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Original Article

Silver spoon effects of hatching order in an asynchronous hatching bird

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The silver spoon hypothesis proposes that individuals which develop under favorable conditions will gain fitness benefits throughout their lifetime. Hatching order may create a considerable size hierarchy within a brood and lead to earlier-hatched nestlings having a competitive advantage over their siblings, which has been illustrated in some studies. However, there have been few explorations into the effect on subsequent generations. Here, using a 15-year-long study, we investigated the long-term fitness consequences of hatching order in the endangered crested ibis, *Nipponia nippon*, a species with complete hatching asynchrony. In this study, we found strong support for silver spoon effects acting on hatching order. Compared with later-hatched nestlings, first-hatched nestlings begin reproduction at an earlier age, have higher adult survival rates, possess a longer breeding life span, and achieve higher lifetime reproductive success. Interestingly, we found carry-over effects of hatching order into the next generation. Nestlings which hatched earlier and became breeders in turn also produced nestlings with larger tarsus and better body condition. Additionally, we found a positive correlation among life-history traits in crested ibis. Individuals which started reproduction at a younger age were shown to possess a longer breeding life span, and the annual brood size increased with an individual's breeding life span. This suggests that the earlier-hatched nestlings are of better quality and the "silver spoon" effects of hatching order cover all life-history stages and next generation effects.

Key words: **silver spoon effect, hatching order, long-term fitness consequence, life history, individual quality, crested ibis.**

INTRODUCTION

A fundamental concept in life-history theory is that organisms are constrained by trade-offs under finite resources (Stearns 1992). The trade-off between fundamental life-history characteristics, such as reproduction and survival, has been extensively documented at the interspecific level (Williams, 1966; Christians 2000; Roff 2002; Walker et al. 2008; Mourocq et al. 2016; Rohr et al. 2016). Within species, however, the direction of the correlation between the costs of reproduction and subsequent survival is inconsistent, and in some cases, even a positive correlation between reproduction and survival is observed (van Noordwijk and de Jong 1986; Wendeln and Becker 1999; Cam et al. 2002; Hamel et al. 2009; Thompson et al. 2016). This variance in observed correlations could be driven by the variation in the amount of resources available to individuals, which is often referred to as heterogeneity of individual quality (Wilson and Nussey 2010). A range of traits have been employed to capture individual quality, including reproductive effort, individuals' size, body condition, and longevity (Wendeln and Becker 1999; Cam et al. 2002; Blums et al. 2005; Hamel et al. 2009; Fay et al. 2016). Heterogeneity among traits is expected to evolve if it can be transferred into the next generation (Wilson and Nussey 2010), which requires that the fitness individuals gain is at least partly a consequence of the quality of their parents, such as genetic quality or investment ability. The long-term consequences of condition during development on fitness hence are at the heart of the life history evolution (Lindström 1999; Sæther et al. 2013).

The conditions during the developmental stage are likely to influence individuals' quality at independence (Haywood and Perrins 1992; Green and Cockburn 2001; Maddox and Weatherhead 2008; Bowers et al. 2011; Minias et al. 2015). Additionally, this influence may be effective for a long time within an individual's lifetime (van de Pol et al. 2006) and may cause not only the variance

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on short-term fitness such as juvenile survival rate (Williams et al. 1993; Sedinger et al. 1995; Badyaev et al. 2002) but may also have delayed consequences on various other fitness components, such as the age of maturity, annual survival rate, annual reproductive success, and breeding life span (Lindström 1999; Cam et al. 2003; van de Pol et al. 2006; Pigeon et al. 2017). If developing under favorable conditions causes an individual to enjoy a fitness advantage throughout life, this is known as the "silver spoon" effect (Grafen 1988). The silver spoon effect has been demonstrated in the context of many factors which affect rearing conditions such as breeding season (Sinervo and Doughty 1996; Einum and Fleming 2000), natal habitat quality (van de Pol et al. 2006), environment condition (Reid et al. 2003; Balbontín and Møller 2015), and food availability (Madsen and Shine 2000; Wong and Kölliker, 2014; Briga et.al. 2017).

The idea of the "silver spoon" effect was based on the influence of conditions' individuals experienced during development on their future phenotype and life-history traits, and these traits should positively correlate with fitness and covariance in the same direction. However, rather than a positive correlation, the life-history traits may also show trade-offs. Current investment is consequently expected to be negatively correlated with future investment (Stearns 1992). For example, high breeding investment in early life may reduce survival rate (Clutton-Brock 1984; Viallefont et al. 1995; Blomquist 2009) and cause earlier senescence (Kim et al. 2011). Given the difficulties associated with monitoring individuals across their lifetime, many studies can provide only limited information about life-history traits (Badyaev et al. 2002; Millon et al. 2011) rather than data on lifetime fitness consequences (Reid et al. 2003), and this may cause an unconvincing explanation about the fitness benefits as a result of developing under favorable conditions. Additionally, some studies report that individuals which develop during unfavorable early-life conditions can adjust their life-history trajectories to achieve similar lifetime fitness (Metcalfe and Monaghan 2001). Exploring the "silver spoon" effect requires: 1) comparing the fitness of individuals born under different early-life conditions at different life stages and 2) demonstrating the presence of a positive correlation, instead of trade-offs, between life-history traits.

Additionally, a cross-foster process was always required to distinguish between the influence of genetic and nutritional effects on development under favorable conditions (Metcalfe and Monaghan 2001; Cartwright et al. 2014), because the positive correlation between life-history traits may occur as a consequence of genetic quality (Partridge and Harvey 1988). The "silver spoon" effect of hatching order, which may to a large degree rule out genetic-driven influences, has rarely been studied over entire lifetimes, with few studies investigating its effect on next generation (Thomas et al. 1999; Cam et al. 2003; Aguirre and Vergara 2007; Martínez-Padilla et al. 2017). Most altricial birds start incubation before clutch completion (Clark and Wilson 1981), resulting in asynchronous hatching which can last from hours to days (Clark and Wilson 1981). Although the function of hatching asynchrony is still debatable (Stenning 1996), the overall consensus is that it causes a significant hierarchy within a brood during the rearing period and as a result, later-hatched nestlings experience more stressful conditions (Magrath 1990; Stoleson and Beissinger 1995; Stenning 1996). Additionally, as a consequence of earlier hatching as well as scramble competition for food and parental care, the dominant nestling will grow faster and fledge in better quality compared with later-hatched nestlings (Slagsvold 1986; Mock and Parker 1997; Maddox and Weatherhead 2008; Bowers et al. 2011). Good fledgling body condition can increase fitness later in life and correlates with higher prebreeding survival rate (Badyaev et al. 2002; Monrós et al. 2002) and future reproduction performance (Haywood and Perrins 1992; Cam et al. 2003). Hatching order, therefore, might affect an offspring's future fitness (Badyaev et al. 2002) as a consequence of a strong "silver spoon" effect. Moreover, although most studies focus on the effects of growth condition on an individual's fitness, it is still poorly understood how conditions experienced early in life are projected into the next generation (carry-over effects). Studies on "silver spoon" effects often investigate the effect of rearing conditions on the number of offspring produced later in life (Millon et al. 2011; Hayward et al. 2013; Douhard et al. 2014) and rarely on the quality of offspring produced.

Here, we examine the "silver spoon" effects of hatching order in a long-lived and long-term monogamous bird, the crested ibis *Nipponia nippon*, not only on comprehensive life-history traits throughout lifetime, but also on the effect on quality of next generation offspring. The crested ibis usually laid 3.04 ± 0.86 eggs (Ding 2004) in a clutch and showed complete hatching asynchrony as a consequence of immediate incubation after laying the first egg. Eggs were usually laid at 1-day intervals with a decline in mass, resulting in broods hatching asynchronously over 5–9 days (Ding 2004). The hatching and fledging order of nestlings in a brood were strictly consistent with laying order (Ding 2004), and the body size hierarchy among siblings remained during development from hatching to fledgling (Ding 2004; Zeng et al. 2017). The earlier-hatched nestlings had 1.82 times higher opportunity to receive food when competing with later-hatched sibling over food provided by the parents (Shi and Cao 2001), and the survival rate from hatching to fledgling declines with hatching order (first hatching = 0.90, second = 0.75, third = 0.71, 169 nestlings from 69 clutches, Ding 2004). Our study has three main objectives. Firstly, to quantify the relationship between life-history traits in the crested ibis, using data obtained over 25 years, and ascertain positive or negative correlations. Secondly, to explore whether condition-dependent effects, which accrue during the juvenile stage, reverberate into the adult stage. And thirdly, to explore whether this effect could carry over into the next generation.

METHODS

Study area and species

The study was carried out at Shaanxi Hanzhong Crested Ibis National Nature Reserve within the range 33°05′ to 33°45′N and 107°25′ to 107°82′E. This area lies on the intersection of the Han River plain and the southern slopes of the Qinling Mountains, China, where the world's only wild crested ibis population is located. The elevation ranges from 400 to 800 m above sea level, and the landscape includes forest, shrub, grass, cropland, open water, built-up areas, and artificial buildings (village and road) distributed throughout the study area. Crested ibis were previously widespread in Northeast Asia before rapidly declining in the early twentieth century. They were even evaluated as extinct in the wild in 1981 (Ding 2004). A small wild population of seven birds (two adult males, two adult females, and three juveniles of unknown gender) was rediscovered in 1981 in Yangxian, Shaanxi Province of central China (Liu 1981). With intense conservation efforts, this unique wild population has been recovered to more than 1100 individuals (Wang et al. 2014) and was recategorized from Critically Endangered to Endangered in 2001 (BirdLife International 2001).

Monogamous crested ibis breed once a year between February and June with both male and female birds contributing to nesting, hatching, and feeding chicks. The crested ibis nests in tall trees close to paddy fields, its main feeding habitat (Ma et al. 2001; Ding 2010) and close to villages (67.1 ± 5.33 m, $n = 415$, unpublished data). The wild population is resident, with only short seasonal movements taking place during summer and winter (Ding 2010). Crested ibis breeding pairs show strong nest site fidelity (95.6%, $n = 113$) and will reuse old nests if not damaged (Ding 2004); hence, there was no breeding dispersal.

Age at first reproduction and lifetime breeding life span

During the breeding season from February to June, the nature reserve staff checked all old nests from the previous year to record whether they were reused or abandoned. They also surveyed the whole breeding area for new nest sites and new nests. The local people were also active in the new nest survey because they are paid for information on new nests. From 1981 onwards, most of the nests (96.5%, $n = 1819$ nests) were GPS located and monitored for brood size. Brood size was determined by counting nestlings as they approached 35 days old, around a week before fledging.

Between 1987 and 1999, nestlings from wild population were banded with a combination of two-colored bands, and from 2000 onwards nestlings were banded with a colored band with a unique number (Ding 2010) which could be easily identified through a telescope. When these banded ibises started breeding, the band numbers of the parents were recorded during incubation and nestling provisioning. On average, 51.8% ($n = 307$) of parents were banded. The age at which an ibis was observed breeding in a new nest without previous reproductive records was recorded as the age of first reproduction. If year of birth and death data was available for an individual, breeding life span was calculated as the number of years in which the bird was observed nesting. Lifetime reproductive success was calculated by the number of nestlings an individual produced during its lifetime. Nestlings were recorded when they approached 35 days old.

To quantify the relationship between life-history traits in crested ibis, we recorded life-history traits of 64 individuals which have produced a total of 300 nests over an individual's lifetime including the age of first reproduction, breeding life span, and lifetime reproductive success.

Effects of hatching order on adult survival rate

In 2003 and 2004, the hatching order of 165 nestlings from 80 broods was confirmed by body size (body mass, length of bill and tarsus, Ding 2004; Zeng et al. 2017) when they were approximately 25 days old. The hatching order can be easily distinguished by body mass and length of tarsus within a brood (Ding 2004) and individual's growth rate declined with hatching order (Estimate ± SE: −3.773 ± 1.396, $X^2 = 7.303$, $P = 0.007$, $n = 16$, unpublished data). Individuals with confirmed hatching order were marked with a uniquely numbered-color band before fledging. After 4 years, when most of these ibises had reached adulthood and started reproducing (average age at first reproduction: 3.0 ± 0.1 years, ranging from 1 to 6 years), we conducted mark-recapture/resighting surveys of adult crested ibis between 2008 and 2017. The resighting history data only included ibis which had previously been observed as sexually mature. The maturity of crested ibis can easily be distinguished by the red featherless face and grey breeding plumage, whereas the nonmature crested ibis is identified by its orange featherless face and white plumage all year round (Ding 2010). Beginning in May of each year, when most nestlings were hatched and the parents were frequently foraging (average hatching data April 28, $n = 190$), we searched the whole breeding colony (confirmed by nature reserve staff each year) for resightings of marked individuals. Each individual's ring number was identified through a telescope (Zeiss Diascope 65T*FL), and the survey was conducted 3 times prior to the end of July. Multiple sightings of the same individual during the same year were classified as a single resighting event. We used this dataset to build individual resight history and estimate adult survival and recapture probability to ascertain whether the individual hatching order had an effect on adult survival. The effects of age at first capture were taken into account (two categories: marked in 2003 or 2004).

To analyze adult survival, we built Cormack–Jolly–Seber models (Lebreton et al. 1992) in MARK (White and Burnham 1999) to estimate annual apparent survival probability (φ) and recapture (re-sighting) probability (p). Survival models were constructed from design matrices that included year, age at first capture, and individual hatching order as factors. The over-dispersion of the most general model φ~ hatching order + age + year/p~ hatching order + year was evaluated using the "median c-hat" goodness-of-fit bootstrap simulation in MARK (White and Burnham 1999). The median c-hat was 1.136. Model selection was conducted using Akaike's information criteria adjusted for small sample size (AICc, Burnham and Anderson 2002), and over-dispersion was taken into account by using the median c-hat to build a quasi-likelihood corrected model selection criterion (QAICc, Anderson et al. 2001; Burnham and Anderson 2002). A subset of models with the lowest QAICc values (ΔQAICc < 2) was used to produce model-averaged parameter estimates (Burnham and Anderson 2002).

Effects of hatching order on individual's life history traits

The influence of hatching order on an individual's life history traits, such as age at first reproduction, lifetime reproductive success, last breeding age, and breeding life span, was estimated by long-term monitoring of crested ibises of known hatching order which were born and marked in 2003 and 2004. From 2005 to 2017, we monitored the first reproduction of 32 out of these 165 individuals and recorded the age at first reproduction. Since some of these individuals were not monitored every year, we only recorded the lifetime reproductive success (brood size), last breeding age, and breeding life span of 21 individuals. From 2005 to 2017, we recorded that these 21 individuals produced a total 96 nests throughout their lifetime. These data were used to estimate the effect of hatching order on annual reproductive success.

The carry-over effects into the next generation

To estimate the effect of a parent's hatching order on the condition of its offspring, we measured the body traits of 23 nestlings (body mass, length of bill, and tarsus) when they were approximately 20 days old. Nestlings were derived from 10 broods produced in 2014 and 2015 (three nests were measured both years) by seven paired parents of known hatching order.

Statistical analyses

We first analyzed the relationship between an individual's breeding life span and last breeding age on the age of first reproduction using linear models. We used a linear model to test the effect of breeding life span and age of first reproduction on lifetime reproductive success. Since the crested ibis' brood size as a count data is often under-dispersed (Lynch et al. 2014), we fitted a generalized linear mixed effect model (GLMM) with Conway–Maxwell–Poisson distribution (Sellers and Shmueli 2010) to analyze the influence of life history parameters on an individual's brood size. Due to the collinearity of breeding life span and the age of last reproduction ($r = 0.806$), the last breeding age was not included in the model. The average brood size of each year and whether a nest was used for the first time were designated as fixed effects, whereas nest identity and year were designated as random effects.

Due to the low frequency of broods containing three nestlings (25.7%, $n = 1348$ nests, from 2004 to 2017) and the low survival rate of the third nestling (see below), we only recorded the life-history data of the first- and second-hatched nestlings. Hence, we analyzed the influence of hatching order (first- vs. second-hatched) on the age of first reproduction, breeding life span, the number of chicks during lifetime, and the last breeding age using a GLMM with normal distribution. The identity of each ibis's nest of birth was designated a random effect to statistically control for the potential influence of a genetic effect.

The effects of hatching order on an individual's brood size were analyzed by fitting a GLMM with Conway–Maxwell–Poisson distribution (Sellers and Shmueli 2010). Hatching order, breeding life span, the average brood size of each year, and their interactions were designated as fixed factors, and the nest identity and year were designated as random effects. Natal dispersal distance was calculated using the "geosphere" package in R (Hijmans et al. 2015), and the effect of hatching order on an individual's natal dispersal was tested by using a one-way ANOVA. We used likelihood ratio to compare the explanatory power of our best fitting models of ibis annual survival rate. We used GLMMs with normal distribution to analyze the relationship between parental hatching order and their nestlings' body traits, whereas nest identity and year were designated as random effects. Since nestling body traits were also influenced by an individual's sex, nestling hatching order, brood size, and hatching date, we used these explanatory variables to build all possible models and then used AICc values (Burnham and Anderson 2002, Supplementary Table S3) to select the most suitable model to test the relationship between parental hatching order and their nestlings' body traits. Because siblings within a brood are of different ages, which influences an individual's body size, we controlled our analyses for individual age which was estimated using a growth model (Zeng et al. 2017).

The GLMMs used to analyze brood size were fitted using the "glmmTMB" package (Magnusson et al. 2017), GLMMs used to analyze the effect of hatching order on life-history traits and nestlings' body traits were fitted using the "lme4" package (Bates et al. 2014), and the survival model was constructed by the "RMark" package (Laake and Rexstad 2014). All analyses were performed in R version 3.1.1 (R Development Core Team; http://cran.r-project.org/).

RESULTS

Relationships between life-history traits

The age at which crested ibis reproduced for the first time was not associated with the age they bred for the last time (Estimate ± SE: 0.038 ± 0.338, DF = 1/68, $t = 0.113$, $P = 0.911$, $r = 0.014$) but declined significantly with breeding life span (Estimate ± SE: −0.776 ± 0.297, DF = 1/68, $t = -2.616$, $P = 0.011$, $r = 0.302$, Figure 1). The older an individual was when it started reproducing for the first time, the shorter its breeding life span. Lifetime reproductive success was significantly positively correlated with breeding life span (LM, Estimate ± SE: 2.325 ± 0.089, DF = 2/67, $t = 26.014$, $P < 0.001$) but not with the age of first reproduction (LM, Estimate ± SE: 0.276 ± 0.229, DF = 2/67, $t = 1.205$, $P = 0.232$).

Life-history traits have an influence on ibis' reproduction. The annual brood size produced by individuals increased with their breeding life span (Figure 2; Table 1) and average brood size produced by the population per year (Table 1). However, an individual's age of first reproduction was not associated with its brood sizes (Table 1).

Effects of hatching order

Reproductive performance

First-hatched nestlings, when compared with second-hatched nestlings, started reproduction at an earlier age (mean ± SE, first nestling: 2.3 ± 0.2 years; second nestling: 3.4 ± 0.4 years, $X^2 = 9.254$, $P = 0.002$, $n = 32$, Figure 3a), had a longer breeding life span (mean ± SE, first nestling: 6.5 ± 1.1 years; second nestling: 3.6 ± 0.8 years, $X^2 = 4.512$, $P = 0.033$, $n = 19$, Figure 3b), and had slightly higher lifetime reproductive success (mean ± SE, first nestling: 14.409 ± 3.472 chicks; second nestling: 6.574 ± 1.744 chicks, $X^2 = 3.790$, $P = 0.052$, $n = 19$, Figure 3c). Hatching order, however, had no effect on the last breeding age (mean ± SE, first nestling: 8.3 ± 1.1 years; second nestling: 8.4 ± 1.1 years, $X^2 = 0.009$, $P = 0.926$, $n = 19$, Figure 3d).

An individual's hatching order was not associated with annual brood size (Table 2). However, there was a significant interaction effect between an individual's hatching order and breeding life span on brood size (Table 2). First-hatched individuals with longer breeding life span had on average larger brood sizes (GLMM, Estimate ± SE: 0.070 ± 0.020, $z = 3.545$, $P < 0.001$, Figure 4). However, there was no relationship between breeding life span and brood size in second-hatched ibis (GLMM, Estimate ± SE: 0.021 ± 0.034, $z = 0.616$, $P = 0.538$, Figure 4), which suggests that the lifetime reproductive success of first-hatched ibis was more reliant on its breeding life span than second-hatched ibis.

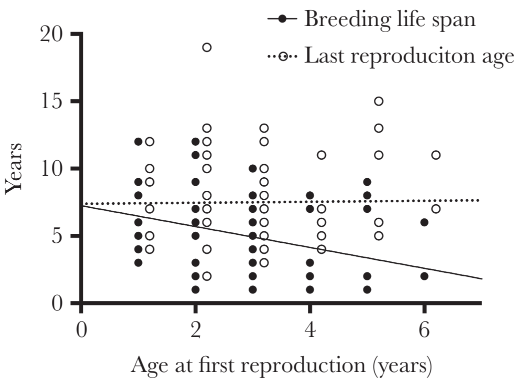

Figure 1

The age of first reproduction in crested ibis was negatively correlated with an individual's breeding life span (closed circles, solid line) and not correlated with an individual's last reproduction age (open circles, dotted line).

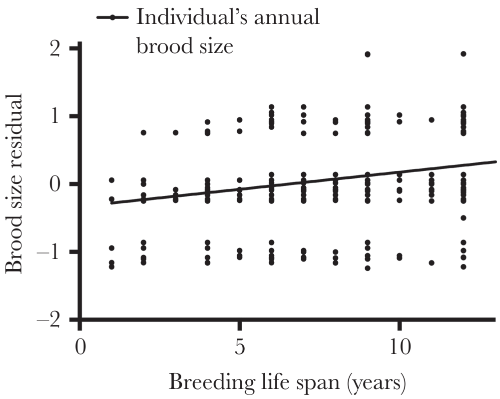

Figure 2
The annual brood size (corrected for average brood size produced in the population per year) increased with breeding life span for individual crested ibis (for statistics, see Table 1).

An individual's hatching order had no influence on its natal dispersal ($F_{1,44} = 0.038$, $P = 0.846$). First-hatched ibises disperse 14.8 ± 2.34 km ($n = 20$) from their birth site to their breeding site, and the natal dispersal distance was similar in second-hatched (14.7 ± 2.02 km, $n = 21$) and third-hatched ibises (16.1 ± 3.41 km, $n = 5$).

Adult survival rate

Of the 165 nestlings marked in 2003 and 2004, 46 individuals (27.9%) were rediscovered during the subsequent decade of research. Model selection favored models which included the effect of an individual's hatching order on the annual apparent survival rate of adult crested ibis (Supplementary Table S1). The first four models (Supplementary Table S1) of annual apparent survival were chosen to build the average model and provided a substantially better fit to the data than a null model ($X^2 = 30.396$, $P < 0.001$, $X^2 = 14.35$, $P = 0.006$, $X^2 = 16$, $P = 0.007$, and $X^2 = 31.846$, $P < 0.001$, respectively). Second hatched individual had lower apparent survival rate than first hatched individuals but not significant (95% CI around estimates narrowly overlapped 0, Supplementary Table S2), and third hatched individuals had the lowest apparent survival rate (Supplementary Table S2). First-hatched nestlings had 13.0% higher apparent survival rates at adulthood than second-hatched ibis (Table 3), and second-hatched nestlings possessed 17.8% higher apparent survival rates than third-hatched nestlings (Table 3).

Next generation

The "parent's hatching order" variable was present in the best models (ΔAIC <2) of the length of nestlings' tarsus and bill and body condition (represented by residuals above and below regression of body mass on tarsus length), but not in the best models of nestling body mass (Table 4). We used the best models which also included "parent's hatching order" as an independent variable to show the relationship between parent's hatching order and nestling's body traits (Table 4). First-hatched parents produced nestlings with longer tarsi (GLMM, Estimate ± SE: −0.808 ± 0.302, $X^2 = 7.135$, $P = 0.008$) and better body condition (GLMM, Estimate ± SE: −0.151 ± 0.067, $X^2 = 5.137$, $P = 0.023$), compared with the nestlings of parents which hatched later. However, there was no significant effect of "parent's hatching order" on nestling's bill length (GLMM, Estimate ± SE: −0.871 ± 0.601, $X^2 = 2.102$, $P = 0.147$).

Table 1
Results of GLMM showing the effects of breeding life-history parameters on crested ibis brood size

Parameter	Estimate	SE	z	*P*
Brood size				
Intercept	−0.266	0.254	−1.046	0.296
Age at first reproduction	0.011	0.016	0.678	0.498
Breeding life span	0.019	0.007	2.735	0.006**
First nesting	−0.083	0.045	−1.828	0.068
Average brood size per year	0.411	0.114	3.607	<0.001***

Significant relationships are indicated as *$P < 0.05$ and **$P < 0.01$.
Data obtained from 300 nests produced by 64 individuals.
The analyses included nest identity and year as random factors.

DISCUSSION

In this study on crested ibis, we found a positive correlation among life-history traits which suggests that heterogeneity of individual quality drives this relationship. We demonstrated a "silver spoon" effect of hatching order: 1) First-hatched nestlings began reproduction at an earlier age, had a longer breeding life span, and achieved higher lifetime reproductive success than second-hatched nestlings. 2) First-hatched nestlings had higher apparent survival rates as adults than second- and third-hatched nestlings. 3) Additionally, the positive correlation among life-history traits was more apparent in first-hatched nestlings. And more importantly, 4) the "silver spoon" effect is projected into the next generation. First-hatched nestlings, once breeders, produced offspring with a larger tarsus and better body condition.

Life-history traits

Life-history theory suggests a trade-off among competitive life-history traits, such as reproduction and survival (Stearns 1992; Roff 2002; Griesser et al. 2017). However, the "individual quality" hypothesis states that the heterogeneity of individual quality predicts a positive correlation between life-history traits (Bergeron et al. 2008; Lim et al. 2014; Fay et al. 2016) and hence reduces the contribution of a single life-history trait on fitness. In this study, we found no support for the "trade-off" hypothesis. Instead of a trade-off among resources, crested ibis show strong support for the "individual quality" hypothesis. Crested ibis recruiting earlier had a longer breeding life span, without reducing their longevity. In the context of the trade-off hypothesis, we would have expected the age at first reproduction to have a negative effect on future reproduction as a consequence of recruiting earlier in the population and higher investment in reproduction (Oli et al. 2002). On the other hand, crested ibis may show an increase in breeding life span because individuals recruiting earlier are of higher quality and achieve higher reproductive success (Fay et al. 2016). Additionally, the brood size produced each year by individuals also increased with their breeding life span and crested ibis show a highly positive relationship between lifetime reproductive success and breeding life span which all support the "individual quality" hypothesis. The relationship between first recruitment age, lifetime reproductive success, and breeding life span hence could be attributed to differences in individual quality.

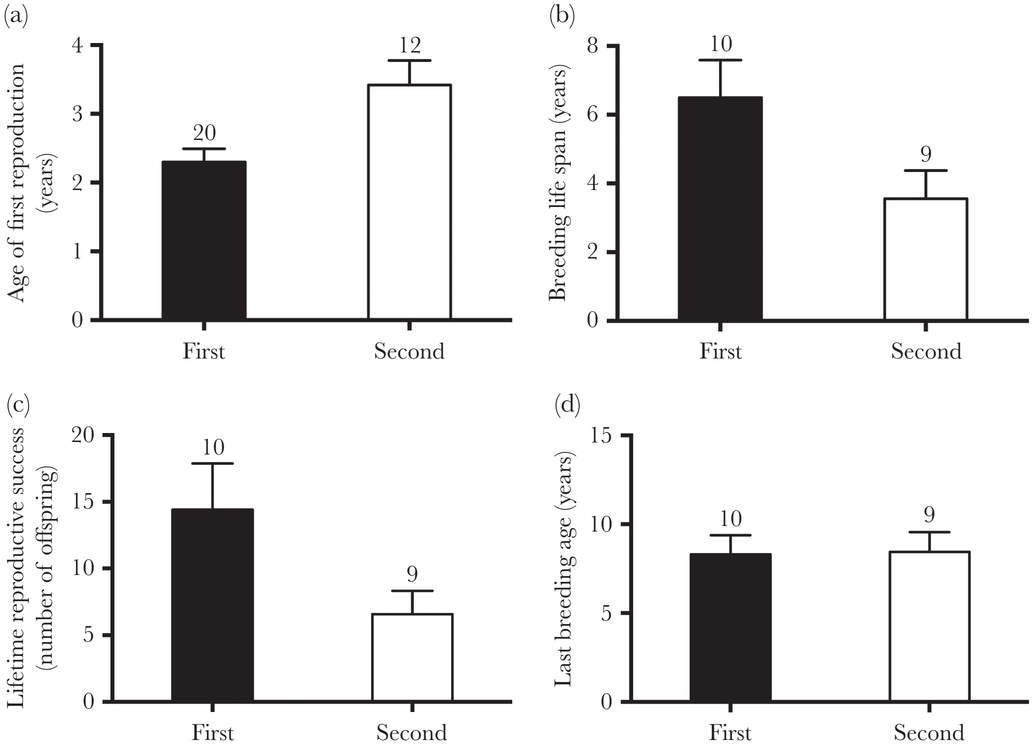

Figure 3
Long-term fitness consequences of hatching order. First-hatched nestling started reproduction at an earlier age than the second nestling (a), had longer breeding life span than the second nestling (b), and slightly higher lifetime reproductive success (number of offspring during lifetime, c). Hatching order had no effect on individual's last breeding age (d). Black bars: first-hatched nestling; white bars: second-hatched nestling.

Table 2
Results of GLMM showing the effects of an individual's hatching order on crested ibis brood size

Parameter	Estimate	SE	*z*	*P*
Brood size				
Intercept	−1.988	1.512	−1.314	0.189
Hatching order	1.092	0.950	1.149	0.250
Breeding life span	0.139	0.036	3.855	<0.001***
Average brood size per year	0.803	0.722	1.112	0.266
Hatching order × breeding life span	−0.057	0.018	−3.087	0.002**
Hatching order × average brood size per year	−0.294	0.445	−0.660	0.509

Significant relationships are indicated as $^*P < 0.05$ and $^{**}P < 0.01$.
Data obtained from 96 nests produced by 21 individuals.
The analyses included nest identity and year as random factors.

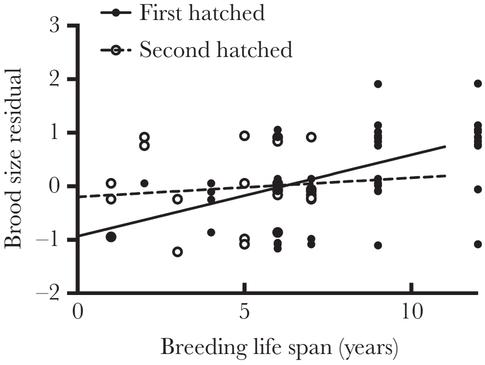

Figure 4
The relationship between an individual's breeding life span and brood size (corrected for average brood size produced in the population per year) each year, which were either first-hatched (*n* = 11) or second-hatched (*n* = 8). For first-hatched nestlings, the brood size increased with an individual's breeding life span (filled circles, solid line, *n* = 57), but not for second-hatched nestlings (open circles, dashed line, *n* = 29).

Silver spoon effect of hatching order

Effects of hatching order

In this study, we found comprehensive evidence that hatching order has long-term fitness consequences throughout life: 1) First-hatched ibises began reproduction earlier than second-hatched individuals, 2) this advantage was consistent throughout life, in that first-hatched individuals had a longer breeding life span than second-hatched ibises, and 3) additionally, first-hatched nestlings had a higher adult annual apparent survival rate compared with second- and third-hatched nestlings, with third-hatched nestlings showing the lowest adult annual apparent survival rate.

In our study, only 27.9% of the marked individuals were rediscovered; however, the survival rate survey was conducted 4 years before the nestlings were marked. An early study showed that the average survival rate of juvenile crested ibis was 0.66 (*n* = 94, Shi and Cao 2001), so we presumed that ibis which had not been resighted had died before the first survey and had not dispersed from the area of

Table 3

Model estimates of hatching order–specific survival probabilities (φ) for crested ibis with standard error (SE), lower 95% confidence limit (LCL), and upper 95% confidence limit (UCL)

Hatching order	φ	SE	LCL	UCL
First	0.949	0.032	0.838	0.985
Second	0.840	0.051	0.723	0.913
Third	0.713	0.138	0.400	0.902

study. The third-hatched nestlings showed the lowest adult annual apparent survival rate in our study. However, there is a possibility that hatching order–biased dispersal is occurring, where third-hatched individuals may be more likely to disperse out of the study area since they are of lower quality and may be more inclined to avoid competition (Hamilton and May 1977). In our study, we also tested the difference in dispersal distance between ibis of different hatching orders. Crested ibis only show natal dispersal (Ding 2010), and we found that hatching order had no influence on the natal dispersal of the crested. The apparent survival rate of crested ibis, therefore, might largely reflect the true survival rate which indicates that first-hatched nestlings may achieve better lifetime fitness.

The fitness consequences of rearing condition are at the heart of evolutionary studies of how parental quality is transferred into offspring (Lindström 1999; Sæther et al. 2013). However, it is difficult to get a good representation of lifetime fitness from limited life-history parameters because of the inconsistent correlation among life-history traits. In our study, although the sample size is limited, we not only showed the advantage associated with earlier hatching for key life-history traits, but also we showed that first-hatched nestlings produced more offspring during their lifetime than second-hatched individuals, which yields strong evidence of the occurrence of fitness benefits from earlier hatching.

Fitness trajectory of "silver spoon" effects

A positive relationship between competing life-history traits is expected, when there is a great difference between individuals' quality (van Noordwijk and de Jong 1986; Reznick et al. 2000). According to our results, the positive correlation between annual brood size and breeding life span was only significant in first-hatched ibis but not in second-hatched ibis (Figure 4). An individual's fitness can be described as the production of offspring throughout its lifetime (McGraw and Caswell 1996), that is, brood size multiplied by breeding life span. First-hatched nestlings therefore show more variance in fitness than second-hatched nestlings. Parental investment often forms a large part of altricial offspring's rearing environment and can affect an offspring's life history (Lindström 1999; Ratikainen and Kokko 2009), which suggests that crested ibis parents should invest more on first-hatched nestlings since there is a positive correlation between life-history traits and a larger variance in fitness. This is contrary to other studies which suggest that females will compensate for the detrimental effects of hatching asynchrony (Gil 2003; Groothuis et al. 2005). It may be important in future studies to examine whether parents allocated their investment according to hatching order in crested ibis.

Fitness transmits to next generation

Despite the fact that hatching order exists in most altricial birds (Clark and Wilson 1981) and some studies report its effect on individuals after fledging (Thomas et al. 1999; Cam et al. 2003; Aguirre and Vergara 2007; Martínez-Padilla et al. 2017), the role of hatching order on the next generation has rarely been reported. In our study, although the sample size is limited, we found that the effects of hatching order can also have an influence on the next generation's performance. Despite the influence from a nestling's own hatching order (body traits declined with nestlings' hatching order, Song et al. 2019), nestlings will have a longer tarsus and with better body condition when parents were earlier-hatched. Body condition in our study was estimated by body mass corrected for tarsus length, which represent that nestlings produced by earlier-hatched parents were larger and under better nutritional status compared with the nestlings of parents which hatched later. Ibises from an earlier hatching order will achieve more resources at the brood stage and can maintain that good condition throughout their lifetime, and they can thus produce offspring of high quality (Clutton-Brock 1984; Lim et al. 2014). However, the classic model about optimal allocation strategy suggests that mothers with more resources should produce offspring of the same size (i.e., the optimum investment per offspring) but in higher numbers (Smith and Fretwell 1974). On the other hand, the heterogeneity of an individual's quality suggests that individuals with better quality will achieve far more success in reproduction and fitness, especially if "silver spoon" effects from a developed condition predict a variance among individuals. In our study, due to better quality, first-hatched ibis not only produced offspring in higher numbers but also of better quality. Fitness is always defined as the genetic contribution to the future generations (Wilson and Nussey 2010), and the influence of parental quality on offspring quality will increase the fitness benefit of hatching earlier, since the individual size at fledging could cause higher prebreeding survival rate (Badyaev et al. 2002; Monrós et al. 2002) and better reproductive performance (Haywood and Perrins 1992; Cam et al. 2003). From an evolutionary perspective, individuals of different hatching orders will have different fitness benefits and different rates of gene propagation.

Table 4

Results of candidate GLMM model selection to assess the effects of parent's hatching order on 23 crested ibis nestling body traits

Parameter	AICc	ΔAICc	Number of parameters	Deviance
Length of tarsus				
HO + HD + PHO	70.586	0.000	7	40.972
HO + HD	71.778	1.192	6	48.010
Length of bill				
HO + HD	73.450	0.000	6	47.798
HO + HD + PHO	74.826	1.376	7	45.357
Body condition				
S + HO + BZ + PHO	244.405	0.000	8	262.415
Body mass				
HO	8.572	0.000	5	−12.498
S	9.613	1.041	5	−10.416
HO + HD	10.178	1.606	6	−23.991

Nest ID and years were entered as random factors. Nestling sex (S), nestlings' hatching order (HO), brood size (BZ), hatching date (HD), and parent's hatching order (PHO) were chosen as parameters for all possible models. The models used to obtain the statistical results shown in "Results" are highlighted in bold.

A fundamental assumption of many evolutionary studies is that the influence of parents or environment on offspring at development could persist into their adulthood, as a result of the long-term fitness consequences of "silver spoon" effects (Trivers and Willard 1973; Cam et al. 2003). Our results suggest that in crested ibises, with complete hatching asynchrony, hatching order has a strong "silver spoon" effect during individual lifetime and even across generations. Early-hatched individuals recruit earlier and possess a longer breeding life span, higher adult apparent survival rate, and lifetime reproductive success. This advantage of earlier hatching may project into the next generations by producing offspring with a larger tarsus and better body condition. Our study provides comprehensive evidence of the "silver spoon" effects of hatching order covering all life-history stages and next generation effects. These advantages of earlier-hatched nestlings throughout their entire life and the long-term effect of hatching order may be the important factors to consider in studies looking at heterogeneity in individual quality.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Authors' contributions: Zitan Song conceived the study, conducted the analyses, and wrote the manuscript; Yuqi Zou, Canshi Hu, and Yuanxing Ye contributed to data collection and result interpretation; Chao Wang and Baoping Qing contributed substantial materials and resources during field work; Jan Komdeur advised on data analyses and manuscript writing and reviewed drafts of the paper; Changqing Ding coordinated the long-term study of crested ibis, conceived the research ideas, wrote the manuscript, and reviewed drafts of the paper. All authors helped draft the manuscript and gave final approval for publication.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Song et al. (2018).

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