

Helpers of the Giant Babax cheat for an immediate reward when they provision the brood

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Abstract Cooperative breeding is a special form of cooperation between dominant breeders and subordinate helpers, in which cheating by helpers happens occasionally. As cheating by helpers will reduce the interest of dominant breeders in them, it is difficult to understand why dominant breeders often tolerate the presence of cheaters within the group. We addressed this in the Giant Babax *Babax waddelli*, a cooperative breeder that breeds exclusively on the Tibetan Plateau. During the nestling period, helpers exhibited three types of non-feeding behaviors when they visited the nest: pseudo-feeding, without food but mimicking food delivery activities; false feeding, delivering plastic debris to nestlings; and contested kleptoparasitism of fecal sacs of nestlings, without delivering food but snatching fecal sacs of nestlings after others delivered food. We found that these non-feeding behaviors of helpers had an obvious aim, to get fecal sacs of nestlings, thus they were considered to be cheating. In response to the cheating of a helper, the female breeder reacted negatively, the male breeder disregarded it, and other

helpers became accomplices. Since helpers contributed nearly 70% to brood provisioning, the benefits that breeders obtained from the presence of helpers outweighed the costs caused by the cheaters. This can explain why dominant breeders do not evict cheaters from the cooperative group. We suggest that a short-term reward may be also an important force driving helpers to cheat in cooperative breeding.

Keywords Cooperative breeding · Cheating · Provisioning behavior · Immediate reward · Dominants

Zusammenfassung

Helfer beim Riesenbabax täuschen bei der Brutpflege für eine umgehende Belohnung

Kooperatives Brüten ist eine spezielle Form der Kooperation zwischen dominanten brütenden Vögeln und untergeordneten Helfern, in der es bisweilen zu Täuschungen durch die Helfer kommt. Da Täuschungen durch Helfer die Interessen der dominanten, brütenden Vögel beschädigen, ist es nicht leicht zu verstehen, warum die dominanten Vögel die Anwesenheit von Betrügern in der Gruppe tolerieren. Wir gingen dieser Frage beim Riesenbabax (*Babax waddelli*) nach, einer kooperativ brütenden Art, die ausschließlich im Hochland von Tibet brütet. Während der Nestlingszeit zeigten die Helfer folgende drei Verhaltensweisen beim Nestbesuch, bei denen sie nicht fütterten: (1) Scheinfüttern, ohne Futter, aber ein Füttern vortäuschend; (2) Falsches Füttern, bei dem sie den Nestlingen Plastikmüll brachten; (3) Kleptoparasitismus von Kotsäcken, bei dem sie Kotsäcke der Nestlinge schnappten, nachdem andere Futter brachten. Wir fanden heraus, dass dieses nicht-fütternde Verhalten

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der Helfer den offensichtlichen Zweck hatte, an Kotsäcke der Nestlinge zu gelangen, und daher eine Täuschung gewesen sein könnte. Die brütenden Weibchen zeigten eine negative Reaktion auf das Täuschungsverhalten der Helfer und die Männchen ignorierten es, während andere Helfer zu Komplizen werden konnten. Da der Anteil der Helfer an der Brutpflege bei nahezu 70% liegt, wird der Schaden durch die Anwesenheit der Betrüger durch den Nutzen der Helfer mehr als aufgewogen. Das kann erklären, warum die dominanten, brütenden Vögel die Betrüger nicht aus der Gruppe verstoßen. Wir geben zu bedenken, dass eine kurzfristige Belohnung auch eine wichtige treibende Kraft sein könnte, die Helfer beim kooperativen Brüten zum Täuschen treibt.

Introduction

Cooperative breeding is a specific form of cooperation that is generally characterized by non-breeding individuals (helpers) assisting a breeding pair (dominants) to raise the young (Brown 1987; Russell 2004). In return for their assistance, helpers are permitted to stay in the territory of dominants and enjoy the benefits of group living, such as access to limited resources, enhanced safety, or even direct reproductive sharing (Gaston 1978; Kokko et al. 2002; Ridley et al. 2008). Thus, the performance of helpers in carrying out their helping duties largely determines whether the cooperation is stable (Magrath et al. 2004).

“Cheating” is a term used to describe animal traits or behaviors that convey dishonest signals or exploit the benefits of cooperation without reciprocation (Sachs and Simms 2006; Ghoul et al. 2014; Riehl and Frederickson 2016). It happens in numerous species, from simple life forms like bacteria to more complex organisms like birds and mammals (Ghoul et al. 2014; Jones et al. 2015). Since cheaters can obtain benefits from cheating such as increased access to mates and enhanced survivorship (Mokkonen and Lindstedt 2015), it is conceivable that cheating is prevalent in inter- or intra-specific competition (Ferriere et al. 2001; Jones et al. 2015; Levin et al. 2015). However, it is difficult to understand why cheating also spreads in cooperative breeding where helpers may be deceptive in provisioning the young, mainly in the form of non-feeding nest visits (Boland et al. 1997; Clutton-Brock et al. 2005). Theoretically, these cheating behaviors of helpers will harm the interest of dominants (Riehl and Frederickson 2016); but in many cases cooperative groups maintain stability despite the presence of cheaters (Sachs and Rubenstein 2007). Why do dominants, once cheated, not evict cheaters from the cooperative group? This question remains a great challenge with regards to the evolution of cooperative breeding.

One reason why cheating of helpers is tolerated by the dominants may be that the cheating behaviors of helpers are not really deceptive. For example, pseudo-feeding (visiting the nest without food) and false-feeding (visiting the nest with food but failing to deliver it to the brood) of helpers have been described in cooperative birds and mammals (Boland et al. 1997; Clutton-Brock et al. 2005; Canestrari et al. 2004, 2010; Young et al. 2013). However, after taking into account the body condition and breeding experience of the non-helpers, as well as the level of brood demand, these studies found that neither pseudo-feeding nor false feeding was a clearly cheating tactic of helpers (Sachs and Rubenstein 2007; Young et al. 2013). Even if some helpers completely refrain from visiting the nest, they are in fact the substitute caregivers that can carry out brood provisioning when other helpers decrease their nest attendance due to sudden environmental change (Baglione et al. 2010). Moreover, helpers may cooperate in other ways than brood provisioning, such as nest defense from predators and courtship feeding of brooding females (Koenig and Dickison 2004; Ren et al. 2016). Thus, it is not enough to categorize a helper as a cheater based only on its reduced effort in brood provisioning.

The other reason for cheater tolerance of dominants may be that breeders obtain more benefits from the presence of helpers. Therefore, cooperating with cheating helpers is better than having no helpers at all. The benefits that breeders may obtain include enhanced group competitive ability over limited resources, a lightened workload and increased reproductive output (Woxvold and Magrath 2005; Johnstone 2011). Under the condition when helpers provide less assistance than they should provide (Baglione et al. 2010), dominant breeders will punish them or even evict them from the group (Mulder and Langmore 1993; Johnstone and Cant 1999). Considering the costs of cheating on cooperation (Riehl and Frederickson 2016), if cheaters are present in a cooperative group and the group remains stable, two preconditions should be fulfilled: the presence of helpers plays a vital role in realizing the interests of dominants; when they get the opportunity to cheat to obtain more benefits, helpers trade off the benefits and costs of cheating so that the interests of dominants do not reduce significantly.

We tested these two preconditions in the Giant Babax (*Babax waddelli*), an obligate cooperative breeder that exclusively inhabits the Tibetan Plateau (Zheng et al. 1987). Generally, the breeding units are composed of three to seven adults including the dominant pair (Lu 2004). Helpers primarily contribute by provisioning nestlings; sometimes they also participate in defending the nest against predators and intruders (Du et al. 2012). Both breeders and helpers exhibit strong territoriality that prevents different groups from mixing. Females of the Giant

Babax produce a typical clutch size of three, with the third egg being significantly smaller than the two eggs laid earlier. Consequently, size hierarchy among nestlings is established due to egg-size variation (Du et al. 2012). During the nestling period, parents adopt an opposing investment strategy by preferentially feeding later-hatched chicks so that the smallest chicks grow faster than their older brood mates (Du et al. 2012).

In this study, we first assessed the roles of breeders and helpers in caring for the young by comparing their nest-visiting behaviors. Then, we examined whether there were non-feeding behaviors when helpers provisioned the brood, and whether these non-feeding behaviors could be considered cheating. Based on the identification of different types of helpers' cheating, we checked the responses that other group members made when they witnessed the cheating of helpers.

Methods

Study area and population

This study was carried out in 2010, 2015 and 2016 in the Xiongse Valley (29°40'N, 91°00'E, 3800–4400 m height), located on the southern bank of the river Lhasa, Tibet Autonomous Region, China. The annual mean temperature is 4.5 °C (the highest monthly temperature is less than 16 °C) and annual precipitation is 570 mm (the highest monthly rainfall is less than 150 mm). Due to the high altitude, low temperature and precipitation, vegetation in the region has a short growing period. Birds breeding there have a shorter breeding season than their counterparts breeding at lower altitudes (Lu 2004; Du et al. 2012). Foraging may be a great challenge for the Giant Babax, especially for adults that raise nestlings. In order to find enough food to feed their young and themselves, the Giant Babax greatly enlarged their dietary range, which even includes spiders and lizards, in addition to coleopteran and lepidopteran insects (Du et al. 2012).

Our study population is distributed at the top limit of the species range, with the breeding density being 0.05 nests/ha in a valley of 300 ha. Breeding pairs start to establish at the end of April. During this process, multiple males (often from three to five individuals) court the female by feeding her. Within 1–2 days after pairing ends, some unpaired individuals are allowed into the group and the remaining ones disappear from the region. There are no extra individuals of the species present in the region throughout the rest of the breeding season. As soon as the cooperative group is formed, group members exhibit obvious territorial behaviors, such as mobbing intruders, including researchers (Du et al. 2012).

Fieldwork

The Giant Babax constructed their nests mainly on *Populus platyphylla* and *Berberis hemleyana*. We could easily locate the nests by observing the territorial behaviors of group members. Then, the nest was visited daily to determine the date of egg laying and incubation, as well as the hatching day. During the nestling period, the growth of nestlings was monitored every 2 days to determine their body weight (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm). After fledging, new fledglings need at least 2 months to beg for food from adults before they can forage independently. Both breeders and some of the helpers continuously provisioned the fledglings.

We captured some adults by trapping following the method of Ren et al. (2016). This procedure did not harm the captured birds. Each captured bird was leg-banded with one numbered aluminum ring and two colorful plastic rings to facilitate individual identification. Based on the brood patch, we could identify male and female breeders (both having a brood patch) from helpers (no brood patch). Due to local religious customs, we were unable to catch all adult birds. So, in some cases we needed to identify individuals by mixing leg rings and behavioral differences between breeders and helpers. Paired males and females took turns incubating and brooding, whereas helpers never incubated and rarely brooded. Incubating and brooding females were fed only by male breeders but not by helpers. Behaviors of group members outside the nest were observed by binocular telescope (Steiner, Germany).

We recorded the provisioning behaviors of adults at the nest using a digital camcorder (ZX1; Eastman Kodak). The camcorder was fixed 1 m above the nest cup after the first chick hatched. Videos were recorded at 1000–1200 hours every 3 days for 28 nests; each contained three nestlings. During this process, we did not visit the nest any longer in order to minimize disturbance on adult behaviors. No nest desertions occurred in our study, indicating that video recording did not have a negative effect on Giant Babax. Finally, we obtained 126 h of footage of adult-provisioning behaviors (4.5 ± 1.4 h, $n = 28$ nests).

Data extraction using video playback

Data were extracted from videos by playing back sequences on the computer. The identity of a nest visitor was determined based on behavior (males and females brooded in sequence, but helpers rarely brooded), and a phenotypic character (the back feather of male is darker than that of the female). Other data included:

1. The number of visitors during one nest visit; if more than one visitor emerged simultaneously, we recorded

whether they interacted with each other (courtship feeding or pecking).

2. Nest-visit duration, from the nest visitor arriving at the nest till departing from the nest or brooding.
3. Whether the nest visitor delivered food to nestlings; if yes, the duration of food delivery was recorded.
4. Whether the nest visitor ate the fecal sac of nestlings, and the time from food delivery until nestling defecation.
5. Whether the nest visitor brooded the nest after food delivery; if yes, the duration of brooding was recorded.
6. Whether there were predators that intruded into the nest.

Based on these data, we estimated:

1. The total provisioning rate of helpers, which was estimated as all feeding bouts performed by helpers per hour.
2. The individual provisioning rate of helpers, which was estimated only for banded helpers.

Helpers of Giant Babax exhibited three types of non-feeding behaviors. The first was pseudo-feeding, i.e., a helper visited the nest without food but mimicked food delivery activity by touching the gape of begging nestlings (Appendix I). The second was false feeding, i.e., a helper fed the nestlings with plastic debris (Appendix II). The last was contested kleptoparasitism of fecal sacs, i.e., a helper did not deliver food to nestlings but snatched their fecal sacs after other provisioners delivered food (Appendix III). We recorded no case where natural predators intruded into the territory of cooperative groups.

Statistical analysis

Our analyses were based on the mean values per nest as independent data. First, we classified nest visits into four types: feeding only, brooding only, feeding and brooding, and no feeding or brooding. Then, we compared the percentage and duration of these four types of nest visits between helpers and breeding pairs using paired-sample *t*-tests (Table 1). The percentages were transformed with an arcsine-square-root function before comparing them with *t*-tests. The total provisioning rates of males/females and helpers, the mean provisioning rates of breeders and banded helpers, and the helpers' contributions to brood provisioning were regressed with nestling age by fitting a linear model. After controlling for nestling age, we compared the total and mean provisioning rates of breeders and helpers using paired-samples *t*-tests. The helpers' probability of non-feeding was regressed with nestling age by fitting a quadratic model.

Statistical analysis was performed using SPSS (version 19.0). Descriptive data are presented as mean \pm SE. The

null hypothesis was rejected when $P < 0.05$; reported probabilities are two-tailed.

Results

The roles of breeders and helpers during the nestling period

Breeding pairs and helpers had different roles during the nestling period. Helpers performed feeding-only nest visits more often than male ($t_{26} = 4.04$, $P < 0.001$) and female breeders ($t_{26} = 8.28$, $P < 0.001$; Table 1). However, the frequencies of helpers brooding the nestlings were significantly lower than those of male (both $t \geq 2.51$, $P \leq 0.02$) and female breeders (both $t \geq 7.15$, $P < 0.001$; Table 1). Helpers spent significantly less time feeding nestlings or brooding during nest visits than male (all $t \geq 4.81$, $P < 0.001$) and female breeders (all $t \geq 7.94$, $P < 0.001$; Table 1). Helpers in 17% of the nest visits delivered no food to the nest and did not brood nestlings, whereas breeding pairs seldom performed no-feeding and no-brooding nest visits (Table 1). These results indicated that helpers mainly performed feeding and that breeding pairs performed brooding.

Helpers made greater contributions to brood provisioning than breeders. Although the total provisioning rates of provisioners all increased with nestling age (male, $R^2 = 0.87$, $F_{1,12} = 79.34$, $P < 0.001$; female, $R^2 = 0.90$, $F_{1,12} = 111.56$, $P < 0.001$; helpers, $R^2 = 0.94$, $F_{1,12} = 171.34$, $P < 0.001$; Fig. 1), the increase of helpers (0.86 ± 0.18 bouts/h per day, $n = 13$) was significantly higher than that of males (0.10 ± 0.06 bouts/h per day, $n = 13$; $t_{12} = 3.80$, $P = 0.003$) and female breeders (0.09 ± 0.06 bouts/h per day, $n = 13$; $t_{12} = 4.46$, $P = 0.001$). As a result, helpers' contribution to brood provisioning increased from 8% on the first day to 71% on the last day ($R^2 = 0.84$, $F_{1,12} = 64.8$, $P < 0.001$; Fig. 2). Helpers' contribution to brood provisioning ($47.32 \pm 4.28\%$, $n = 28$ nests) was significantly higher than that of males ($27.05 \pm 2.27\%$; $t_{27} = 2.75$, $P = 0.01$) and females ($25.63 \pm 2.08\%$; $t_{27} = 3.03$, $P = 0.005$).

At the individual level, the mean provisioning rates of breeders (1.90 ± 0.11 bouts/h per day, $n = 14$) did not differ from those of helpers (1.79 ± 0.33 bouts/h per day, $n = 14$; $t_{13} = 0.48$, $P = 0.640$). Although both rates increased with nestling age (breeders, $R^2 = 0.97$, $F_{1,12} = 389.91$, $P < 0.001$; helpers, $R^2 = 0.93$, $F_{1,12} = 154.81$, $P < 0.001$), the increase in helper rates (0.27 ± 0.12 bouts/h per day, $n = 13$) was larger than that of breeders (0.10 ± 0.02 bouts/h per day; Fig. 3), although the difference did not reach a significant level ($t_{12} = 1.15$, $P = 0.27$).

Table 1 Frequency of feeding and brooding nestlings by the breeding pair (male and female) and helpers at Giant Babax nests

Group members	Helper (<i>n</i> = 27)		Male breeder (<i>n</i> = 28)		Female breeder (<i>n</i> = 28)	
	Proportion of visits (%)	Duration of visit (s) (%)	Proportion of visits (%)	Duration of visit (s)	Proportion of visits (%)	Duration of visits (s)
Feeding only	81 ± 2	7 ± 4	35 ± 8	33 ± 3	15 ± 5	37 ± 6
Brooding only	1 ± 3	78 ± 35	11 ± 3	569 ± 89	37 ± 5	539 ± 103
Feeding and brooding	1 ± 4	143 ± 51	53 ± 7	980 ± 168	48 ± 5	614 ± 113
No feeding, no brooding	17 ± 2	20 ± 12	1 ± 1	3 ± 2	–	–

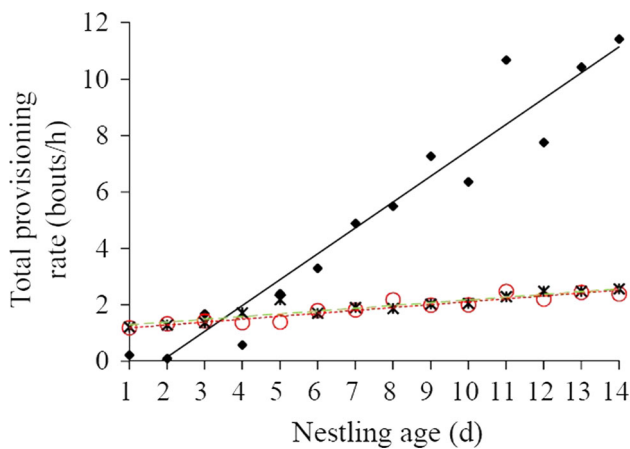


Fig. 1 Variation in the total provisioning rates of males (stars and dashed line), females (empty circles and dotted line) and helpers (filled diamonds and solid line) with nestling age (days; *d*) of the Giant Babax in the Xiongse Valley during 2015 and 2016

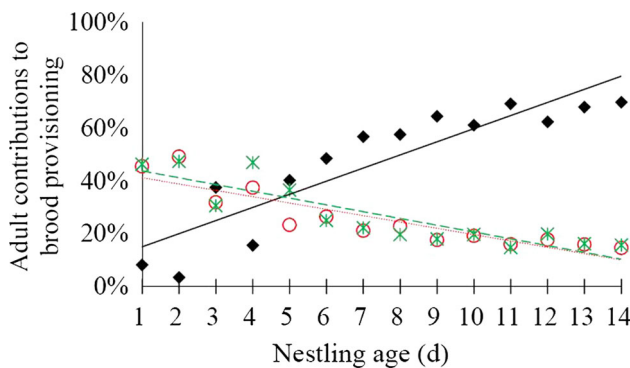


Fig. 2 Variation in the contributions of males (stars and dash line), females (blank circles and dotted line) and helpers (filled diamonds and solid line) to brood provisioning with nestling age of the Giant Babax in the Xiongse valley during 2015 and 2016

Three types of non-feeding behaviors of helpers

Compared with breeding pairs that brooded nestlings in their non-feeding nest visits (Table 1), helpers performed

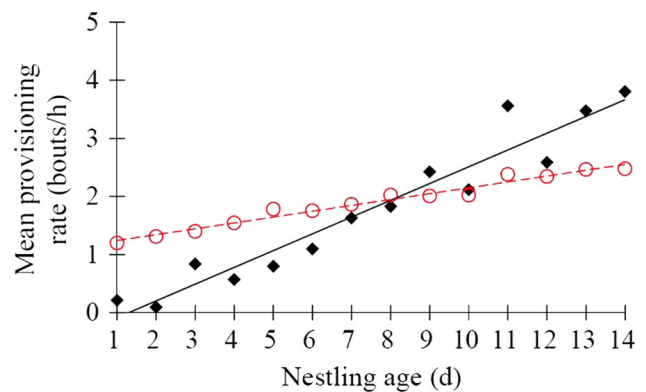


Fig. 3 Variation in the mean provisioning rates of breeders and helpers with nestling age of the Giant Babax in the Xiongse Valley during 2015 and 2016

three types of non-feeding behaviors when they visited the nest without food, or after they finished food delivery in a feeding bout (Table 2). Obviously, helpers carried out pseudo-feeding or false feeding more frequently than did the male and female breeder (all $P < 0.001$; Table 2). However, the contested kleptoparasitism of fecal sacs of nestlings by helpers was equal to that of the female breeder ($t_{26} = 0.57, P = 0.57$) and higher than that of the male breeder ($t_{26} = 4.67, P < 0.001$; Table 2).

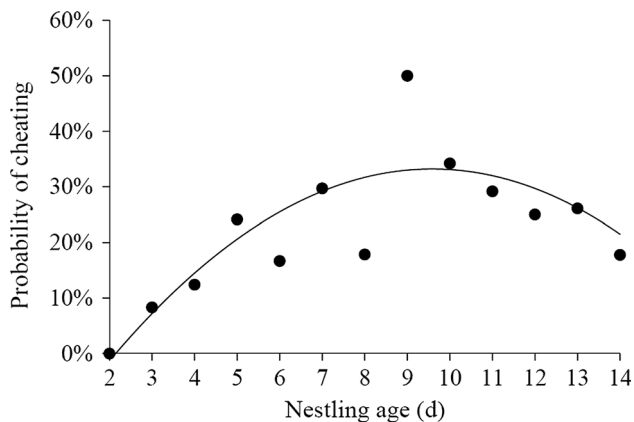
These non-feeding behaviors of helpers changed significantly with nestling age ($R^2 = 0.68, F_{2,10} = 10.59, P = 0.003$; Fig. 4). Before the nestling age of 9 days, the probability of non-feeding behaviors of helpers increased ($t = 4.08, P = 0.002$); thereafter, it decreased ($t = -3.53, P = 0.005$; Fig. 4).

Contested kleptoparasitism of fecal sacs

Nestlings never defecated if they did not obtain food; when they were fed, they defecated in 47% ($\pm 3\%$, $n = 28$) of cases. After food delivery, no matter whether the fed

Table 2 Frequency of different types of non-feeding behaviors by helpers and the breeding pair (male and female) at Giant Babax nests

Types of non-feeding behaviors	Proportion of nest visits by group members (%)		
	Helper ($n = 27$)	Male breeder ($n = 28$)	Female breeder ($n = 28$)
Pseudo-feeding	13 ± 2	1 ± 1	0
False feeding	3 ± 1	0	0
Contested kleptoparasitism of fecal sacs of nestlings	13 ± 2	4 ± 2	22 ± 6

**Fig. 4** Variation of helpers' cheating probability with nestling age of the Giant Babax in the Xiongse Valley during 2015 and 2016

nestling defecated or not, all nest visitors spent some time waiting for the nestlings to defecate. The wait of helpers until nestling defecation was shorter (13.8 ± 0.4 , $n = 28$) than that of males (16.5 ± 0.5 , $n = 28$; $t_{27} = 4.58$, $P < 0.001$) and females (21.1 ± 0.5 , $n = 28$; $t_{27} = 10.34$, $P < 0.001$).

Generally, it was the provisioner that obtained and ate the fecal sac. However, sometimes, the kleptoparasitism of fecal sacs of nestlings was contested by other individuals (Table 3). A greater proportion of kleptoparasitism events by helpers were contested by the breeding female (Appendix V) rather than by other helpers ($t_{22} = 1.78$, $P = 0.09$) and the breeding male ($t_{22} = 2.29$, $P = 0.03$; Table 3). The breeding male was confronted by helpers and

the breeding female equally ($t_{24} = 0.04$, $P = 0.97$). For the breeding female, other individuals seldom contested her when she ate the fecal sac (Table 3). These results indicated that kleptoparasitism of fecal sacs of nestlings in the Giant Babax was not a nest-cleaning activity but an attempt to eat the fecal sac.

Responses of other group members to non-feeding behaviors of helpers

Other group members made different responses to these non-feeding behaviors of helpers. When helpers contested the fecal sac of nestlings after males provisioned the brood, males often disregarded this non-feeding behavior of helpers (Appendix IV; in 87.50% of cases, i.e., seven of eight; $\chi_1^2 = 4.50$, $P = 0.03$). By contrast, females often punished the helper by pecking at it if it performed pseudo-feeding (Appendix I; 66.67% of the cases, i.e., eight of 12) or prevent helpers from continuously carrying out false feeding behavior (Appendix II, 83.33% of the cases, i.e., ten of 12; $\chi_1^2 = 6.00$, $P = 0.01$). These results indicated that males and females responded differently to the non-feeding behaviors of helpers (Fisher's exact test in crosstable, $P = 0.005$).

When another helper witnessed the false feeding behavior of a helper, it immediately became an accomplice to the behavior, by feeding the nestling on the plastic debris together with the first helper (three cases; Appendix VI).

Table 3 Proportions of contested and non-contested kleptoparasitism (fecal sac taken by an individual not feeding nestlings) within the group

Kleptoparasitism of fecal sac by group members	Kleptoparasitism not contested (%)	Kleptoparasitism contested by group members (%)		
		Helper	Breeding male	Breeding female
Helper ($n = 23$)	70 ± 7	7 ± 3	3 ± 3	20 ± 7
Breeding male ($n = 28$)	88 ± 5	6 ± 3	–	6 ± 4
Breeding female ($n = 28$)	99 ± 1	1 ± 1	0	–

Discussion

In the Giant Babax breeding on the Tibetan Plateau, helpers made greater contributions to brood provisioning than both parents. During the process of brood provisioning, helpers adopted three types of non-feeding behaviors that may be considered cheating, including pseudo-feeding, false feeding, and contested kleptoparasitism of fecal sacs of nestlings. As adult birds can get some nutrients from eating the fecal sac of nestlings (McGowan 1995; Burns 2016), obtaining a fecal sac may be an immediate reward driving helpers to cheat.

Why are non-feeding behaviors of helpers considered cheating?

According to the definition of cheating as “exploiting the benefit of cooperation without paying commensurate costs” (Sachs and Simms 2006; Sachs and Rubenstein 2007), we think that these non-feeding behaviors of helpers in the Giant Babax may be actual cheating because helpers obtained or intended to obtain fecal sacs (a benefit because of the nutrients within it) but delivered no food to the nest (paying no commensurate cost). However, there are alternative opinions regards whether pseudo-feeding behaviors of helpers can be considered actual cheating (McDonald et al. 2008). First, pseudo-feeding helpers may be inexperienced or of low quality. Thus, they may be unable to find and deliver the same amount of food as the breeders (Arnold et al. 2005; Baglione et al. 2010). By comparing both the total and mean provisioning rates between helpers and breeders (Figs. 1, 4), this possibility can be discarded because helpers are also good at foraging and delivering food to chicks. Second, when the food demand of chicks is lower than that of helpers, a helper may eat the food itself, hence false feeding occurs (McDonald et al. 2007). In the Giant Babax, non-feeding helpers visit the nest with no food at all. Therefore, it is impossible that these false feeding behaviors have resulted from an estimation of food demand of the brood. Third, when helpers provisioned the chicks with plastic debris, they may be making a mistake. If so, we cannot explain though why helpers themselves do not eat the plastic debris since Giant Babax eats as many as 11 food types, including butterflies, moths, and lizards (Du et al. 2012). The last possibility is that helpers may have allocated their efforts to other tasks such as nest defense (Koenig and Dickson 2004; Ren et al. 2016). However when we recorded the provisioning behaviors of adults, no natural predators intruded the territory of the cooperative groups. Thus, this possibility can also be excluded.

In cooperatively breeding species, pseudo-feeding or false feeding behaviors of helpers may advertise their

compliance with the cooperative agreement [pay-to-stay hypothesis (Kokko et al. 2002); social prestige hypothesis (Zahavi 1995)], which may benefit cheating helpers in a long-term involvement in future reproduction. In the Giant Babax, however, we found that three types of non-feeding behaviors of helpers significantly correlate with a short-term benefit, i.e., getting the fecal sacs from nestlings. Given that this kind of nutritional benefit from eating the fecal sacs of nestlings has been reported in many altricial birds (McGowan 1995; Burns 2016), it appears that helpers must pay to get them, by performing the majority of brood provisioning (Taborsky 1984; Bergmüller et al. 2005). So, to get this immediate nutritional reward may be an important incentive driving helpers to cheat.

Group members make different responses to cheating

In cooperative groups, helpers often reduce but do not cease their parenting efforts completely (Boland et al. 1997; Clutton-Brock et al. 2005). To compensate the reduced parenting efforts of cheating helpers, other group members have to increase the amount of parenting, hence their benefits will be reduced (Legge 2000). Depending on the effect of cheating on their fitness, it is understandable that other group members will respond differently to cheaters. In the Giant Babax, female breeders usually peck at cheaters to prevent helpers from cheating continuously (Appendix I–II), and even snatch fecal sacs after helpers deliver food to nestlings (Appendix V). As female breeders are the most dominant in the group [being active in mate selection at the beginning of the breeding season (Lu 2004; Du et al. 2012)] and are more nutritionally stressed than other group members, cheating of helpers will greatly reduce the potential benefits that these females could obtain from ingesting fecal sacs of nestlings. So, female breeders of the Giant Babax will make negative responses to cheaters. By contrast with female breeders, male breeders did not exert punishment on cheaters even when they witness their cheating behaviors (Appendix IV). The reason for this may be that male breeders are less nutritionally stressed than female breeders because they have more time to forage for food (Table 1).

It is interesting to note that other helpers became accomplices when they witnessed the cheating behavior of a helper (appendix VI). This indicates that helpers in a cooperative group of Giant Babax have the same interests. For them, to become the accomplice of a cheater adds no overt costs but brings obvious benefits if they can stimulate the nestlings to defecate. The plastic debris delivered to the nestlings by cheating helpers is made of potato or corn starch that can degrade naturally in the environment. If it could be digested by birds, it would be very easy for them

to obtain this plastic debris. But none of the Giant Babax had fed on plastic debris before (Du et al. 2012), indicating that plastic debris is only a false bait used by cheaters to stimulate nestlings.

Why does cooperation not break down in the presence of cheaters?

The reduced contributions of helpers to brood provisioning, no matter whether they are cheating or not, seldom cause a break down of the cooperative groups (Canestrari 2004; McDonald et al. 2007). On the one hand, this is because helpers may undertake other tasks within the group, such as nest defense (Koenig and Dickison 2004; Arnold et al. 2005). On the other hand, breeders may obtain more benefits from the presence of helpers, even if helpers cause some costs by cheating. In the Giant Babax, although cheating behaviors occurred, the provisioning rates of helpers increased with nestling age (Figs. 1, 4) and their cheating probabilities decreased when nestlings needed more food in the later nestling period (Fig. 4). Consequently, helpers' contributions to brood provisioning increased with nestling age (Fig. 2). Compared with the benefits of a lightened workload (nearly 70% of food delivery), the costs caused by helpers' cheating (consumption of fecal sacs of nestlings) are significantly minor to both male and female breeders. So, even if helpers cheat, neither breeding parent of the Giant Babax evicts these helpers from the group.

In conclusion, by investigating the cheating behaviors of helpers and the responses of other group members in the Giant Babax, we suggest that cheating may evolve in cooperative breeding. When dominant breeders can obtain more benefits from the presence of helpers within the nest, they may endure the occurrence of cheating by helpers. For the helpers, short-term benefits may be another important factor driving them to cheat.

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