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Parental dependence on the nest's spatial cues in offspring recognition decreases with nestling growth in the azure-winged magpie

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Abstract

In altricial birds, to address which cues are used by parents to recognize their offspring, and when they switch between cues during reproduction, it has not been well determined. In this study, we address this question in a Tibetan population of the azure-winged magpie *Cyanopica cyanus*, by examining the dependence of parents on a nest's spatial position in offspring recognition. During the egg and nestling phases, azure-winged magpie nests were translocated to new positions across various distances from their original site, and parental responses to the translocated nests were investigated. Our findings show that a nest's spatial position is not connected with the survival of its young, but might be used as a cue in parental offspring recognition. When nests are translocated to a new position within a certain distance, parents could recognize their nests and returned to resume their parenting behaviors. Parental dependence on the nest's spatial position in offspring recognition is higher during the egg phase than during the nestling phase, and it decreases with the growth of nestlings. After nestlings reach a certain age, the nest's spatial position was no longer used by parents as the single cue for offspring recognition. These findings suggest that azure-winged magpies switch their cues in offspring recognition during the different stages of reproduction. After parent–offspring communication has been established, the offspring's phenotypic traits may become a more reliable cue than the nest's spatial position in offspring recognition.

Key words: homing, nest spatial position, nest translocation experiment, offspring recognition

Inclusive fitness theory has been hypothesized as having a strong influence on behaviors (Hamilton 1964), which is established on an implicit precondition that individuals are able to recognize kin and nonkin (Fletcher and Michener 1987; Hepper 1991). To confirm the validity of this precondition, exploring the cues that animals use in kin recognition becomes an important theme. To date, studies in altricial birds have revealed that parents use various cues in recognizing their offspring that are connected with their visual, auditory, or olfactory systems (Hughes et al. 1994; Roper 1999; Freake 2001; Jouventin and Aubin 2002; Johnson and Freedberg 2014).

Moreover, these cues differ not only between species, but also between different life-history stages within species (Beecher et al. 1986; Johnson and Freedberg 2014). Thus, it is important to demonstrate the variation of offspring recognition cues to confirm the validity of inclusive fitness theory.

In altricial birds, it has been widely reported that parents do not rely on 1 single cue to recognize their offspring throughout the whole reproductive period (Dugatkin 2014). For example, in the bank swallow *Riparia riparia*, parents only need to remember the location of their nest during the nestling stage; whereas they have to

remember the vocal features of their offspring to avoid delivering food to other fledglings after fledging (Beecher et al. 1986; Pfennig and Sherman 1995). In the cliff swallow *Petrochelidon pyrrhonota*, parents recognize their offspring via the song before they fledge while using facial markings after they fledge (Medvin et al. 1992; Johnson and Freedberg 2014). This switch of offspring recognition cues by parents may be related to the development of offspring. During the egg phase when the features of eggs seldom change (except that an event of nest parasitism occurs, Ortega 1998), remembering where the eggs have been laid is undoubtedly simpler and more efficient for parents than learning and identifying the egg features (Waldman 1987). However, during the nestling phase, when the features of chicks change greatly, learning the nestlings' phenotypic characteristics may become more important for parents to recognize their offspring (Johnson and Freedberg 2014). This is not only because remembering where the chicks are no longer especially useful after they fledge, but because parents gradually establish communication with their offspring through identifying the nestlings' phenotypic characteristics, such as the voice (Marques et al. 2011). Therefore, parents' switching of cues in offspring recognition is assumed to relate with the growth of offspring. To date, which cues are used by parents to recognize their offspring, and when they switch between cues during a reproduction, has not been well determined.

The nests of altricial birds have been considered to play a key role both in protecting and in recognizing the dependent offspring. On the one hand, the architectural structure of a nest can provide the nestlings a stable and secure microhabitat (Brown et al. 1992; Martin 1993; Windsor et al. 2013). On the other hand, the spatial position of a nest can transmit a homing cue to parents (Hughes et al. 1994; Hutchinson and Gigerenzes 2005; Houston et al. 2007; Dell'Ariccia et al. 2015). Since nestlings cannot move between physically separated nests, homing implies that parents can direct parental care for their offspring (Jouventin and Aubin 2002). Therefore, remembering the nest's position becomes a widespread mechanism for offspring recognition, that is, the "rule of thumb" (Hutchinson and Gigerenzes 2005; Houston et al. 2007). In such circumstances, it should be easy to address which cues are used by parents and when they switch between cues by experimentally manipulating the spatial position of a nest.

The azure-winged magpie *Cyanopica cyanus* is a cooperatively-breeding corvid that is distributed widely in East Asia. In the past 2 decades, its distribution has gradually expanded to the Tibetan Plateau (Ren et al. 2016; Gao et al. 2018). Although there are many studies reporting that azure-winged magpies in other geographic populations may be parasitized by the common cuckoo *Cuculus canorus* (Kleven et al. 1999; Andou et al. 2005) or the great spotted cuckoo *Clamator glandarius* (Soler et al. 2003), no cases of nest parasitism by cuckoos have occurred in the Tibetan population (Da et al. 2018). Nonetheless, a recent study based on parentage analysis has revealed a high frequency of extra-pair copulations in the Tibetan population, which produce young unrelated to either the paired male or female (Gao et al. 2018). Interestingly, both sexes did not reduce their parental care for a mixed brood, suggesting that azure-winged magpies might be unable to differentiate between their offspring and unrelated young (Gao et al. 2019). Moreover, a cross-fostering experiment performed in the Tibetan population indicates that foster parents do not reject foreign nestlings until it is 10 days old (Da et al. 2018), suggesting that offspring recognition in the azure-winged magpie may be connected with nestling age. Therefore, the azure-winged magpie may be an ideal system to experimentally investigate the variation of cues used by parents in offspring recognition.

In this study, we assume that 1) parental dependence on the nests' spatial position in offspring recognition decreases with the growth of offspring and differs between the egg and nestling phases and 2) parents switch the cues from the nest's spatial position to the offspring phenotypic traits after parental–offspring communication is established. To test these 2 assumptions, azure-winged magpie nests were experimentally translocated to a new position, and parental responses to their manipulated nests were examined.

Material and Methods

Study area and population

This study was carried out at the Luqu County, Gansu Province, China (102.5°E, 34.6°N, mean altitude 3,400 m), during 2012–2018. This region has typical alpine meadow characteristics, being cold (mean annual temperature 2.3°C) and humid (annual precipitation 782 mm). The landscape changes from alpine meadow to Qinghai spruce *Picea crassifolia* conifer forest, with an ill-defined transitional zone of shrubs that are composed mainly of *Berberis hemsleyana*, *Hippophae rhamnoides*, and *Salix caprea*. These shrubs are distributed either on islands in the river or along the riverbank (Figure 1A). As a colonial species, azure-winged magpies construct most of their nests on *H. rhamnoides* and *S. caprea* in a highly-clumped pattern. Nest density in different colonies, which is calculated as the total number of active nests per hectare that complete their clutches in a breeding season, ranges between 20 and 180 nests/ha (Ren et al. 2016).

The Tibetan population migrates between their wintering and breeding sites. Around mid-April every year, adults migrate from their wintering site at lower altitude to the breeding site at a higher altitude. Generally, experienced breeders return to their previous colony, and do so earlier than inexperienced breeders. Although they seldom construct their nest at the previous site, they usually occupy the previous territory or a new territory in its vicinity. This territorial fidelity in many studied species reflects that individuals have a spatial memory of their territories (Schlossberg 2009), which seems also true in the azure-winged magpie.

Field data collection

Active nests were systematically searched for within the shrubs at the end of April. For each located nest, its contents were checked daily to monitor the date when the female laid her 1st egg, when she
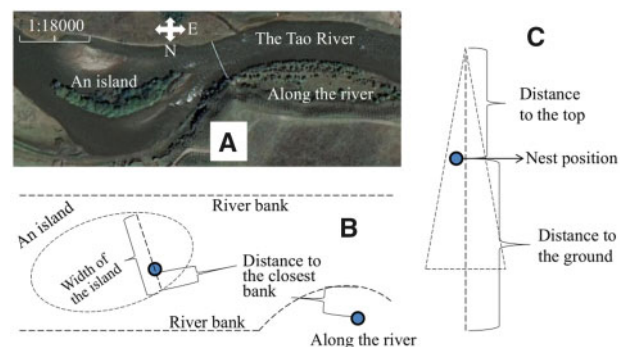
Figure 1. One example of azure-winged magpie nests that were distributed on an island or along the riverbank in our study area (**A**). Measurements of the horizontal position of a nest, including the distance to the closest bank and the width of the island (**B**). Measurements of the vertical position of a nest, including the distance to the top of shrub and to the ground (**C**).

commenced the all-day incubation, and when the 1st nestling hatched. According to these data, the incubation days of a nest (the 1st date of all-day incubation being set as 1) and the nestling age of a brood (the 1st day of the 1st nestling hatched being set as 1) could be determined. Other data regarding life-history traits were also collected following the procedure of Gao et al. (2018).

Data regarding a nest's spatial positions included the shrub species on which the nest was built, its distance to the closest bank and the width of the island (Figure 1B), as well as its distance to the top of the shrub and to the ground (Figure 1C). The nest's horizontal position on an island was then standardized by calculating the ratio of its distance to the closest bank to the width of the island. The nest's vertical position on a shrub was standardized by calculating the ratio of its distance to the ground to the shrub height. All active nests were monitored throughout the breeding season to see whether parents fledged at least one offspring, which was used as an index of nest survival.

Design of nest translocation experiment

A nest translocation experiment was designed and carried out either during the incubation or nestling phase. In the experiment, a randomly selected nest was translocated to a new position by cutting off the branch on which the nest was positioned. This cut branch was affixed with metal wire to another branch, which varied both in the direction (downwards, upwards, or horizontally) and in the distance (ranging from 0.5 to 6 m) away from the original site of the nest. This procedure changed only the nest spatial position but not the nest architectural characteristics, and it was completed within 5 min for all the manipulated nests. After the nest translocation was finished, behaviors of adults were recorded by a digital camcorder (ZX1; Eastman Kodak Company, Rochester, NY, USA) that was fixed on a branch 1 m diagonally above the nest. Behavioral recordings lasted for 2 h, examining whether parents returned to their manipulated nest and resumed their parenting behaviors (i.e., incubating eggs during the egg phase, and provisioning nestlings during the nestling phase). As a control, the cut branch for 135 nests (96 during the incubation, 39 during the nestling period), in which parents did not return within the 2 h of experiment, was connected to its original position with sticks and metal wire. This procedure was completed within 2 min for all manipulated nests. Parental behaviors were recorded by the same method to check whether they returned to their nest at the original site.

During 7 years of this study, we manipulated 219 azure-winged magpie nests in the translocation experiment. Of these, 116 nests were translocated during the egg phase, and 103 nests during the nestling phase. To minimize the disturbance coming from local herdsmen, all translocated nests were selected from colonies on the island. Furthermore, all experiments were carried out only on sunny days to minimize the influence of weather. During the 2 h of experiment, we patrolled the boundary of a colony to prevent any predators from approaching the manipulated nests.

The procedures of nest translocation and animal measurement are under the Wildlife Conservation Law of China (20170101).

Statistical analysis

Nests' distance to the closest bank, which was arcsine square-root transformed before being used in the analysis, was compared between islands and along the riverbank using an independent sample t-test. The nests' horizontal position on an island was linearly regressed against the width of the island. The nests' vertical position on the *H. rhamnoides* or *S. caprea* was compared with their counterparts along the riverbank, respectively, using an independent sample t-test.

A generalized linear model was fitted to examine the effect of a nest's horizontal and vertical position on its survival (set as response variable, with binomial distribution). Predictor variables included the clutch initiation date, nesting density in a colony, and the nest's horizontal and vertical position. As the Tibetan population spanned the initiation of breeding for 2 months, the nesting density in a colony was calculated as the instantaneous number of active nests during the experiment per hectare in the colony.

A generalized linear mixed model (GLMM) was fitted to test the factors that might influence whether a female returned to her manipulated nest during the egg phase (set as the dependent variable, with binomial distribution and a logit link function). Fixed effect variables included the nesting density in a colony, incubation days of the nest, and the nest's translocation distance and direction. The year and colony identity were introduced into the model as random effects to estimate their relative contributions to the variance of female likelihood during the egg phase.

Another GLMM was fitted to test the factors that might influence whether parents returned to their manipulated nest during the nestling phase (set as the dependent variable, with binomial distribution and a logit link function). Fixed effects included the nesting density in a colony, nestling age, the nest's translocation distance, and direction. The year and colony identity were introduced into the model as random effects to estimate their relative contributions to the variance of parental likelihood during the nestling phase.

To compare whether parents had different dependence on their nests' spatial position between the egg and nestling phases, the likelihood that parents returned to their manipulated nests, which was obtained by fitting the GLMMs, was regressed with the translocation distance both during the incubation and nestling period.

Statistical analysis was performed by R (version 3.4.4). Descriptive data are presented as mean ± standard error of mean. Null hypotheses were rejected when $P_{2\text{-tailed}} < 0.05$.

Data accessibility

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hmgqnk9ck.

Results

In the Tibetan azure-winged magpies, the nests' distance to the closest bank on an island (11.48 ± 0.71 m, $n = 190$) was significantly shorter than that of nests along the riverbank (16.52 ± 1.09 m, $n = 99$; $t_{244} = 3.76$, $P < 0.001$). The nests' horizontal position on an island increased significantly with the width of the island ($F_{1,88} = 7.37$, $P = 0.01$). The nests' vertical position on the *H. rhamnoides* (0.327 ± 0.015, $n = 132$) or on the *S. caprea* (0.390 ± 0.024, $n = 68$) was significantly lower on islands than their counterparts along the riverbank (*H. rhamnoides*: 0.410 ± 0.021, $n = 63$; $t_{193} = 3.23$, $P = 0.001$; *S. caprea*: 0.501 ± 0.032, $n = 38$; $t_{104} = 2.76$, $P = 0.01$). Nest survival of azure-winged magpies was significantly positively correlated with the nesting density in a colony, but unrelated to the clutch initiation date and the nest's horizontal or vertical positions (Table 1).

Parental responses to nest translocation during the egg phase

Of the 116 nests that were translocated to a new position during the egg phase, females in 26 nests returned back and resumed the incubating. In the remaining nests, females did not return, or returned but did not resume the incubating within the 2 h of experiment. The likelihood that a female returned and resumed the incubating was significantly negatively influenced by the nest's translocation distance, but unrelated to the nesting density in its colony, and the incubation days (Table 2). Females in nests that were translocated downwards were more likely to return and resume the incubating

than those translocated upwards or horizontal (Table 2). Between-colony difference contributed to the individual variance in female responses more than that between years (Table 2). In the control, females returned and resumed incubation in most manipulated nests (91 of 96 nests) that were affixed to their original site.

Parental responses to nest translocation during the nestling phase

Of the 103 nests that were translocated during the nestling phase, parents in 58 nests returned and continued to provision the brood. In the remaining nests, parents either did not return or returned but did not provision the brood. The likelihood that parents returned and continued to provision the brood was significantly positively influenced by the nesting density in their colony and nestling age, but negatively influenced by the nests' translocation distance (Table 3). Compared with breeders in nests that were translocated upwards, breeders were more likely to return and continue to provision their offspring in nests that were translocated horizontally or downwards (Table 3). Between-year differences contributed to the variance of parental responses more than that between colonies (Table 3). In the control, parents returned and continued to care for the brood in all the 39 nests that were affixed to their original site.

Table 1. Factors that might be correlated with the nest survival of Tibetan azure-winged magpies, examined by fitting a general linear model

Generalized linear model parameters Predictor variables	$\beta \pm$ SEM	χ^2	df	P
Intercept	-1.29 ± 0.96	1.80	1	0.18
Clutch initiation date	0.02 ± 0.03	0.77	1	0.38
Nesting density	0.29 ± 0.07	17.83	1	<0.001
Vertical position	-0.55 ± 1.40	0.15	1	0.70
Horizontal position	-0.18 ± 1.19	0.02	1	0.88

Table 2. Factors that might influence whether females return to their manipulated nests during the incubation period to resume incubating

Generalized linear mixed model parameters Fixed effects	$\beta \pm$ SEM	n	t^a
Intercept	-2.427 ± 4.388	116	-0.553
Nesting density	0.001 ± 0.008	116	0.096^{NS}
Incubation days	0.159 ± 0.103	116	1.551^{NS}
Translocation distance	-6.446 ± 1.579	116	-9.576^*
[b]Translocation direction			
Downwards	8.239 ± 4.441	95	1.868
Horizontal	0.305 ± 6.676	12	-0.046
Random effect variables	Variance $\pm$ SD	n	Results of VCA
Year	0.003 ± 0.055	116	0.022
Colony	0.023 ± 0.151	116	0.167
Residuals	0.112 ± 0.334	116	0.812

The year and colony are set as random effect variables. [a] Correlation was significant (**) or not (NS). [b] Nests translocated upwards ($n = 9$) was set as the baseline. VCA, variance component analysis; SEM, standard error of mean; SD, standard deviation.

Table 3. Factors that might influence whether adults returned to their manipulated nest during the nestling period and continued to provision the brood

Generalized linear mixed model parameters Fixed effect variables	$\beta \pm$ SEM	n	t^a
Intercept	-0.340 ± 0.148	103	-2.305^*
Nesting density	0.002 ± 0.001	103	2.981^*
Nestling age	0.079 ± 0.010	103	7.982^*
Translocation distance	-0.245 ± 0.031	103	-8.009^*
[b]Translocation direction			
Downwards	0.960 ± 0.152	84	6.301^*
Horizontal	0.747 ± 0.166	11	4.500^*
Random effect variables	Variance $\pm$ SD	n	Results of VCA
Year	0.017 ± 0.129	103	0.168
Colony	0.0001 ± 0.001	103	0.001
Residuals	0.084 ± 0.290	103	0.831

The year and colony are set as random effect variables. [a]Correlation was significant (*) or not (NS). [b] Nests translocated upwards ($n = 8$) was set as the baseline. VCA, variance component analysis; SEM, standard error of mean; SD, standard deviation.
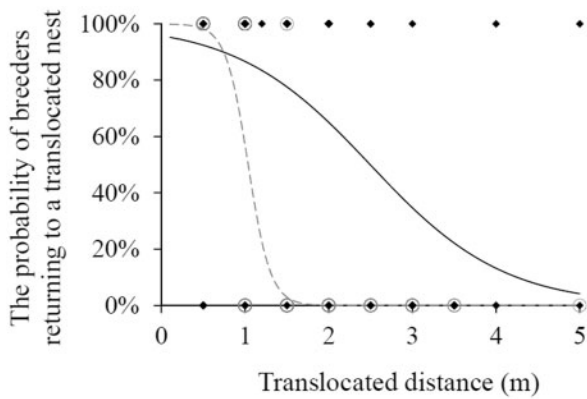
Figure 2. The probability of breeders returning to a manipulated nest as a function of its translocated distance during the incubation (circles and dashed line) and nestling periods (diamonds and solid line). Some circles contain diamonds within them because 2 data points are overlapped at that distance.

For the parents within the nests that were translocated downwards, they were more likely to return to their manipulated nests during the nestling phase than that during the egg phase (Figure 2).

Discussion

In the Tibetan azure-winged magpies, our experimental findings reveal that parents will return and resume their parenting behaviors even if their nests have been translocated to a new position. The likelihood that parents return to a manipulated nest differs between the egg and nestling phases, and varies with the translocation distance and the growth stage of nestlings.

By testing the factors that might influence the nest survival of azure-winged magpies, we find that a nest's spatial position is not connected with its survival. This thus greatly reduces the possibility that our experimentally translocated nests had been abandoned because of the enhanced exposure to natural predators. In altricial birds, nest site selection is an essential adaption to the existence of natural predators (Martin 1993; Newton 1994). By carefully choosing where to construct their nests (Nilsson 1984; Shields 1984; Goodnow and Reitsma 2011; Hansell 2011), parents can provide a safe shelter to their dependent offspring. In the Tibetan population, azure-winged magpies tend to construct their nests close to the center of an island and at a lower position of the shrubs on the island than along the riverbank. This choice of nest spatial position helps parents to cope with the high risk of nest predation in our study area, which is caused mainly by magpies *Pica pica* and domestic cats *Felis catus* (Ren et al. 2016). As predators for nests on an island only come from the air, to construct their nests close to the island center and a shrub's lower position might reduce the risk of being attacked by natural predators. More importantly, as a colonial breeding species, the highly-clumped nesting pattern of the Tibetan azure-winged magpie facilitates all breeders in a colony to defend their nests together from predators (Ren et al. 2016). Hence, the nesting density in a colony has a positive relationship with the nest survival (Table 1). In our experiment, all manipulated nests were located on the island. Therefore, parental abandonment of a translocated nest would not be due to the nests' enhanced exposure to predators, but more likely be a consequence of uncertainty in recognizing their offspring.

Parental responses in the nest translocation experiment indicate that a nest might more likely function as a cue for offspring recognition in the Tibetan azure-winged magpies than simply protecting offspring. Generally, a nest carries 3 types of cues, the spatial position and architectural characteristics, which seldom change with the growth of offspring (Hutchinson and Gigerenzes 2005; Houston et al. 2007), and the offspring phenotypic traits, such as the nestlings' calling that changes with their development (Medvin et al. 1992). When we performed the nest translocation experiment, none of a nest's architectural characteristics and the phenotypic traits of either eggs or nestlings had changed remarkably within the 2 h of experiment. Consequently, it is unlikely that negative parental responses to their translocated nest, either during the egg (Table 2) or nestling phase (Table 3), resulted from their perception of a cue connected with the nest's architectural characteristics or the offspring's phenotypic traits. On the contrary, these results support that parents use the nest's spatial position as a cue of offspring recognition. Under such a mechanism, any nestlings that emerge outside the nests will be identified unrelated to parents (Hutchinson and Gigerenzes 2005; Houston et al. 2007). Obviously, a nest that was translocated to a new position will affect parental memories of their nests. The farther a nest is translocated, the greater parental memories will be affected. If a nest is translocated a distance far from its original site, parents will become uncertain whether the nest belongs to them. Accordingly, the likelihood that parents returned to their manipulated nest decreased with translocation distance (Tables 2 and 3). One point needs to be noticed is that the Tibetan azure-winged magpies are more likely to return to a nest translocated downwards than upwards. One possible explanation may be that azure-winged magpies have experienced in the natural environment events that move their nests downwards, such as in cases of falling due to strong winds or being dislodged by predators. But nests will not move upwards or horizontally under natural circumstances. This might influence their memory of the nests' spatial position in offspring recognition.

The dependence by parents on the nest's spatial position in offspring recognition differed between egg and nestling phases (Figure 2), and decreased with the development of nestlings (Table 3), which implies that azure-winged magpies might switch between cues in offspring recognition during reproduction. During the experiment performed at different incubation days (during the egg phase) or nestling ages (during the nestling phase), egg signals change imperceptibly, but nestling signals change quickly. Nestlings have the ability to establish communication with their parents, such as via an acoustic or visual signal, after a certain age (Medvin et al. 1992). Therefore, it is understandable that parents make no reaction to the change of incubation days during the egg phase (Table 2), but significantly respond to the change of nestling ages during the nestling phase (Table 3). In a previous study on the Tibetan azure-winged magpie that involved a cross-fostering experiment, parents began to reject a foreign nestling after it was 10 days old (Da et al. 2018), indicating that parents can recognize their offspring from unrelated nestlings based on the phenotypic traits of nestlings. So, it can be confirmed that decreased parental dependence on the nests' spatial position in offspring recognition with nestling age (Figure 2) is a consequence of switching cues for recognizing their offspring. Because parent–offspring communication has been established via vocal or visual signals (although which signals are the determinant remains unknown in the azure-winged magpie), using such signals as the cue in offspring recognition will be more efficient for parents than simply using the nests' spatial position. Consequently, when nestlings are older, parents can return and resume the provisioning of offspring even their nests have been translocated farther than when nestlings are young (our dataset deposited on Dryad).

Whether parents returned to a manipulated nest and resumed their parenting behaviors reflects their willingness to provide further parental care for the brood. As proposed by Robert Trivers (1972), the level of ongoing parental investment to a given brood is expected to vary with what they have invested, because the costs of future investment incurred by abandoning current offspring increase with the stage of reproduction. This hypothesis has been supported by findings that birds defend their nests against predators more strongly during the nestling phase than during the egg stage (Brunton 1990). In the Tibetan azure-winged magpies, breeders are more likely to commence a 2nd brood if their 1st brood failed during the egg phase than during the nestling phase (Du Bo, unpublished data), implying that the costs incurred by nest failure during the nestling phase are higher than during the egg phase. Thus, parental tradeoffs between the benefits and costs of abandoning an uncertain nest may be a possible explanation for why parents are more willing to return to a manipulated nest during the nestling phase than during the egg phase, even at the exact same translocation distance (Figure 2). However, without the integration of offspring recognition, this alone cannot explain why parental willingness toward a manipulated nest did not change with the days of incubation (Table 1), as well as why parental response to a manipulated nest changes with the nest's translocation distance (Table 2). So, it seems more likely that as parents have invested more energy to current reproduction when their offspring approach the nestling phase, they are more willing to examine whether the nestlings within a farther translocated nest are their own offspring. Under this condition, switching cues from the nest's spatial position to the offspring's phenotypic traits may be a more reliable mechanism for parents to correctly recognize their offspring.

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Conflict of Interest

The authors declare no any conflicts of interest to other government organization bodies.

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