old offspring from different brood sizes to evaluate whether adult survival varied as a function of brood size. We assessed variation in life history traits related to fitness consequences with brood sizes. For under-dispersed count data (age of first reproduction, reproductive success per year, number of fledglings per successful year), we used GLMM with Conway–Maxwell–Poisson (CMP) error distribution (Sellers and Shmueli 2010); breeding lifespans were modeled using GLM with Poisson error distribution; and lifetime reproductive successes were analyzed in GLMM with a Poisson error structure. We treated brood size, age of first reproduction, and breeding lifespan as fixed effects and natal year as random effects. We used these variables to build all model structures and used $\Delta \mathrm{AIC_C}$ to select the most supported model (Burnham and Anderson 2002) to explain the variation in lifetime reproductive success. We tested the relationship between breeding lifespan and lifetime reproductive success using a linear model. Finally, we used GLMM with CMP error distribution to examine whether brood size is repeatable for pairs; we treated years as fixed effects and pair ID as random effects.

Survival modeling was performed using the program MARK (White and Burnham 1999), and other analyses were undertaken in R version 4.0.5 (R Core Team 2021). The glmmTMB package was used to perform GLMM with CMP error distribution (Magnusson et al. 2017; Brooks et al. 2019), the lme4 package was used to perform GLM or GLMM with normal and Poisson error distribution (Bates et al. 2015), and the MuMIn package (Bartoń 2016) was used to build all possible models and calculated $\Delta \mathrm{AIC_C}$ for each model structures. Data are expressed as mean ± SE, $\alpha = 0.05$ in all tests.

Results

Brood size and life history traits of Crested Ibis

Between 1990 and 2018, we collected data on a total of 1694 broods in wild Crested Ibis. The average brood size was 2.12 ± 0.02 (range: 1 – 4 nestlings, Fig. S1), and the most common brood size was two (51%). The average of age of first reproduction, breeding lifespan, and lifetime reproductive success were 2.60 ± 0.10 years old (range: 1 – 4 years old, $n = 90$ individuals), 6.79 ± 0.44 years (range: 1 – 18 years, $n = 71$ individuals), 11.59 ± 0.95 fledglings (range: 0 – 33 fledglings, $n = 71$ individuals), respectively.

Variation in nestlings' quality

The results of a GLMM for body mass of wild Crested Ibis showed that day age, brood size, hatch order, sex, and most of their interactions significantly affected the body mass of

Table 1 Performance of the generalized linear mixed models examining variation in body mass for wild Crested Ibis. Significant effects are shown in bold

	Body mass ($n = 537$)		
Term	Estimate ± SE	t	p
Intercept	390.81 ± 64.20	6.09	**< 0.001**
Day age	36.19 ± 2.65	13.64	**< 0.001**
Brood size	144.56 ± 24.14	5.99	**< 0.001**
Hatch order	− 230.32 ± 21.65	10.64	**< 0.001**
Sex	94.25 ± 32.66	2.89	**< 0.05**
Day age × brood size	− 7.49 ± 0.99	7.57	**< 0.001**
Day age × hatch order	10.78 ± 0.78	13.78	**< 0.001**
Day age × sex	− 6.45 ± 1.20	5.38	**< 0.001**
Brood size × hatch order	2.22 ± 5.08	0.44	0.662
Brood size × sex	32.57 ± 9.05	3.60	**< 0.001**
Hatch order × sex	− 29.93 ± 8.20	3.65	**< 0.001**
Random effects	Variance	SD	
Brood ID	3264.71	57.14	
Year	64.08	8.01	
Residual	2080.16	45.61	

nestlings before fledging (Table 1). After controlling for the effects of the variables including day age, hatch order, sex, and their interactions, mean body mass residuals increased as brood size approached three and then decreased (mean residuals, one nestling: − 1.67, two nestlings: − 0.03, three nestlings: 0.38, four nestlings: − 0.76, Fig. 1), indicating that the quality was highest when the number of nestlings was three in the wild population of Created Ibis.

Variation in apparent survival of offspring as adults

Using the "median *c*-hat" approach in the program MARK, *c*-hat = 1.26 was used to adjust for over-dispersion in the data. Model selection results showed that the first two models of apparent survival were supported ($\Delta QAIC_C < 2.0$). Although the best-supported model does not include brood size, the inclusion of brood size slightly reduced the AIC_C weights of the model (Table S1). Based on a χ^2 distribution, the second best-supported model [$\varphi(BS)\ p(.)$] fits the data equally well compared to the first model ($\chi^2 = 3.54$, $df = 2$, $P = 0.171$), suggesting that variation in survival of offspring as adults could be explained by differences in natal brood size. Since the second-best model is nearly as well supported as the best model. To avoid model selection uncertainty, we calculated an average estimate for survival rate by averaging over all models with an AIC_C weight > 0 in the candidate model set. Individuals from one-nestling broods had the lowest adult survival (Table S2, Fig. S2). Individuals from two-nestling broods had relatively higher survival rate than from one-nestling broods, but this difference was not significant (estimate ± SE: 0.97 ± 0.59, 95% CI 0.17–2.12, Table S2, Fig. S2). Individuals from three-nestling broods had slightly higher survival rate than from two-nestling broods and had 7% higher survival rates than from one-nestling broods (estimate ± SE: 1.37 ± 0.62, 95% CI 0.16–2.58, Table S2, Fig. S2).

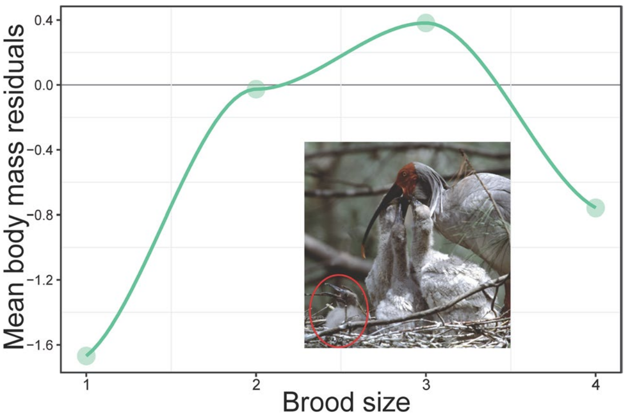

Fig. 1 The effects of brood size on mean body mass residuals, after controlling for the effects of year, sex, day age, hatch order, and their interactions in wild Crested Ibis, 2013–2018. Line fit via loess smoothing. The photograph (©Jingquan Jiao) shows a four-nestling brood; three are grapping for foods from adult, but the other (red circle), which is significantly smaller, cannot obtain foods

Variation in lifetime reproductive performance

A summary of vital life history traits related to long-term fitness consequences is presented in Table S3. The age of first reproduction did not differ among offspring from different brood sizes (Table 2, Fig. 2A), though the individuals from three-nestling broods, when compared with one- and two-nestling broods, had significantly longer breeding lifespan (Table 2, Fig. 2B). Likewise, the individuals from three-nestling broods had higher average reproductive success per year, as counted as young fledglings. Furthermore, when only successful breeding years in breeding lifespan were counted, the average number of fledglings per year had similar variation, although it was not significant (Table 2, Fig. 2C).

The most supported model ($\Delta AIC_C = 0.0$) explaining variation in lifetime reproductive success included the effect of brood size, age of first reproduction, and breeding lifespan (Table 3). Individuals from three-nestling broods had 22.0% higher lifetime reproductive success than those from two-nestling broods and had measurements twice as high as those from one-nestling broods; individuals from two-nestling broods had 65.9% higher lifetime reproductive success than those from one-nestling broods (mean ± SE, one-nestling brood: 6.56 ± 1.93, range: 1 − 20, *n* = 9; two-nestling brood:

Table 2 Models examining variation in life history traits related to lifetime reproductive performance in wild Crested Ibis, 1990–2018. Beta coefficients with 95% confidence intervals not overlapping zero are in bold

Term	Lifetime reproductive performance (model type)			
	Age of first reproduction (GLM, CMP)	Breeding lifespan (GLM, Poisson)	Reproductive success per year[a] (GLM, CMP)	No. fledglings per successful year[b] (GLM, CMP)
Intercept	0.821 (0.594; 1.048)	2.847 (2.181; 3.463)	0.209 (− 0.087; 0.504)	0.416 (0.140; 0.691)
Brood size − 2	0.188 (− 0.060; 0.437)	**− 0.937 (− 1.639; − 0.196)**	0.173 (− 0.161; 0.506)	0.060 (− 0.250; 0.369)
Brood size − 3	0.128 (− 0.126; 0.383)	**− 0.926 (− 1.609; − 0.202)**	**0.363 (0.031; 0.694)**	0.242 (− 0.063; 0.547)

[a] Lifetime reproductive success/breeding lifespan. [b] Lifetime reproductive success/reproductive success years in breeding lifespan

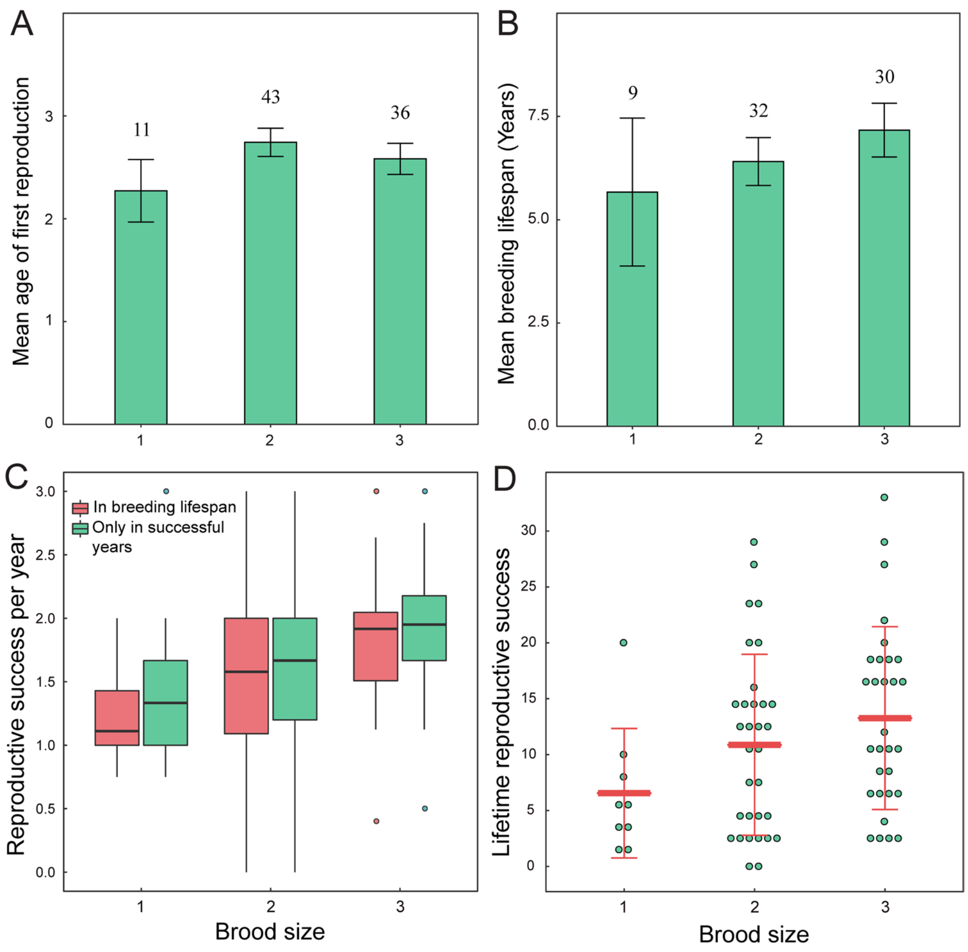

Fig. 2 Variation in mean age of first reproduction (**A**), mean breeding lifespan (**B**), reproductive success (number of fledging) per year in entire breeding lifespan and only in successful breeding years (**C**), and lifetime reproductive success (number of fledging during lifetime) (**D**) of individuals with natal brood size for wild Crested Ibis ($n = 71$). Bars represent SD, and the numbers above the columns represent the sample size in **A** and **B**. The boxes in **C** show the median, interquartile range, whiskers (indicating 1.5 × the interquartile range), and outliers. Red lines in **D** represent mean ± SD

Table 3 Performance of the generalized linear mixed models used to explain variation in lifetime reproductive success ($n = 71$) of wild Crested Ibis, 1990–2018

Model structure	*df*	ΔAIC$_C$	Weight	logLik
BS + AFR + BL	6	0.00	0.51	− 198.53
BS + BL	5	0.75	0.35	− 200.10
AFR + BL	5	3.10	0.11	− 201.28
BL	4	5.21	0.04	− 203.50
BS	4	80.25	0.00	− 241.01
AFR + BS	5	81.66	0.00	− 240.56
Null	3	86.13	0.00	− 245.08
AFR	4	87.24	0.00	− 244.51

AFR was the age of first reproduction; *BS* was the brood size; *BL* was the breeding lifespan

10.88 ± 1.43, range: 0 − 29; $n = 32$; three-nestling brood: 13.27 ± 1.49, range: 2 − 33, $n = 30$, Fig. 2D). Individuals that started breeding at the age of 2 had relatively high lifetime reproductive success compared to those at older ages or at only 1 year old (Fig. 3A). Additionally, the lifetime reproductive success of individuals positively correlated with their breeding lifespan (estimate ± SE: 1.858 ± 0.136, $df = 1/73$, $t = 13.689$, $R^2 = 0.716$, $P < 0.001$, Fig. 3B), and the most productive individual breeding 16 years produced a total of 33 fledglings.

Variation of brood size across years

Based on the 65 pairs that bred for at least 2 years, the result of GLMM showed that brood sizes are significantly influenced by the year in which breeding occurred (estimate ± SE: 0.016 ± 0.007, 95% CI 0.003–0.03). This finding suggests that brood sizes of an individual pair varied from year to year: in some years, the mean brood size was very small (e.g., 1993), but in the other year (e.g., 1994), all pairs could produce at least three nestlings. Moreover, the variability of brood sizes within each year was smaller in 2001–2018 than in 1990–2000 (Fig. 4), and we found that the proportion of broods of three decreased from 35% in 1990–2000 to 23% in 2001–2018, while the proportion of broods of two increased from 21 to 49% in the same time periods, respectively. Hence, broods of two offspring are the most common in the wild population of Crested Ibis.

Fig. 3 **A** The variation in lifetime reproductive success of individuals started breeding at different ages. Violin plots (green) show the range and distribution of the data; the widest portions of the plots demonstrate where the data is most likely to be distributed, and the black dots indicate outliers. The boxes in violin plots show the median, interquartile range, and whiskers (indicating 1.5 × the interquartile range). **B** The positive relationship between breeding lifespan of individuals and their lifetime reproductive success for wild Crested Ibis, 1990–2018. Shaded area represents the 95% credible interval

Discussion

In this study, we investigated the correlations between brood size, offspring quality, and lifetime fitness in a natural population of a long-lived bird. In general, our results demonstrated positive correlations between brood size and body mass, adult survival, and lifetime reproductive success of offspring, indicating that offspring quality increases with natal brood size. Specifically, we demonstrated four novel findings regarding the Crested Ibis. First, nestlings' body mass (a proxy of offspring quality before fledging) increases with brood size up to broods of three, whereas broods of four are rare, and the body mass of nestlings in these broods was lower compared to those in broods of three. Second, offspring from three-nestling broods had higher adult survival and lifetime fitness than those from one- or two-nestling broods. Third, the most common brood size (two nestlings) is smaller than broods with the highest offspring quality (three nestlings) and production (four nestlings). Finally, the broods in the wild population significantly varied across years.

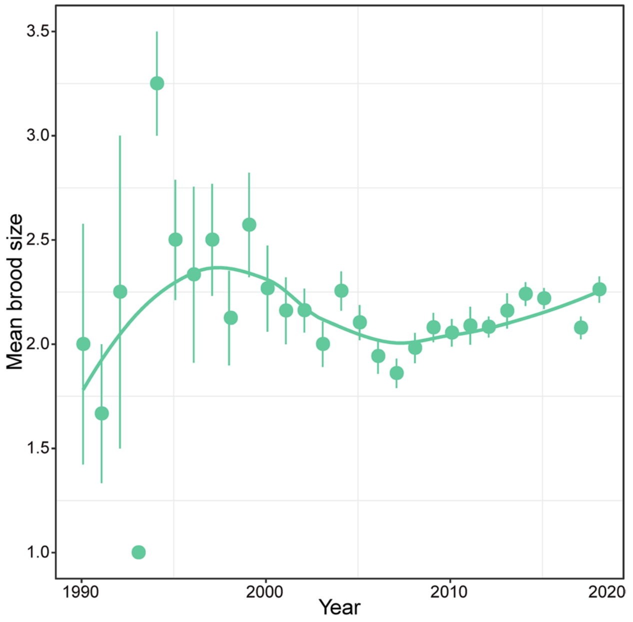

Fig. 4 The variation of mean brood size across years in the wild Crested Ibis population, 1990–2018. Bars represent SD, line fit via loess smoothing

Relationships between brood size and nestlings' quality

A key concept of life history theory is the trade-off among life history traits under the fact that resources are limited, such as when offspring number increases but offspring quality declines (Jacobsen et al. 1995; Ricklefs 2000; Roff et al. 2006). For example, in long-lived barn owls (*Tyto alba*), the body mass of nestlings was lower in enlarged than reduced broods (Roulin et al. 1999). For great tits (*Parus major*), reduced broods produced larger-sized nestlings than control and enlarged broods (Rytkönen and Orell 2001). Though this quantity-quality trade-off seems to be inevitable, some studies have observed that such trade-offs only under certain circumstances (e.g., resources scarcity) (Gillespie et al. 2008); if parental care varies significantly or if there is spatiotemporal variation in resource richness, this correlation between offspring quantity and quality may be weak or even positive (van Noordwijk and de Jong 1986; Emery Thompson et al. 2016). Our study of a population of wild Crested Ibis found that nestlings' body mass increases with brood size until the offspring number exceeds broods of three. Even though broods of four are rare, this finding may suggest that different processes are at play; the quantity-quality trade-off can be observed when the brood size is greater than three due to an observed decrease in the body mass of the nestlings, but the lower quality of smaller broods (one or two nestlings) are the consequences of other constraints.

The negative process is similar to the results found in studies of other altricial birds (Rytkönen and Orell 2001; Parejo and Danchin 2006). Although parents with four broods could fledge more offspring, these nestlings' body mass declined. We believe that the reduction of nestlings' body mass in broods of four is a result of competition and limitation of food resources (Lack 1947; Fig. 1). Ding (2004) reported that malnutrition due to food shortage is the primary cause of nestling mortality (accounting for 40%, $n=91$), therefore limiting the ability of parents to rear more high-quality nestlings. Moreover, even though we did not explicitly conduct brood size manipulation experiments, researchers exploited egg-replenishment habits in the birds throughout the early stage of the species rescue process in order to increase egg production of captive Crested Ibis. When all or part of the eggs were taken artificially, a female could continuously lay five to six eggs, but the hatching success of these eggs and the developmental quality of nestlings declined, and the survival of female was often challenged (Ding 2004). Hence, these results suggested that we can still expect to observe a quantity-quality trade-off when brood sizes are greater than a given size in natural broods under limited resources conditions; even if the upper bound of offspring number is rarely encountered in nature, the quality of nestlings decreases when parents produce more offspring that exceed this given size.

Effects of brood size on adult survival and their lifetime fitness

The conditions during an individual's developmental period may have a long-term influence on adult survival and fitness once they become independent (Harrison et al. 2011; Minias et al. 2015). To test this long-lasting effect, we investigated other metrics of quality in this study (aside from body mass) such as adult survival and lifetime reproductive performance. Results derived from the program MARK showed that the best-supported model on apparent survival allowed survival to be a constant; this is because the survival rate of offspring after 2 years old (adult survival) was estimated in this study, and the variation of adult survival is generally smaller than that of young or sub-adults in Crested Ibis (Ding 2004). As such, we observed a relatively small shift in adult survival among brood sizes. Nonetheless, we still detected some support for variation in adult survival with brood size. Offspring from three-nestling broods had significantly higher adult survival than those from one- and two-nestling broods, which was consistent with the pattern of changes in the body mass of nestlings. Indeed, our results are similar to those in studies on other long-lived species. For example, in black brant, larger goslings also have subsequent survival advantages (Sedinger et al. 1995; Sedinger and Chelgren 2007). These results verify the existence of a long-lasting effect in long-lived species; that is, the quality during the growth period could influence the survival of individuals when they are adults (Owen and Black 1989).

As for lifetime fitness, long-term data (29 years) on the Crested Ibis revealed that lifetime reproductive performance differs among brood sizes. Individuals from three-nestling broods had a significantly longer breeding lifespan, higher reproductive success per year, and higher lifetime reproductive success than those from smaller broods. Although no differences in age of first reproduction among brood sizes were detected, we found that individuals who reproduced relatively early had higher lifetime reproductive success because these individuals had a longer breeding lifespan (Song et al. 2019), and breeding lifespan positively was correlated with lifetime reproductive success for Crested Ibis. The number of fledglings per year in breeding success years does not significantly change, but individuals from three-nestling broods have significantly higher reproductive successes per year in their entire breeding lifespan; this finding suggests that individuals from three-nestling broods have higher reproductive success rates, while individuals from smaller broods are more likely to fail to reproduce. Moreover, breeding lifespan also reflects adult survival, which further supports the reliability of the estimated survival from the MARK program. With these results considered together, we demonstrate that Crested Ibis demonstrates the long-term effect of early body conditions on later life performance. The higher quality (e.g., higher body mass) of individuals during growth not only conveys higher survival when they are adults, but also higher lifetime fitness consequences. Since broods of four nestlings are rare, broods of three nestlings are the largest normally observed in the population. Thus, we concluded that offspring quality (body mass, adult survival, lifetime reproductive success) overall increases with brood size, and offspring from broods of three nestlings had the highest quality in a natural population of Crested Ibis.

What factors are responsible for the most common brood size and lower offspring quality reared in these broods?

Based on our results, we conclude that the most common brood size is smaller than broods with the highest offspring quality and production in the Crested Ibis population—a phenomenon common in other bird species (Lepage et al. 1998; Loonen et al. 1999; Leach et al. 2017). Why are smaller broods most common in the population? One possible explanation is that parents tend to consistently produce broods of a given size because of a particular heritable component (Boag and van Noordwijk 1987). However, we failed to find evidence to support this hypothesis, because the brood size of individual pairs varied significantly from year to year. These findings instead indicated that environmental conditions (e.g. climate, food resources) in a given year have a profound effect on brood size. For instance, the mean temperature between March and May in 1993 is significantly lower, and the precipitation is heavier than in 1994 (Wang and Zhai 2001). Low temperature and heavy precipitation not only resulted in food resource scarcity and low food availability, but also in some partial depredation or mortality for Crested Ibis (Ding 2004), eventually resulted in smaller mean brood size in 1993 compared to 1994. Similarly, in little penguin (*Eudyptula minor*), a sharp decline of food resource was associated with low annual reproductive output (Kowalczyk et al. 2014). These results suggest that small broods (e.g., only one or two nestlings) are more common in resource-poor years. Overall, the results we presented in this article showed that the variability of brood sizes within each year was smaller after 2000, which resulted from the proportion of broods of three decreased while the proportion of broods of two increased, and this variation in brood size was mainly due to changes in clutch size (e.g., producing three nestlings need at least three or four eggs, but the proportion of clutches of these eggs significantly declined after 2000, XX et al. unpublished data). As stated by the "egg-production limitation" hypothesis, clutch size is limited by the nutrients accumulated during the egg formation period (Lack 1967; Rohwer 1992). Indeed, since the rediscovery in the mountains in 1981, with the increasing population size, Crested Ibis has rapidly dispersed from their original breeding range (mountains) to new habitat (plains) since 2000 (Ye et al. 2022), and the proportion of pairs breeding in plains has been higher than in mountains habitat (Wang et al. 2014, 2020). A recent study on this species revealed that high-quality food resources were relatively insufficient in plains in the early breeding season because of different tillage methods (Xu et al. 2022). In plains, most of the croplands are planted with dryland farming (such as wheat, rape) in winter and the next spring, resulting in a serious shortage of ideal foraging grounds (winter-flooded paddy fields) and food resources (aquatic organisms) for the Crested Ibis. Hence, we believe that this spatiotemporal variation in resources determined variation in clutch sizes, and poor access to high-quality food supply led the broods of two to be the most common brood size in the wild population of the Crested Ibis.

Why do individuals from small broods have lower quality (lower body mass, adult survival, and lifetime reproductive success)? We believe resources also play a critical role; high availability of resources and successful foraging can lead to good growth condition and fitness advantage, not only by strengthening survival but also by having a positive influence on reproductive performance (Weimerskirch 2018). As mentioned above, in resource-rich years or in their original habitat (in mountains, a number of winter-flooded paddy fields provide abundant, high-quality food resources), pairs not only could produce three nestlings but are capable of raising them successfully (e.g., higher body mass). While in resource-poor years, food shortage causes malnutrition in nestlings (Ding 2004), affecting their long-term survival and fitness consequences. In addition, with the increasing population size and nest density, food resources for the Crested Ibis are insufficient during breeding seasons in recent years (Ye et al. 2017, 2022; Song 2018), resulting in many small, low-quality broods. This finding aligns with previous studies on other bird species (Herzog 2002; Rushing et al. 2016; Calvert et al. 2019). For instance, barnacle goose (*Branta leucopsis*) parents that have better access to local food supply would strengthen the growth of their offspring (Larsson and Forslund 1991). In American Redstart (*Setophaga ruticilla*), individuals occupying high-quality habitat benefit to improve reproductive success (Smith and Moore 2005). Canada jays (*Perisoreus canadensis*) that dispersed to territories of lesser quality also experienced lower nest success rates (Fuirst et al. 2021). On the other hand, some studies reported the influence of heritable component on the growth and body size of offspring in birds (Sedinger et al. 1995; Hamel et al. 2009). For example, Nicolai and Sedinger (2012) showed that goslings that grow most rapidly also produce goslings with the highest mean fitness in black brant geese. Although Song et al. (2019) found that the quality of parents could be transmitted to the next generation in the asynchronous hatching Crested Ibis, as the earlier-hatched nestlings had better quality and this advantage may help them as adults produce offspring with high quality. We did not show evidences supporting the heritable component in this study due to data sparseness of parental quality.

In conclusion, our results suggest that offspring quality increases with brood size, and offspring from three-nestlings broods have the highest quality. We also found that broods of individual pairs vary from year to year, and the proportions of different brood sizes changed after 2000, coinciding with the dispersal of the Crested Ibis population.

Thus, we believe that our results support the resource limitation hypothesis, and this long-term study provides an explanation for why the most common brood size is two nestlings; how spatiotemporal variation in resources plays an important role in brood size and subsequent fitness determination; and how only pairs with access to high-quality resources are able to produce larger broods of nestlings that achieve higher body mass and subsequent fitness advantages, whereas others in poor-quality habitats were restricted to a small, poor-quality broods. We found that broods of four are rare, and the body mass of nestlings from broods of four is lower compared to broods of three, which may be suggestive of a trade-off, and we may still expect to observe quantity-quality trade-off when brood size is greater than a given size in natural broods under limited resources condition. As part of a series which aims to understand the long-term variation in the life history of endangered Crested Ibis, this paper demonstrated the correlation between brood size and offspring quality; in a future work, we hope to explore the spatiotemporal variation in pace-of-life and its driving mechanisms, to understand more fully the ecological implications of life history evolution.

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Author contribution CD and XX conceived the study; YY, CW, BQ, and ZS contributed to the data collection; XX and YY analyzed the data; CD and XX led the writing of the manuscript; EB advised on manuscript writing and reviewed the drafts of the paper.

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Data availability The datasets used in this work are available in the Dryad Digital Repository, https://doi.org/10.5061/dryad.x95x69pjx.

Declarations

Ethics approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. All fieldwork was conducted with the permission and cooperation of Shaanxi Hanzhong Crested Ibis National Nature Reserve and approved by the Ethic and Animal Welfare Committee of Beijing Forestry University (Approval No. EAWC_BJFU_2022010). This work was part of a long-term, ongoing conservation and research project for endangered Crested Ibis, which does not have any harmful influence to the Crested Ibis.

Conflict of interest The authors declare no competing interests.

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