



Begging is an honest signal of hunger in a communally nesting bird with low genetic relatedness

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Abstract

Kin selection theory predicts that conflict over resource allocation will intensify as relatedness between dependent young and adult caregivers decreases. As inclusive fitness constraints on dishonest signalling relax, begging behaviour is less likely to be a reliable indicator of hunger or condition. Therefore, dishonest signalling is expected to be especially prevalent in communally breeding species, for which offspring survival often depends on care from both related and unrelated adults. We evaluated the scope for conflict and its consequences for dishonest signalling in the greater ani (*Crotophaga major*), a communally nesting cuckoo in which multiple unrelated pairs lay in the same nest. Using video recordings of nearly 2500 feeding events across 10 nests, we demonstrate that begging behaviour is a reliable signal of hunger, with hungrier nestlings begging more intensely. We also show that begging may communicate reliable information about condition in the long term, with smaller nestlings begging more intensely than their larger broodmates. Ultimately, larger nestlings and those who begged more intensely were more likely to receive food, indicating that both begging signals and scramble competition influence resource allocation. Together, our results indicate that honest begging signals can persist even when caregivers and young are unrelated.

Significance statement

Offspring solicit food from their adult caregivers through a variety of begging behaviours. These behaviours can convey important information about offspring hunger and/or long-term condition, but may be exaggerated, if offspring attempt to gain more than their proportionate share of resources. We examined whether offspring exaggerate their begging behaviour, such that it is not a reliable indicator of their hunger or condition, in the greater ani. Greater anis breed communally, with multiple pairs sharing a single nest simultaneously such that nestlings are fed by both their parents and unrelated adult caregivers. Theory predicts that begging should be less reliable if offspring and caregivers are unrelated, but we found that greater ani begging behaviour reliably communicated hunger, and potentially long-term condition, to adults. This study is the first to evaluate begging signal reliability in a communally breeding species.

Keywords Communal breeding · *Crotophaga major* · Greater ani · Honest signalling · Inclusive fitness · Parent–offspring conflict

Introduction

In animal families, asymmetries in the inclusive fitness benefits derived from parental investment lead to potential conflict over the amount and allocation of resources, both

between parents and offspring and among offspring themselves (Trivers 1974; Macnair and Parker 1979; Godfray 1995). Theoretically, offspring are selected to solicit greater investment than parents are selected to give and may therefore exaggerate aspects of their hunger, body condition, and fitness potential in order to gain a disproportionate share of resources (Trivers 1974). Parents may still use these begging behaviours to make decisions about how to optimize resource allocation, but the information they receive may not be perfect. The degree to which begging behaviours are honest depends partly on the relatedness among signallers and receivers. Indirect fitness costs, including the reduced

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survival of related current and future siblings, typically limit family conflict and unreliable signalling to some degree, such that begging signals can be fully reliable indicators of offspring fitness under certain conditions (Parker et al. 1989; Grafen 1990; Godfray 1991; Romano et al. 2012). But as genetic relatedness among adult caregivers and dependent young decreases, conflict is predicted to intensify, and begging behaviour is less likely to be a reliable indicator of offspring hunger or condition.

Empirical data tend to support this prediction: Numerous comparative studies demonstrate that offspring who are likely to compete against half-siblings, whether in the current brood (due to extra-pair matings) or in a future brood (due to parental divorce or death), appear to be less honest than those whose parents are monogamous or likely to breed together again in the future (Briskie et al. 1994; Long 2005; Caro et al. 2016b; Peignier et al. 2019). Similarly, increased competition, in the form of additional contemporaneous siblings or a greater likelihood of future siblings, is often associated with an increase in dishonest or exaggerated begging (Godfray 1995; Leonard et al. 2000; Caro et al. 2016b; but see Thompson et al. 2013). If begging signals are less likely to be reliable, adult receivers may ultimately prioritize information about hunger and condition from other sources instead, such as publicly available cues and the outcome of direct competition over access to parental resources (McRae et al. 1993; Krebs 2001; Smiseth et al. 2003).

For species that breed communally, the potential for family conflict should be especially high and the honesty of begging behaviour especially weak. Communal breeding systems are widely distributed across animal taxa, found in birds (Vehrencamp and Quinn 2004), mammals (Lewis and Pusey 1997; Hayes 2000; Federico et al. 2020), and insects (Zink 2005; Komdeur et al. 2013). In these social groups, multiple reproductive adults provide care to a shared brood of offspring, often indiscriminately and without reliable kin recognition (Manning et al. 1995; Gilchrist 2004; Young 2017). Even if adult co-breeders are first- or second-order kin, the average genetic relatedness among adult caregivers and dependent young is typically lower than that of noncommunal breeders (e.g. Koenig and Pitelka 1979; Manning et al. 1995; Eberle and Kappeler 2006). Moreover, the inclusion of multiple broods in a single den or nest often leads to increased competition for resources, despite the presence of additional caregivers, potentially further favouring dishonest solicitation (Kacelnik et al. 1995; Hodge et al. 2009; Caro et al. 2016b).

However, family conflict and the honesty of begging signals have received little attention in communal breeders (Bell 2007; Bebbington et al. 2018), and there are several aspects of communal breeding that may actually help to maintain begging signal honesty. In communal groups that persist for multiple seasons, the fitness interests of caregivers and offspring can be aligned despite low genetic relatedness,

since unrelated broodmates or caregivers may remain in the group and provide care to future siblings (e.g. Packer and Pusey 1982). Exploiting co-breeders for significantly more resources than they are selected to provide may therefore lead to considerable indirect fitness costs: Changes in group composition can lead to reduced reproductive success in subsequent years (Ebensperger et al. 2016), and, even if co-breeders remain in the group, their condition may be diminished such that they are unable to provide adequate care to an offspring's future siblings (Santos and Nakagawa 2012). Additionally, honest begging signals could also persist through direct fitness costs. Exaggerated solicitation could increase the likelihood of predation (e.g. McDonald et al. 2009) or may simply be limited by energetic costs (Godfray 1991; Chappell and Bachman 2002; Mock et al. 2011). The latter is observed in some obligate avian brood parasites, who are unrelated to their host caregivers and yet for whom begging behaviour still honestly communicates their hunger level (Hauber and Ramsey 2003; Lichtenstein and Dearborn 2004; but see Rivers 2007). Investigating the potential role of relatedness on the expression of selfish begging behaviour can also elucidate how signaller costs and receiver benefits work to constrain or facilitate cooperative behaviours. For example, if signal honesty varies between species with similar levels of within-brood relatedness, this could indicate that inclusive fitness costs and benefits themselves may play a more important role in determining honest signalling.

In this study, we examined begging behaviour in the greater ani (*Crotophaga major*), an obligate communally nesting cuckoo with a high potential for conflict over resource allocation. Greater anis live in social groups composed of two to three unrelated breeding pairs, all of whom contribute to and care for their shared brood (Riehl and Jara 2009; Riehl 2011). Adults are unable to recognize their own offspring (Riehl and Strong 2015), and each female contributes two to four eggs to the incubated clutch, leading to large broods in which nestlings compete for resources against full siblings, unrelated nestmates, and sometimes half-siblings (Riehl and Jara 2009; Riehl 2012, 2016). Low within-brood genetic relatedness (Riehl 2016) and provisioning by both related and unrelated adult caregivers may favour dishonest begging signals.

We evaluated begging signals and their effects on resource distribution among greater ani nestlings in 10 communal broods. First, we tested whether the intensity of begging signals accurately reflects measures of nestling hunger (Grodzinski and Lotem 2007; Mock et al. 2011): if so, begging intensity should be positively correlated with hunger level, and if not, we expected to find no relationship between begging behaviour and hunger level. We controlled for the possibility that begging signals may also convey information about nestling need or quality at the ultimate level (Mock et al. 2011; Caro et al. 2016a; Gurguis and Duckworth 2022)

by including body size, as a measure of nestling condition in the long term, as a covariate. Adults may be able to judge body size even without nestling begging behaviour, through cues or structural ornaments, but this information could be reinforced and communicated more effectively through begging signals, particularly in a crowded nest environment (Wild et al. 2017). Second, we determined the degree to which begging behaviour (whether honest or dishonest) actually influenced whether a nestling was likely to receive prey during a given feeding event, given direct competition among nestmates and information about nestling condition already visible to adult receivers (i.e. body size). We then evaluated whether the resulting resource allocation patterns were consistent with favouring nestlings in good condition (with high probability of surviving to fledge) or nestlings in poor condition (who presumably would benefit most from the next prey item).

Methods

Study system

Greater anis are long-lived birds (15–20 years; CR unpubl. data) that form groups of two or three socially monogamous breeding pairs; while we have occasionally observed single pairs and groups of four at our study site, they have never bred successfully (Riehl and Jara 2009; Riehl 2011, 2012). Adult group members are genetically unrelated to their groupmates: Nestlings almost always disperse to join unrelated co-breeders rather than remaining to breed with their natal group ($N=340$ of 341 nestlings; Riehl 2011), and average genetic relatedness among adult co-breeders is not significantly higher than random chance (Riehl 2011). Pairs are predominantly genetically monogamous but occasionally produce extra-pair offspring within the group (12–19% of nestlings; Riehl 2012). In about 20% of groups, breeders are assisted by nonbreeding helpers, who may be retained offspring from a previous brood or unrelated immigrants (Riehl and Jara 2009; Riehl 2021). Breeding pairs can remain in the same group for a decade or more (Riehl and Strong 2018), and group stability and between-pair bonds are likely to be under strong selection: females who have nested together previously are less likely to skip breeding in the current year (Smith and Riehl 2020) and achieve better reproductive success than females who have never nested together before (Riehl and Strong 2018).

Since the number of adults contributing young to the brood increases with group size, average within-brood relatedness—and the likelihood of an adult feeding its own offspring in a given feeding event—decreases slightly with group size. In broods that do not experience predation,

groups with two breeding pairs produce an average of 6.37 nestlings (\pm SE = 0.12), and the mean dyadic relatedness among nestlings is $r=0.21$ (\pm SE = 0.02), whereas groups with three breeding pairs produce 8.53 nestlings (\pm SE = 0.28) among which $r=0.13$ (\pm SE = 0.02; data from Riehl 2012). Adults are unable to recognize their own offspring and provide care indiscriminately (Riehl and Strong 2015). Nestlings typically hatch over a period of 1–3 days, which leads to competitive asymmetries that are most pronounced between the first- and last-hatched nestlings (Riehl 2016). Last-hatched nestlings are significantly more likely to die of starvation than both first-hatched nestlings and middle-hatched nestlings; overall, starvation accounts for 7.6% of nestling mortality and occurs in 26.4% of all broods (and 41.2% of broods that do not experience predation; Riehl 2016). Adult males are on average 10 g heavier than females; this sexual size dimorphism emerges about 2 days after hatching (T. Hendrix and CR, unpubl. data).

Data collection

From June to August 2018, during the greater ani breeding season, we collected data on begging and provisioning behaviour at our long-term field site within the Barro Colorado Nature Monument (BCNM) in central Panama. Managed by the Smithsonian Tropical Research Institute, the BCNM consists of Barro Colorado Island and several mainland peninsulas surrounding Lake Gatún.

We studied 10 focal groups whose brood sizes ranged from two to 11 nestlings (mean \pm SE = 5.2 ± 0.89) and whose group sizes, including breeders and nonreproductive helpers (present in six groups), ranged from four to eight adults (mean \pm SE = 5.5 ± 0.40 ; Table S1). Five groups contained three breeding pairs, while the others contained two pairs (Table S1). Genetic analyses confirmed that all breeding pairs contributed offspring to the communal clutch. At the brood level, average genetic relatedness for nestlings within the same brood ranged from $r=-0.09$ to $r=0.31$ (mean \pm SE = 0.14 ± 0.04 ; $N=10$ broods; Supplemental Methods). Because we followed specific focal groups, it was not possible to use blinded methods when collecting data. We checked nests every other day during incubation and daily after hatching began, in order to identify nestlings and install small video cameras (Contour + 2 or Roam3 models) to record provisioning events. At hatching, nestlings were marked on the head and back using non-toxic paint pens; marks were refreshed daily. When nestlings were 2–3 days of age, we took blood samples by puncture of the brachial vein for later molecular sexing and genotyping. Cameras were attached to external battery packs (Anker Astro E1s) and secured to nearby branches approximately 1 foot away from the nest with zip ties. Nestlings are capable of prematurely fledging at 5–6 days after hatching if disturbed, so

we were limited to a maximum of 5 days of video footage per nest.

We installed the video cameras as early as possible each day, typically between 0700 and 0900 h. Prior to installing the cameras, nestlings were weighed daily in a small cloth bag attached to a spring scale, and their mass was recorded to the nearest gramme. Tarsus and culmen length were measured using dial callipers, to the nearest millimeter. We then used these raw measurements to develop our body size metric, representing condition in the long term. We used principal component analysis through the “prcomp” function in R v. 4.0.2 (R Development Core Team 2020) to reduce mass, tarsus, and culmen length into a single principal component which explained 96% of the variation. The variables were centred and scaled to have unit variance before being decomposed. In the few instances in which we could not obtain all measurements for a nestling in the field ($N = 13/281$ sets of nestling measurements), we used linear regression models based on the other measurements to predict the missing value(s). Nestlings who had higher principal component scores were assumed to be in better condition than those with lower scores.

Video data

Three observers watched and annotated the nest camera footage using ELAN software v. 5.9 (The Language Archive 2020), identifying all instances in which an adult brought prey back to the nest (“feeding events”). We observed 2 477 feeding events in total. Observers recorded the start time (when the adult came into contact with the nest) and end time (when the nestling who ultimately swallowed the prey made contact with the prey item) of each event to the nearest tenth of a second. Interobserver reliability for subsequent behavioural measures was assessed using Cohen’s kappa statistic; observers exceeded a kappa of 0.75 on all measures (Kaufman and Rosenthal 2009; Hallgren 2012). Kappa values were calculated using the “irr” package in R (Gamer et al. 2019).

For each nestling in each feeding event, observers recorded its maximum begging intensity, its closest proximity to the adult, and its maximum height above the floor of the nest for the duration of each feeding event. Begging intensity was scored on a five-level scale from zero to four. Nestlings at level zero did not beg at all; those at level one had an open gape; those at level two had an open gape and an outstretched neck; those at level three had an open gape and some wing movement; and those at level four had an open gape and sustained wing flapping (adapted from Redondo and Castro 1992).

Proximity and height were scored as binary variables. Nestlings who were closest to the adult or reached the highest were scored as “closest” or “tallest,” respectively.

Multiple nestlings could be closest or tallest during a given feeding event, either simultaneously or at different points during the event. Nestlings who were never closest to an adult or never reached the highest were scored as “not closest” or “not tallest,” respectively. If multiple adults were present during a feeding event, proximity was not scored ($N = 613/2 477$ feeding events excluded). Observers also recorded which nestling ultimately received the prey item and the size of that prey relative to the length of an adult’s bill on a five-point scale (XS–XL). If no nestling received the prey (e.g. it was swallowed by an adult or dropped outside the nest), observers recorded the feeding event as “unsuccessful” and did not record the above behavioural data ($N = 153/2 477$ feeding events excluded).

At the start of each feeding event, each nestling’s hunger level was approximated by calculating the amount of time, in hours, that had elapsed since it had last received prey. At the first feeding event of each day, nestlings were assumed to have the same hunger level, equivalent to the amount of time elapsed since filming began; after this first feed, hunger levels began to diverge. Nestlings for whom more time had elapsed were assumed to be hungrier than nestlings who had been fed more recently. All nestlings were fed at least once per day.

Hypothesis testing and statistical analysis

All data were analysed using R v. 4.0.2 (R Development Core Team 2020). We used mixed-effects models to examine (1) whether hunger level and body condition accurately predict begging intensity and (2) which nestling behaviours and characteristics influence whether a nestling is fed during a given feeding event. We used an information-theoretic approach in which global models included all predictors of interest and “best-subsets” models were identified using Akaike’s information criterion, corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). Best-subset models were those that were within 2 AIC_c units of the top performing model, unless they differed from the top model by the inclusion of only one additional parameter, per Arnold (2010). Candidate models were evaluated against a null model containing only the intercept and random effects using likelihood ratio tests conducted in the package “rcompanion” (Mangiafico 2021). Only data from days when full broods were present were considered when fitting models (i.e. only after all nestlings had hatched in a given nest).

First, we evaluated whether nestling begging behaviour was correlated with nestling hunger and condition. Using the package “ordinal” (Christensen 2019), we ran a mixed-effects ordinal regression with absolute begging intensity as the response variable; nestling ID nested

within group ID as random effects; time in hours since a nestling had last been fed (“hunger”) as the main fixed effect; and nestling body size, the size of the last prey item that a nestling consumed, and brood size as covariates. We also included an interaction between brood size and the main effect of hunger. We considered body size as a covariate because other studies have shown that nestling begging behaviour can be associated with multiple types of information, including hunger and condition, which could affect our hunger result if not accounted for (Gurguis and Duckworth 2022). We included the size of a nestling’s last meal (coded as an ordinal variable) to control for the effect of prey size on how long before a nestling felt hungry and included brood size and its interaction to control for differences in competitive environment and relatedness that could influence begging behaviour. As brood size increases, average relatedness among nestmates decreases, since increases in brood size are typically due to the addition of another breeding pair to the social group. We use brood size instead of number of breeding pairs as a covariate here because brood size is the proximate cue that would be most available to nestlings to gauge the likely relatedness of their nestmates (and therefore the optimal honesty of their begging signals). To reduce multicollinearity in the model, we mean-centred all four main effects (Iacobucci et al. 2016); variance inflation factors, calculated using the “car” package (Fox and Weisberg 2019), were < 2 after mean-centring (Table S2).

Second, to determine whether begging behaviour actually influences allocation decisions, given that adults can observe relative nestling size even without behavioural cues, and that size also influences direct competition among nestlings, we ran a mixed-effects logistic regression using the package “lme4” (Bates et al. 2015) with whether each nestling was “fed” or “not fed” as the binary response variable; nestling ID nested within group ID as random effects; and relative begging intensity, height, proximity, relative body size, sex, and brood size as fixed effects. We initially ran separate regressions that included either absolute or relative measures of begging intensity and body size. Relative begging intensity was calculated as the difference between an absolute begging score and the brood’s average score for a given feeding event; relative body size was calculated as the difference between a nestling’s body size and the brood’s average body size for a given day. Models with absolute measures either failed to converge or had higher AIC_c values than models with relative measures, so we used relative values in the final subsetting process for this model (see Table S3). Variance inflation factors were < 2 , without mean-centring (Table S4). Sex could not be determined for two nestlings, whose data were excluded from this model.

Ethical note

While being measured and marked, nestlings were held for less than 10 min. We observed no adult aggression toward marked nestlings in this study, and the randomly assigned paint colour (blue, green, or purple) did not influence whether or not a nestling received prey (one-way ANOVA with nestling ID nested within group ID as random effects: $\chi^2_2 = 0.27$, $P = 0.87$; see also Table S5). Adults occasionally pecked at the video cameras when they were first installed, but quickly stopped. After installation, adults resumed feeding within 17 min on average (± 13 min SD), which matches the usual period between feeding events (AGS and CR unpubl. data).

Results

Begging, hunger, and condition

To determine whether greater and begging signals are reliable indicators of hunger, we first fit a model to evaluate the effect of the time since a nestling had last been fed on begging intensity. The resulting best-subset model included hunger, body size, size of the last meal, and brood size as significant predictors (Table 1; Table S6). The next-best subset was the global model ($\Delta AIC_c = 1.93$), which differed from the top model only by the inclusion of the interaction term, which was not significant (Table S7). Hungrier and smaller nestlings begged at significantly higher intensities than nestlings who had recently been fed and begged more intensely than larger nestlings (Fig. 1). This relationship may have been driven by differences in the probability of begging at the highest intensity (level four; blue lines in Fig. 1) or not begging at all (level zero; pink lines in Fig. 1): hungrier and smaller nestlings were more likely to beg at the highest intensity, while less hungry and larger nestlings were slightly more likely not to beg at all. Hungrier and smaller nestlings were also slightly more likely to beg at intensity level two. Because hunger and nestling size were both retained in the best-subset model, with low levels of multicollinearity (variance inflation factors < 2 ; Table S2), it appears that both predictors separately affect begging intensity.

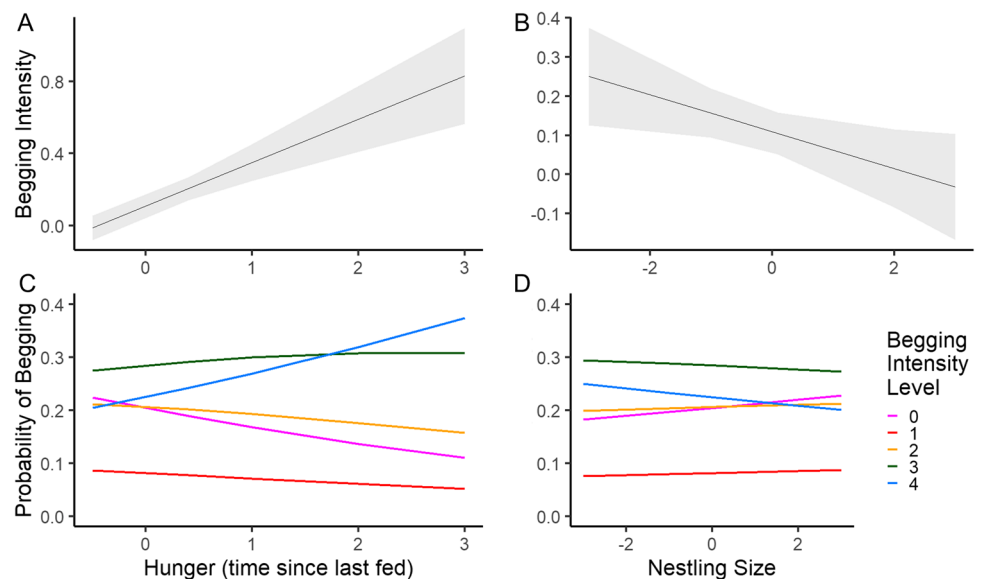
The size of a nestling’s last-consumed prey item had a significant effect on its begging intensity, along with the time that had elapsed since it had last received that prey item; nestlings who had recently eaten a small meal begged more intensely than nestlings who had recently eaten a large meal (Table 1). As brood size increased, the likelihood of begging at a high intensity significantly decreased. Neither of the interaction terms involving brood size was retained in the best-subset model (Table 1).

Table 1 Results of a best-subset mixed-effects ordinal regression predicting the effect of nestling hunger (the time in hours since last fed), along with nestling body size, brood size, and the size of a nestling's last-consumed prey item, on begging intensity in communal broods of greater ani nestlings

Response variable: begging intensity					
Fixed effect	Odds ratio	SE	Z	P	95% CI
Hunger (time since last fed)	1.272	0.056	5.469	< 0.0001	1.167, 1.387
Nestling body size	0.954	0.019	-2.326	0.0200	0.917, 0.993
Size of last meal	0.382	0.045	-8.133	< 0.0001	0.304, 0.483
Brood size	0.934	0.021	-3.078	0.0021	0.895, 0.976
Random effect		Variance	SD		
Group ID		0.008	0.091		
Group ID: Nestling ID		0.120	0.347		

A two-way interaction between brood size and hunger was included in the full model, but was not retained in the best-subset model. Begging intensity and prey size were scored on discrete 5-point scales (0=no begging, 4=most intense begging; XS–XL). Nestling ID and group ID were included as nested random effects

Fig. 1 Model-estimated effects of nestling hunger and nestling body size on begging intensity as a continuous latent variable (A and B, respectively) and on the probability of begging at a given level of intensity (C and D, respectively) in communally breeding greater anis. Shading in (A) and (B) represents 95% confidence intervals. Data are mean-centred



Resource allocation

After determining that begging intensity was associated with nestling hunger, nestling body size, size of the last meal, and brood size, we then evaluated whether begging influences adult allocation decisions by testing which factors predict the probability of whether a nestling receives prey during a given feeding event. The resulting best-subset model retained the following predictors: relative begging intensity, proximity, height, relative body size, and brood size, all of which were highly significant ($P < 0.001$; Table 2). The next-best subset ($\Delta AIC_c = 1.88$) was the global model, which included all previous predictors plus nestling sex, which was not a significant predictor by itself (Tables S8 and S9).

Relative begging intensity was positively and significantly associated with receiving prey: The more intensely a nestling begged, the greater the probability that it would be fed, when controlling for hunger and body size (Table 2). A nestling's

proximity to the provisioning adult and its height above the floor of the nest were also positively associated with receiving prey; height was significantly associated with body size, but proximity was not (Tables S10 and S11). Larger nestlings were more likely to receive prey than were smaller nestlings in the same brood, and as brood size increased across groups, the probability of any given nestling receiving prey decreased, when controlling for hunger and begging intensity (Table 2).

Discussion

In this study, we evaluated whether low genetic relatedness in a communally breeding bird is associated with dishonest and exaggerated nestling begging behaviour. Contrary to this hypothesis, we found a significant positive association between greater ani nestling begging intensity and hunger and a significant negative association between begging intensity and body

Table 2 Results of a best-subset mixed-effects logistic regression predicting the binary probability of whether a greater ani nestling in a communal brood received prey during a feeding event (0 = not fed, 1 = fed)

Response variable: fed or not fed (binary)					
Fixed effect	Coefficient	SE	Z	P	95% CI
Brood size	-0.223	0.023	-9.564	<0.0001	-0.280, -0.179
Height	1.601	0.087	18.467	<0.0001	1.432, 1.772
Proximity	0.691	0.086	8.008	<0.0001	0.522, 0.860
Relative begging intensity	1.071	0.050	21.559	<0.0001	0.974, 1.169
Relative body size	0.220	0.060	3.647	0.0003	0.100, 0.341
Random effect	Variance	SD			
Group ID	0.013	0.116			
Group ID: Nestling ID	0.017	0.132			

Begging intensity was scored on a discrete 5-point scale and standardised to the average intensity in a nest for each feeding event. Nestling body size was standardised to the average size among nestmates on a given day. Proximity and height were binary (0 = not closest to adult or not tallest, 1 = closest to adult or tallest)

size, suggesting that begging is an honest signal of hunger and that it could also communicate reliable information about nestling long-term need. Begging signals influenced how adults allocated resources within the nest, along with factors like nestling height and proximity to the provisioning adult, which suggest that scramble competition may also have an effect on resource allocation. Additionally, we found that begging intensity was influenced by the size of a nestling's most recent meal and that, unexpectedly, begging intensity decreased as the number of nestlings in a brood increased.

Our finding that ani begging behaviour correlates with hunger is not necessarily surprising and aligns with the results of several studies on brood parasites, who continue to signal their hunger honestly even though they are genetically unrelated to both of their host parents and to all of their host nestmates (Lichtenstein 2001; Hauber and Ramsey 2003; Lichtenstein and Dearborn 2004; Soler et al. 2012). However, signal honesty had not previously been investigated for communally breeding species, whose within-brood relatedness may be closer to that of brood parasites' than to pair-nesting species. It appears that, for greater ani nestlings, begging behaviour represents a reliable signal of hunger, communicating information about immediate nestling need (Mock et al. 2011), although manipulative experiments would be necessary to fully confirm the results of this observational study. That postural begging reliably communicates hunger may be explained by the direct fitness costs associated with begging, which only the hungriest nestlings may be able and/or motivated to offset (Lotem 1998; Kilner 2001). We found that hungrier ani nestlings were increasingly likely to beg at level four, the highest intensity level, which is distinguished by sustained wing flapping. This may be the most salient postural signal for adult receivers, who typically evaluate nestlings in crowded, chaotic nests, but it may also be one of the most energetically expensive to produce (Kilner 2001; Rodríguez-Gironés et al. 2001; Hauber

and Ramsey 2003), and it may also expose nestlings to increased predation risk (McDonald et al. 2009).

In addition to direct fitness costs, indirect fitness costs may also play a role in maintaining an honest signal of hunger. A greater ani parent's ability to breed again and to care for a brood of future offspring is contingent not only on their condition, but also on that of their co-breeders, since all adults in their communal breeding group contribute to incubation, provisioning, and defending the nest. Since group composition is fairly stable between breeding seasons (Riehl 2011; Smith and Riehl 2020), co-breeders caring for nestlings in the present brood are likely to care for the brood's future siblings, too. Nestlings may therefore be invested not only in their parents' survival, but also in that of their co-breeders and, in line with current understanding of parent-offspring conflict theory, may benefit from honestly signalling their hunger and allowing all adults to more closely achieve their ideal distribution of resources. The role that unrelated group members may play in realizing indirect fitness benefits should not be overlooked when evaluating the scope of family conflict in communal breeders.

These results highlight the important effect that factors beyond relatedness can have on constraining the expression of selfish signalling behaviour and facilitate cross-species comparisons to better understand variation in family conflict. For example, while the cost to greater ani nestlings of exploiting unrelated adult caregivers may be sufficiently high to limit exaggerated begging, the same may not be true for one of their congeners, the groove-billed ani (*C. sulcirostris*), who can nest successfully either as a single pair or in a communal group (Vehrencamp 1978). Their cost of exploitation may be lower than for greater anis, who are obligate communal breeders with few alternative reproductive options if co-breeders are unavailable for the next breeding season. Little is currently known about begging signal honesty in the other Crotophaginae cuckoos or in other communal

breeders, and much more work is needed to understand how factors beyond relatedness influence family conflict and begging signalling across different social systems.

In addition to conveying an honest signal of hunger, begging behaviour may also communicate signals of offspring need or quality (Mock et al. 2011; Gurguis and Duckworth 2022), which we accounted for by including a composite measure of nestling body size, as a proxy for long-term condition, in our model of begging behaviour. Overall, body size was a significant predictor of begging intensity, even when controlling for hunger: Smaller ani nestlings were more likely to beg at level four, while larger nestlings were more likely to beg at level zero (no begging). This suggests that greater ani begging behaviour could also be an honest signal of need, with only nestlings in poor body condition, who would receive the greatest marginal fitness benefit from the next prey item, willing to pay the costs of begging at such high intensities (Godfray 1991). In many species, body size is a significant predictor of whether nestlings will survive the risky post-fledging period (Lindström 1999; Schwagmeyer and Mock 2008; Jones et al. 2017) and may be an important piece of information for adult receivers. However, our metric of body condition may already be publicly available to provisioning adults, violating the signal of need assumption that begging signals transmit otherwise cryptic information (Godfray 1991; Mock et al. 2011). Still, some theoretical models demonstrate that if public information can instead be more efficiently and reliably communicated through a signal, receivers may preferentially attend to this signal instead of relying on publicly accessible cues (Wild et al. 2017). Given that ani nests are typically crowded spaces, with nestlings occasionally standing on top of each other and only slight differences in body size among those hatched on the same day, an apparently redundant signal of condition could nevertheless be important for adults (Wild et al. 2017). Given the correlative nature of our results, additional experiments that manipulate nestling body size, estimate actual survival rates, and consider truly cryptic measures of condition are necessary to evaluate whether begging behaviour is actually a signal of long-term need for greater ani nestlings. Additionally, other signals that we were unable to measure in this study, such as begging vocalisations or skin and gape colouration, may also play a role in communicating information about hunger and/or condition to adult receivers (Kilner 1999; Sacchi et al. 2002).

An unexpected result from our study was that begging intensity decreased with brood size. Given the potential for increased competition in larger nests, as well as a slight decrease in intra-brood relatedness, we might predict that begging intensity should increase as brood size increases. However, we found the opposite. Because broods are typically larger in three-pair groups compared to two-pair groups (8.53 nestlings ± 0.28 SE versus 6.37 nestlings ± 0.12 SE; Riehl 2012), it is possible that a simultaneous increase

in caregivers may have sufficiently offset the nutritional demands of larger broods, actually reducing competition (Bebbington et al. 2018). Another possibility is that adults could have reduced the costs of competition by synchronizing their nest visits, leading to a more equal distribution of resources as shown in Taiwan yuhinas (*Yuhina brunneiceps*) (Shen et al. 2010). However, both of these possibilities are unlikely in this study population: Other work has demonstrated that per capita prey availability is actually constant regardless of brood or group size (AGS and CR, unpubl. data), and there is no evidence that adult anis synchronize provisioning trips. An alternative explanation for the decrease in begging intensity is that more asynchronous hatching in larger broods may in fact limit competition among nestmates by establishing clearer age and size hierarchies among them (Mock and Ploger 1987; Magrath 1990; Ostreiher et al. 2012). In larger broods, adults typically begin incubation several days earlier, relative to clutch completion, than in smaller broods, which causes nestlings to hatch over a period of several days and establishes these competitive asymmetries (Riehl 2016). Prior work has shown that hatching asynchrony itself is probably a non-adaptive consequence of communal laying rather than an adaptive strategy for parents (Riehl 2016), since brood reduction is higher in asynchronous broods; but the proximate consequence of asynchrony may be to accentuate competitive differences among nest-mates and reduce overall begging intensity.

Begging signals played a significant role in determining how resources were allocated among nestlings, with those who begged more intensely more likely to be fed. However, nestling size and other predictors related to size, like height and proximity to the provisioning adult, were also significant positive predictors of whether a nestling received prey. A bias toward larger nestlings coincides with our observations of brood reduction in this species, occurring in 41.2% of non-depredated broods (Riehl 2016); if adults only have sufficient resources to raise a portion of their brood, they are more likely to allocate those resources to offspring in the best condition and with the greatest chance of survival (Caro et al. 2016a). However, the degree to which greater ani adults might actually control this allocation pattern and whether brood reduction represents an adaptive adult strategy is unclear. Video observations showed that while adults often seemed to try to select a particular nestling to feed, placing a prey item in multiple nestlings' gapes before finally releasing it, nestlings were sometimes able to reach up and over their broodmates to take prey from adults just as they arrived. We also observed apparent interceptions of prey items, in which an adult seemed to move prey toward one nestling's gape only for another nestling to block its path and take the prey item instead. In larger broods, where competitive asymmetries are more pronounced, last-hatched nestlings receive proportionally less than they do in smaller

broods, despite comparable prey availability, suggesting that scramble competition could supersede adult control over resource allocation (AGS and CR, unpubl. data). Ultimately, determining whether brood reduction is adaptive will require experimental manipulations of hatching asynchrony and prey availability and long-term monitoring to quantify the fitness consequences of losing nestlings and nestmates to starvation.

Taken together, our results support the idea that some reliability in “parent-offspring” signalling systems can be maintained even when the average relatedness among signallers and receivers is low. Multiple selective pressures, acting on both direct and indirect fitness, are likely to support honest signalling and, in many systems, may be operating simultaneously. Future studies should focus on teasing apart the relative impacts of kin-derived and socially derived indirect fitness on the scope and resolution of family conflict. In particular, the potential importance of social relationships among unrelated individuals on indirect fitness warrants further examination, especially in small, stable groups with alloparental care.

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Data availability All data generated or analysed during this study are included in this article and its supplementary information files.

Declarations

Ethics approval All methods were approved by the Institutional Animal Care and Use Committees of Princeton University (protocol #10034) and the Smithsonian Tropical Research Institute (protocol #2017–0626–2020). The use of animals adheres to the guidelines set forth by the Animal Behavior Society.

Competing interests The authors declare no competing interests.

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