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Original Article

A diagnosis model of parental care: How parents optimize their provisioning strategy in brood reduction?

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Abstract

Altricial birds often display biased preferences in providing parental care for their dependent offspring, especially during food shortages. During this process, such inflexible rules may result in provisioning errors. To demonstrate how parents optimize their provisioning strategies, we proposed a "diagnosis model" of parental care to posit that parents will undergo a diagnosis procedure to test whether selecting against some particular offspring based on phenotype is an optimal strategy. We tested this model in an asynchronous hatching bird, the Azure-winged Magpie *Cyanopica cyanus*, based on 10 years of data about demography and parental provisioning behaviors. Given their higher daily survival rates, core offspring (those hatched on the first day) merits an investment priority compared with their marginal brood mates (those hatched on later days). However, a marginal offspring also merited a priority if it displayed greater weight gain than the expected value at the early post-hatching days. Parents could detect such a marginal offspring via a diagnosis strategy, in which they provisioned the brood at the diagnosis stage by delivering food to every nestling that begged, then biased food toward high-value nestlings at the subsequent decision stage by making a negative response to the begging of low-value nestlings. In this provisioning strategy, the growth performance of a nestling became a more reliable indicator of its investment value than its hatching order or competitive ability. Our findings provide evidence for this "diagnosis model of parental care" wherein parents use a diagnosis method to optimize their provisioning strategy in brood reduction.

Key words: brood reduction, parental care, provisioning strategy, weight gain.

In altricial birds, parents need to provide sustained, costly care to their dependent offspring until they can survive on their own (Williams 2018). To maximize reproductive fitness, parents have to make decisions to select against some offspring based on their ability in the resource acquirement (Lack 1947; Mock and Forbes 1995) and the reproductive values that they estimate for those offspring (Slagsvold 1997; Forbes 1999; Hasselquist and Kempenaers 2002; De Ayala et al. 2007). The sacrifice of lower valued nestlings (i.e. brood reduction) has often been observed in altricial birds when resources are limited, and this is widely accepted to represent an adaptive response of parents to poor breeding conditions (Lack 1947; Stoleson and Beissinger 1997; Forbes et al. 2002; Du et al. 2014; Fan et al. 2017; Da et al. 2018). In most species, brood reduction victims often die in the first few postnatal days, a time when the intensity of potential sibling rivalry is lowest and parents can support all nestlings (Slagsvold and Wiebe 2007). The decision to sacrifice nestlings in such a stage reflects a proactive selection by parents to disproportionately allocate care to higher valued offspring and avoid the high costs of investing offspring with lower survivorship. Thus, how parents optimize their provisioning strategies in selection among brood mates has long been a focus question in studies of parental investment (Forbes and Mock 1998).

Since prioritizing high-valued offspring can maximize their reproductive fitness, parents can make errors in selecting against a particular offspring in brood reduction. The main reason of making errors in brood selection is that altricial birds often use offspring phenotypic signals, such as size (Forbes 1999), age (Mock and Forbes 1995), coloration (De Ayala et al. 2007), and sex (Hasselquist and Kempenaers 2002), as the estimation of their investment values. The problem is that offspring phenotype does not always advertise their investment values honestly. For example, offspring in asynchronous hatching species are often classified into core (nestlings hatching on the first day) and marginal (nestlings hatching on later days), with core offspring usually being larger and hence more competitive than their marginal brood mates in the early nestling period (Mock and Forbes 1995). It is common that parents have given their provisioning priority to core offspring than to marginal ones in order to enhance their reproductive fitness (Jeon 2008; Forbes and Wiebe 2010). However, marginal offspring are of lower competitive than core offspring just because they are younger (Mock and Forbes 1995; Forbes 1999; Krist 2011), not because they have lower quality (Parker et al. 2002; Krauss and Yasukawa 2013) than the latter. If an additional unit of resource has been allocated to a marginal offspring, it can result in a higher reproductive return to parents than what is allocated to a

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core offspring (Godfray 1991; Krauss and Yasukawa 2013). Moreover, in some altricial birds, marginal nestlings can grow faster than their core brood mates, although they are smaller at the beginning of the nestling period because of their younger age (Da et al. 2018). Therefore, it implies that parents give provisioning priority always to core offspring can result in a risk of sacrificing some marginal offspring with potentially higher investment value. Under this condition, a strategy for parents to identify which marginal offspring have higher investment value than core offspring should have been favored by natural selection. Then, selecting for high-value marginal offspring against low-value core offspring may be a better investment strategy than giving priority always to core offspring.

To investigate how parents optimize their provisioning strategy in brood selection, we propose a new model of parental care—the diagnosis model (Figure 1A)—to demonstrate that parents in asynchronously hatching nests can use a diagnosis strategy to identify which marginal offspring have higher investment value and hence are worth of provisioning in priority. This model posits that parents adjust their provisioning strategy at different stages of the nestling period (i.e. the diagnosis, decision, and determination stages at different nestling ages, Figure 1A): they first provision the brood by giving food to every nestling that begged at the diagnosis stage, then bias food toward those high-value nestlings at the decision stage (i.e. making negative response to the begging of low-value nestlings), and after brood reduction try to raise all remaining nestlings at the determination stage. At the start of the nestling period when parents are able to satiate all nestlings because of their low food demand, parents deliver food to each nestling that begs to fulfill their food demands. In this case, if offspring display differences in growth performance, such as weight gain which is generally an indicator of future success of offspring (McCarty 2001), their investment value can be advertised honestly by their growth performance. This provisioning strategy can be treated as a diagnosis method for parents to detect offspring with higher investment value, no matter whether they are core or marginal ones. Under this condition, prioritizing their parental care always to these high-value nestlings can make parents realize higher reproductive fitness than always prioritizing parental care to core nestlings (Figure 1B). Therefore, the model first predicts that the growth performance of a nestling at the early stage (but not only their hatching order) determines its subsequent fate (i.e. fledging success at the end). Moreover, if a diagnosis strategy does exist, parents should change their provisioning behaviors after diagnosis, that is, at the decision stage (Figure 1A), because those detected low-value core and marginal offspring will be sacrificed. Consequently, the diagnosis model predicts secondly that, no matter what strategies, parents should respond more positively to the begging of nestlings at the diagnosis stage (i.e. the proportion of fed nestlings being higher because any begging nestlings would be fed) and then less positively to the begging of nestlings (i.e. the proportion of fed nestlings being lowered because low-value nestlings would obtain no food) at the subsequent decision stage (Figure 1C).

We tested the validity of the diagnosis model of parental care in the azure-winged magpie, *Cyanopica cyanus*, by studying parental provisioning behaviors with nestling age. In a population that breeds on the Tibetan Plateau, most azure-winged magpie nests hatch asynchronously (Da et al. 2018); hence nestlings in a nest can be classified into core and marginal offspring. In the past 10 years, demographic data of this Tibetan population show that the mean number of core nestlings (2.6 ± 0.04, n = 705 nests) is higher than that of marginal ones (1.9 ± 0.05, n = 705 nests), and the fledging number of

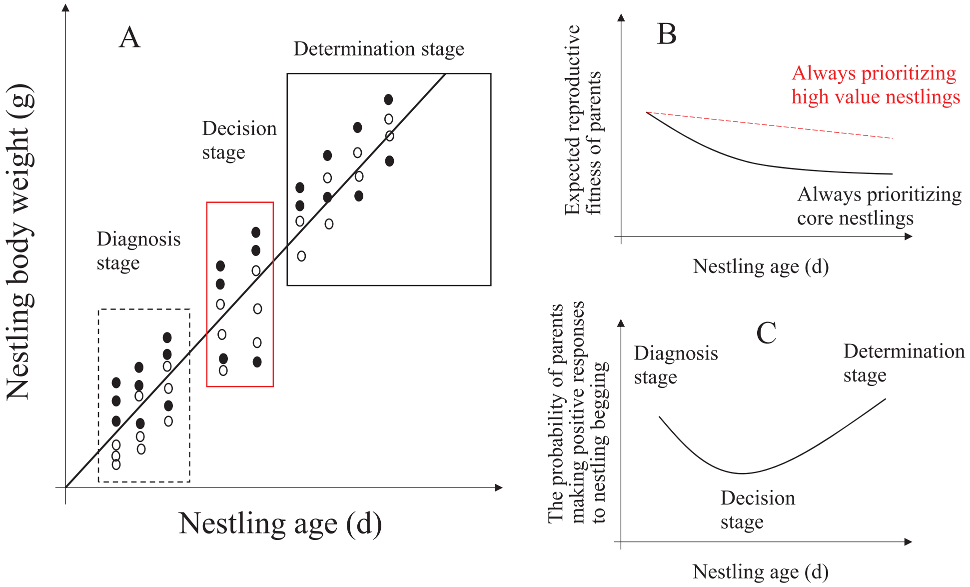

Figure 1. A "diagnosis model" of parental care in altricial birds with asynchronous hatching (A). It posits that parental care in altricial birds should be divided into 3 stages: the diagnosis stage, in which parents carry out a diagnosis strategy to identify the growth performance of core (filled cycles) and marginal offspring (blank cycles); the decision stage, in which parents reach a decision of which chick will be selected against (for instance, 1 core and marginal offspring with the lowest body weight); the determination stage, in which parents try to fledge all the remaining chicks (2 core and marginal offspring). It predicts that 1) the strategy of "always prioritizing highly valued nestlings" can realize higher reproductive fitness than the strategy of "always prioritizing core nestlings" (B), and 2) parents make more positive responses to nestling begging at the diagnosis stage and less positive response at the decision stage (C).

core nestlings (2.3 ± 0.05, n = 671 nests) also higher than that of marginal ones (1.6 ± 0.05, n = 671 nests; Zhu 2022). Although parents tend to adopt a "brood survival" strategy for provisioning nestlings (Da et al. 2018), brood reduction can occur in both core and marginal offspring (Zhu 2022). As azure-winged magpie is a regurgitation-feeding species (Ren et al. 2016), parents usually allocate food among more nestlings in a single feeding bout compared with parents of insectivorous birds (Du et al. 2014). Therefore, the azure-winged magpie becomes an excellent system to address how parents optimize their provisioning priority at different stages of the nestling period.

Here, we first compared the daily survival rate (referring to the proportion of individuals that were alive on day d–1 but died on day d) and hatching body weight between core and marginal offspring to confirm that provisioning core offspring in priority was a better investment strategy but could make errors as some marginal offspring with potentially higher investment value might be selected against. Next, we tested whether the growth performance of a nestling (its absolute body weight and relative weight gain between 2 checking days) at the early stage significantly determined its fate at fledging. Finally, we tested the variation of parental provisioning behaviors with nestling age by evaluating 1) the proportion of fed nestlings in each feeding bout and 2) parental responses to the begging behaviors of nestlings.

Material and Methods

Study area and population

This study was performed in Luqu County (34.6°N, 102.5°E, 3,400 m above sea level), Gansu Province, China, from 2012 to 2020. This region has a high-altitude climate with an annual average temperature of 2.3 °C and precipitation of 680 mm. The local vegetation consists of a typical alpine meadow, and the shrubs of *Berberis hemsleyana*, *Hippophae rhamnoides*, and *Salix caprea* are distributed in clusters along both sides of the Tao River. Azure-winged magpies prefer constructing their nests in *H. rhamnoides* and *S. caprea*. Given the clustered distribution of shrubs, Tibetan azure-winged magpie nests are divided into a series of colonies. Breeders in each colony construct their nests in a highly clumped pattern, and the nesting densities in different habitat patches ranged from 20 to 180 nests/ha (Ren et al. 2016).

Breeding parameters

We systematically searched for active nests in the shrubs each year. An active nest was monitored throughout the breeding season until all offspring fledged or were preyed upon by predators following the method described in Ren et al. (2016) and Da et al. (2018). Eggs and nestlings were individually marked according to their laying and hatching orders. The Arabic numeral was marked on the eggshell or a nestling's head, respectively, using a black permanent marker pen (Deli Group Co., LTD), which caused no nest abandonment by the azure-winged magpie adults. Data on breeding parameters used in this study included 1) laying date of the first egg in the earliest nest (set as day 1); 2) clutch initiation date of each nest (laying date of the first egg, standardized according to day 1) and incubation duration; 3) clutch size, brood size, and fledgling number; 4) hatching date (the first nestling hatched in a nest) and fledging date; 5) whether a nestling was core or marginal offspring; and 6) nestling body weight in each of the first 5 days and every 2 days thereafter of the nestling period. Weight gain of a nestling was estimated as the mean daily difference of body weight between 2 checking days.

A nest was considered successful if the social pair fledged at least 1 offspring. Any eggs or nestlings that disappeared before fledging were recorded. There were 3 causes of reproductive failure: 1) nest predation, which usually resulted in complete reproductive failure (occurring in 38.22% of 984 nests in 9 years); 2) conspecific nest raiding, which usually caused partial reproductive failure (occurring in 21.04% of 984 nests in 9 years); and 3) starvation (occurring in 11.48% of the 984 nests in 9 years, 92.41% (146 of 158) of starved nestlings at the age of 5–8 days). Based on video recordings or signs of nest predation, the reasons for a nestling's disappearance could be exactly determined (Ren et al. 2016). If an entire brood disappeared within a single day, nest predation was considered the reason for failure. If a nestling that grew normally disappeared 1 day, conspecific raiders were considered the reason of failure; however, if a nestling that grew abnormally (body weight did not increase between 2 checking days) disappeared, starvation was considered the reason of such a failure.

Once nestlings hatched, adult birds that provisioned the broods were captured by scalable loops (Da et al. 2018), under the Wildlife Conservation Law of the Tenth National People's Congress of China (28 August 2004). Each captured individual was leg banded with 1-numbered aluminum ring and 2 different-colored plastic rings to allow individual identification. After adult banding, parental provisioning behaviors were recorded by digital camcorders (ZX1; Eastman Kodak Company). A camcorder was fixed 1 m diagonally above the nest after both parents had been leg banded. The recording procedure caused no apparent disturbance to adults that delivered food to the brood or warmed the nestlings (Ren et al. 2016). The recording lasted between 09:00 and 12:00, and was performed at least every 2 days for a nest. Parental provisioning videos used in this study added up to more than 3,800 h of footage and covered 560 nests (mean ± SEM, 6.80 ± 0.18 h).

Parental provisioning behaviors

Data used to examine parental provisioning strategies were extracted from the video recordings by playback on the computer. First, we collected data on parental behaviors in a feeding bout. These data included 1) the identity of a nest visitor (identified according to the colors of its plastic rings) and whether it delivered food to the brood'; 2) amount of food delivered to the brood (i.e. the number of regurgitations); and 3) the number of nestlings that obtained food. We then extracted data on nestling behaviors in the feeding bout. These data included 1) the number of nestlings that displayed begging behaviors (such as head raising, gaping, and neck stretching); 2) the identity of the first nestling that displayed begging behaviors; 3) the number of nestlings that obtained food or not; and 4) whether a nestling that obtained no food in the feeding bout (unfed nestling) displayed begging behaviors. Based on these data, we calculated the proportion of fed nestlings in each feeding bout.

Statistical analysis

To confirm whether core offspring had higher reproductive value than their marginal brood mates, we first calculated the daily survival rate of core and marginal offspring based on the 9 years of demographic data using the software MARK (version 6.1, Cooch and White 2010). A generalized linear model was fitted to examine the effects of nestlings' age (continuous variable) and identity (core or marginal, factorial variable) on their daily survival rate (set as dependent variable after arcsine square root transformed, normal distribution). Moreover, we compared the hatching body weight between core and marginal offspring in the same nests using a paired sample *t*-test.

A nestling's growth performance (its absolute body weight and relative weight gain between 2 checking days) in the first 3e post-hatching days was indexed by the differences in its body weight (Appendix I in Supplementary Material) and weight gain (Appendix II in Supplementary Material) from the mean values of both parameters at the population level. The body weight of core and marginal offspring in a nest was first averaged, respectively, which was then averaged according to different brood sizes in each of the first 3 post-hatching days (Appendix I in Supplementary Material). The ultimate mean values were used as an indicator of the expected body size of azure-winged magpie nestlings. Accordingly, the expected value of weight gains of nestlings in the second and third post-hatching days was calculated (Appendix II in Supplementary Material). A generalized linear mixed model (GLMM) was fitted to test whether a nestling's growth performance in the first 3 post-hatching days determined its fate at the end of a breeding season (whether it fledged successfully or not, being set as the dependent variable, with binomial distribution), in which the brood size was also included as fixed effect variables, and the year and nest identity were used as random-effect variables.

To investigate how parental provisioning behaviors change with nestling age, we used 3 variables as proxies of parental provisioning strategies: the proportion of fed nestlings in 1 feeding bout, whether a nestling that first displayed begging behaviors was fed, and whether an unfed nestling begged in a feeding bout. Linear regression was carried out by setting the 3 variables as dependent variables, respectively. As there may be other factors potentially affecting the 3 dependent variables rather than nestling age, we fitted GLMMs to control for them by saving the predicted value of each dependent variable as the newly standardized variable. In the first GLMM, the proportion of fed nestlings in 1 feeding bout was set as the dependent variable (normal distribution), and fixed effects included brood size, amount of food delivered per feeding bout, and nestling age. In the second GLMM, whether the first begging nestling obtained food was set as the dependent variable (binomial distribution), and fixed effects included the amount of food delivered per feeding bout, the number of begging nestlings, and nestling age. In the third GLMM, whether an unfed nestling displayed begging behaviors in the feeding bout was set as the dependent variable (binomial distribution), and fixed effects included the amount of food delivered per feeding bout and nestling age. Year and nest identity were used as random effects in all 3 models.

All statistical analyses were carried out using R (version 3.5.0, R Core Team 2018). Descriptive data were presented as mean ± SEM. The null hypothesis was rejected when $P_{\text{2-tailed}} < 0.05$.

Results

In the past 9 years, we monitored the entire fate (from egg to fledging) of 705 azure-winged magpie nests that produced 1,865 core and 1,309 marginal offspring. There were 1,550 core and 1,044 marginal offspring that successfully fledged. At the population level, the daily survival rate of nestlings increased significantly with their age ($\beta \pm SE = 0.75 \pm 0.08$, $\chi^2 = 90.62$, $df = 1$, $P < 0.001$), and was significantly greater for core nestlings than for marginal ones ($\beta \pm SE = 5.12 \pm 0.81$, $\chi^2 = 39.45$, $df = 1$, $P < 0.001$; Figure 2A). At the nest level, an average of 88.95% (±1.17%, $n = 666$ nests) of core offspring fledged successfully, which as significantly higher compared with their marginal brood mates (70.79 ± 1.69%, $n = 666$ nests; $t_{665} = 12.34$, $P < 0.001$). Concerning the hatching body weight, core offspring (4.64 ± 0.15 g, $n = 102$ nests) were significantly smaller than that of their marginal brood mates (4.84 ± 0.20 g, $t_{101} = 3.11$, $P = 0.002$; Figure 2B).

Effects of a nestling's early growth performance on its fledging success

A GLMM examining the effects of a nestling's early growth performance on its fledging success revealed a pronounced difference between core and marginal nestlings (Table 1). Whether a core nestling could successfully fledge or not was unrelated to its body weight or weight gain relative to the expected values at the early stage, that is, their fledging probability was independent of their growth performance. However, whether a marginal nestling could fledge or not was significantly related to its weight gain but unrelated to its body weight relative to the expected value at the early

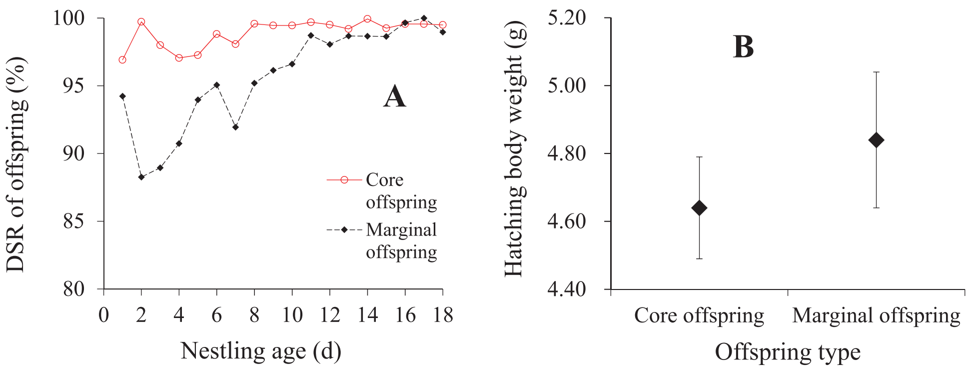

Figure 2. Comparison between core and marginal offspring in their daily survival rates (A, open circles, core offspring; closed diamonds, marginal offspring) and hatching body weight (B).

Table 1. A GLMM examining factors that might affect whether a nestling fledged successfully at the end of a breeding season.

Parameters Fixed effects	Core offspring (n = 97)			Marginal offspring (n = 247)		
	$\beta \pm SE$	z	P	$\beta \pm SE$	z	P
Intercept	0.17 ± 1.01	0.17	0.87	1.02 ± 1.32	0.78	0.44
Brood size	0.05 ± 0.18	0.28	0.78	0.07 ± 0.22	0.33	0.74
Weight gain relative to expected value at the early stage	-0.14 ± 0.32	-0.44	0.66	0.89 ± 0.29	3.05	0.002
Body weight relative to expected value at the early stage	0.19 ± 0.17	1.08	0.28	0.004 ± 0.108	0.04	0.97

Table 2. A GLMM examining factors that might affect the proportion of nestlings that obtained food in a feeding bout

Fixed effects	$\beta \pm SE$	n	t	P
Intercept	0.411 ± 0.082	1,042	4.983	0.003
Brood size	−0.071 ± 0.011	1,042	−6.718	<0.001
Amount of food delivered per feeding bout	0.074 ± 0.004	1,042	19.409	<0.001
Nestling age	0.009 ± 0.002	1,042	4.428	<0.001

stage (Table 1), that is, a marginal offspring can have a higher fledging probability only when it displayed faster growth than the expected value at the begging of the nestling period. The faster the marginal nestling grew relative to the expected value at the early stage of nestling period, the higher the probability that it could fledge successfully.

Variation of parental provisioning behaviors with nestling age

A GLMM examining factors that might affect the proportion of fed nestlings in a feeding bout revealed a negative effect on brood size and positive effects on the amount of food delivered per feeding bout and nestling age on the dependent variable (Table 2). After controlling for brood size and food amount delivered per feeding bout, the standardized proportion of fed nestlings in a feeding bout differed significantly between early (66.69 ± 2.13%, $n = 5$ days) and later stages (56.73 ± 3.36%, $n = 11$ days; $t = 6.04$, $df = 14$, $P < 0.001$) of the nestling period (Figure 3). The significantly larger proportion of fed nestlings at the early than at the later stages of nestling period indicated that parents delivered food to as many nestlings as possible in each feeding bout at the beginning; thereafter, they greatly reduced the number of nestlings that could obtain food in a feeding bout.

A GLMM examining the factors that might affect whether the first begging nestling was fed in a feeding bout revealed a significant negative effect of the number of begging nestlings on the dependent variable (Table 3), indicating that the larger the number of nestlings that displayed begging behaviors in a feeding bout, the lower the probability that the first begging nestling was fed. After controlling for the number of begging nestlings and the amount of food delivered per feeding bout, the probability that the first begging nestling was fed varied with nestling age following a quadratic pattern ($R^2 = 0.588$, $F_{2,13} = 9.28$, $P = 0.003$; Figure 4A), indicating that parents responded to the begging behaviors of nestlings more positively at the early stage while less positively at the subsequent stage.

A GLMM examining factors that might influence whether an unfed nestling in a feeding bout displaying begging behaviors revealed a positive effect on nestling age on the dependent variable (Table 4). After controlling for the amount of food delivered per feeding bout, the probability of an unfed nestling displaying begging behaviors also varied with nestling age following a quadratic pattern ($R^2 = 0.726$, $F_{2,13} = 17.21$, $P < 0.001$; Figure 4B). Thus, it suggested that a nestling was unfed by parents at the early stage because it did not display begging behaviors; however, a nestling was unfed by parents at the subsequent stage because it was rejected by parents when displaying begging behaviors. In another word, parents responded to nestling begging behaviors more positively at the early stage while less positively at the subsequent stage.

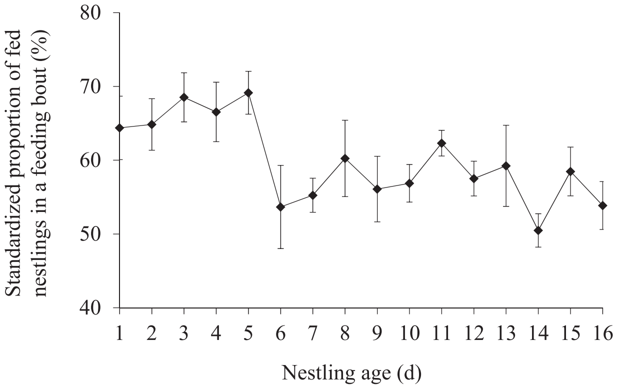

Figure 3. Variation in proportion of fed chicks in a feeding bout with nestling age.

Discussion

In this study, we proposed a "diagnosis model" of parental care and tested it in the Tibetan azure-winged magpies based on 9 years of data on demography and provisioning behavior. By comparing the daily survival rate and hatching body weight between core and marginal offspring, we first proved the necessity of a diagnosis strategy in brood reduction. Then, we found that when a marginal offspring displayed above-average growth performance, its fledging success could be greatly enhanced, which confirmed that a diagnosis stage did exist in the azure-winged magpie. By investigating the

Table 3. A GLMM examining factors that might affect whether the first begging nestling obtained food in a feeding bout

Parameters Fixed effects	*β* ± *SE*	*n*	*z*	*P*
Intercept	2.557 ± 0.623	2,572	4.108	<0.001
Amount of food delivered per feeding bout	0.050 ± 0.038	2,572	1.312	0.190
The number of nestlings that begged	−0.212 ± 0.080	2,572	−2.641	0.008
Nestling age	0.022 ± 0.018	2,572	1.205	0.228

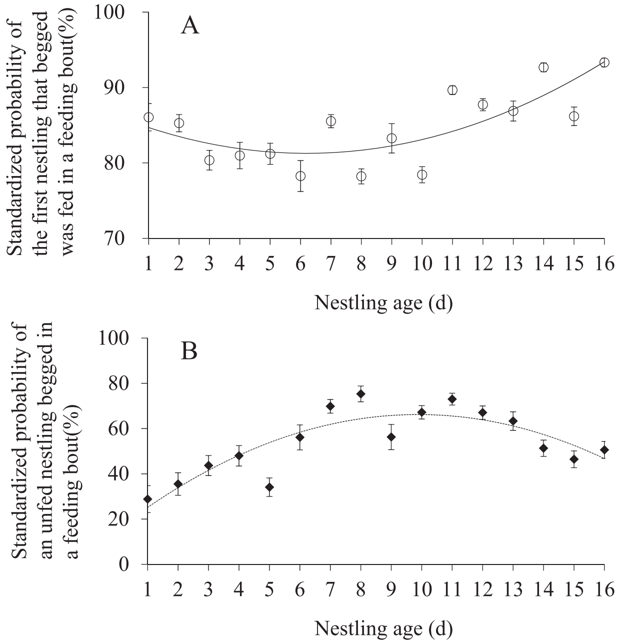

Figure 4. Variation in the probability that the first chick that begged was fed (A) and that an unfed chick begged food (B) in a feeding bout with nestling age.

Table 4. A GLMM examining factors that might affect whether a nestling that obtained no food displayed begging behaviors in a feeding bout

Parameters Fixed effects	*β* ± *SE*	*n*	*z*	*P*
Intercept	−0.084 ± 0.435	2,600	−0.193	0.847
Amount of food delivered per feeding bout	−0.031 ± 0.022	2,600	−1.421	0.155
Nestling age	0.053 ± 0.015	2,600	3.477	0.001

variation of parental provisioning behaviors with nestling age, we found that parents responded to the begging behaviors of nestlings more positively at the early stage while less positively at the subsequent stage, which further provided evidence that the consequence of a diagnosis strategy had altered the provisioning priority of parents.

The long-term demographic data on the growth and survival of azure-winged magpie nestlings indicate that although core offspring merit the investment priority, it remains necessary for parents to perform a diagnosis strategy so that those high-valued marginal offspring can be detected at the beginning of the nestling period. In most multi-nestling broods of altricial birds, it is common that parents bias their provision of limited resources to more competitive offspring (Forbes and Glassey 2000; Forbes et al. 2001; Jeon 2008), which has long been considered an adaptive strategy to food shortage. Since more competitive offspring can outcompete their less competitive brood mates in accessing parental resources, brood reduction can occur and thus reduce the nestling period, as well as the risk of nest predation (Du et al. 2014; Fan et al. 2017). In the Tibetan azure-winged magpie where asynchronous hatching is common (Da et al. 2018), core offspring had a significantly higher daily survival rate than their marginal brood mates (Figure 2A), suggesting that they have higher reproductive value than their parents. From the perspective of investment theory, prioritizing provisioning to core offspring is a secure investment strategy (Trivers 1974; Elton et al. 2013). But it is key to note that the higher competitiveness of core offspring compared to marginal ones is simply a byproduct of asynchronous hatching (Jeon 2008; Forbes and Wiebe 2010), not an honest signal of offspring reproductive value. Comparison between core and marginal offspring revealed that core offspring have significantly smaller hatching body weight than marginal offspring (Figure 2B), and that their mean body weight and weight gain overlapped (Appendices I and II). Therefore, if parents can identify marginal offspring with higher investment value via a diagnosis strategy, selecting for these marginal offspring will be a strategy superior to give more-or-less automatic priority to core offspring.

During the process of diagnosis, azure-winged magpie parents rely largely on the nestlings' growth performance to distinguish the investment values of offspring. When parents of altricial birds maximize reproductive success via an optimized provisioning strategy, the reliability of offspring phenotypic signal in advertising their investment value plays a key role in determining parental investment priority (Forbes 2009). A series of studies of shrub-nesting birds on the Tibetan Plateau have revealed that when parents distributed more food or equal amounts of food to marginal than to core nestlings, marginal nestlings can grow faster and hence fledge synchronously with their elder brood mates (Fan et al. 2017; Da et al. 2018; Li et al. 2020). It implies that growth rate can be an honest signal of offspring in correlating with their fledging success. Our findings in the Tibetan azure-winged magpie indicate that marginal offspring with greater weight gain than the expected value were more likely to be selected for by parents in subsequent stage and fledge successfully (Table 1). Compared with the hatching body weight or hatching order, the growth performance of marginal offspring at the early stage greatly influenced the decision of parents. As a result, it can be confirmed that parents had based on the nestlings' growth performance to detect those marginal offspring with higher investment value.

In altricial birds, the provisioning priority of parents reflects their selection among different types of offspring.

Empirical tests of life history theory have confirmed that an uneven distribution of food within a brood will result in some offspring being selected against (Davis et al. 1999; Hatchwell 1999; Smiseth et al. 2003; Li et al. 2020; Fan et al. 2021). Our findings in the Tibetan azure-winged magpie uncover that parents use a diagnosis strategy at the early stage to assess those offspring worthy of continued investment, in which they provide food to all nestlings that displayed begging behaviors. For example, parents provisioned a larger proportion of offspring in a single feeding bout (Figure 3), which implies that every nestling that begged would be provisioned. Moreover, they responded positively to offspring begging at the early stage, that is, feeding a nestling once it begged first (Table 3, Figure 4A) and did not feed a nestling that did not beg (Table 4, Figure 4B). By fulfilling the needs of each nestling, parents create a fair opportunity allowing all offspring to exhibit different growth performances. Although the positive response of parents to offspring begging seems also to be explained by the low food demands of nestlings and parental capacity of delivering adequate food during the few post-hatching days, this interpretation cannot explain why the growth performance of a nestling significantly determined its fledging success (Table 1). Obviously, those marginal offspring with greater growth performance acquired parental provisioning priority, it is a consequence of diagnosis strategy of parents. Another consequence of the diagnosis strategy is that parents make less positive responses to nestling begging at the subsequent stage of the diagnosis (Figure 4), that is, they decline to give food to some particular nestlings. This result accords with the second prediction of the diagnosis model (Figure 1C). As these victim nestlings have been detected by parents after a positive response to nestling begging at the early stage, it provides further evidence for the existence of a diagnosis strategy.

In conclusion, our study of parental provisioning behaviors in the Tibetan azure-winged magpie suggests that parents use a diagnosis strategy to reduce the probability of making errors in selecting against some marginal offspring with potentially higher investment value. At the diagnosis stage, parents depend more likely on a nestling's early growth performance rather than its hatching order to estimate its investment value. As a result, parents can optimize their provisioning strategy by selecting for some marginal offspring in the case of brood reduction.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Ethics

Adult sampling and nestling banding were authorized by the Wildlife Conservation Law legislated by the Tenth National People's Congress of China (20040828).

Conflict of Interest Statement

The authors have no conflict of interest to any other organizations or individuals with regarding to the publication of this manuscript.

Data Availability Statement

The data used in this study are openly accessible at https://doi.org/10.5061/dryad.s7h44j19j.

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