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Signaling for food and sex? Begging by reproductive female white-throated magpie-jays

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Abstract

Food begging is common in nutritionally dependent young of many animals, but structurally homologous calls recur in adult signal repertoires of many species. We propose eight functional hypotheses for begging in adults; these stem from observations in birds but apply broadly to other taxa in which begging occurs. Adult cooperatively-breeding white-throated magpie-jays (*Calocitta formosa*) use loud begging vocalizations, particularly near the nest site during reproduction. We analysed the social context and behavioural phenology of loud calling and allofeeding in this species and compared these with predictions from each functional hypothesis. We found that reproductive females are the primary producers of beg calls, and their begging peaks during the fertile period when reproductive conflict among males and females was highest. Loud begging rates correlated positively with provisioning rates, but females called more in the pre-incubation fertile period than after they initiated incubation. Based on the context, phenology and active space of the signal, we conclude that female loud begging vocalizations function to signal nutritional need to group members, but also have been evolutionarily co-opted to advertise fertility to potential extra-pair partners. The location of calling is likely a consequence of nest guarding by breeding females to prevent intraspecific brood parasitism.

Keywords

Begging; *Calocitta formosa*; Cooperative breeding; Courtship feeding; Corvidae; Fertility advertisement; Dual-function communication; Signal repertoire

Among birds and mammals, nutritionally dependent offspring frequently produce specialized vocal and visual displays in anticipation of being fed (Bradbury & Vehrencamp 1998; Budden & Wright 2001). In birds, nestlings typically produce quiet, high frequency begging vocalizations when potential feeders (e.g. parents transporting food) approach. When nestlings fledge these calls often become louder, more localizable and individually

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distinctive (Redondo 1991). Studies of food begging by nutritionally dependent young animals have focused on the reliability of these signals as indicators of nutritional need (Redondo & Castro 1992; Kilner & Johnstone 1997; Brilot & Johnstone 2003); on the inherent conflicts of interest between signallers and receivers and among competing signallers (Godfray 1991; Godfray 1995; Johnstone 1996); and on the costs of food begging in terms of energy expenditure and risk of predation (Haskell 1994; Leech & Leonard 1997; Bachman & Chappell 1998; Haskell 1999; Rodriguez-Girones et al. 2001).

In some mammals and birds, adults also produce calls homologous to the food begging calls of young (e.g. Feistner & McGrew 1986; Ruiz-Miranda et al. 1999; Robbins 2000; Otter et al. 2007;). Here, we use the conventional term 'begging' to denote such calls by adults, without meaning to imply any particular function. A variety of songbirds produce adult begging calls, including the European robin (*Erithacus rubecula*; Tobias & Seddon 2002), black-capped chickadee (*Poecile atricapillus*; Otter et al. 2007), and the yellow-billed shrike (*Corvinella corvina*; Grimes 1980), but adult begging calls have been most frequently documented within the family Corvidae (e.g. Skutch 1960; Verbeek 1972; Hardy 1979; Buitron 1983; Lawton & Lawton 1985; Buitron 1988; Heinrich et al. 1993; Langen 1996a; Verbeek & Caffrey 2002). In birds, adult begging is often restricted to nesting females, who produce these calls in association with allofeeding. Additionally, in some species both sexes produce these vocalizations during aggressive social interactions (Heinrich et al. 1993; Woolfenden & Fitzpatrick 1996). It is notable that although allofeeding of breeding females during courtship and incubation is common in birds (Lack 1940), many fewer species are reported to use loud adult begging vocalizations.

Based on the literature and our own familiarity with the natural history of the behaviour, we have identified eight plausible functional hypotheses for loud begging calls by adult birds and mammals. The first three hypotheses apply to those species for which adults of both sexes produce these vocalizations. (1) The *atavism hypothesis* proposes that adult loud begging is a non-adaptive reemergence of the vocal behaviour of nutritionally-dependent young that is stimulated by their food-begging. If so, begging by adults will only occur when nutritionally-dependent young are producing loud begging calls, and begging will not elicit feeding by other adults. (2) The *deception hypothesis* proposes that adults deceive others into feeding them by begging during the same period when young are also actively begging. Thus begging by adults will occur when young are begging, and will result in adult callers receiving food that was intended for nutritionally-dependent offspring. (3) The *appeasement hypothesis* posits that begging during conflict signals submission (Heinrich et al. 1993). If so, begging by adults will occur primarily during aggressive interactions and will be given most often by social subordinates.

The remaining five hypotheses apply to species for which loud begging is largely confined to breeding females, as is the case for the majority of bird species for which this vocalization has been documented. The first two hypotheses focus on begging as an advertisement of nutritional need. (4) The *breeder need hypothesis* proposes that reproductive females direct begging calls at their mate and other potential allofeeders as a signal of nutritional need. Begging calls by breeding females elicit allofeeding, which increases reproductive success via multiple nonexclusive mechanisms such as enhanced egg production, improved incubation constancy, or improved female condition leading to higher future reproductive success through shorter intervals between reproductive bouts or higher breeder survivorship (Lack 1940, Nesbit 1977, Lifjeld & Slagsvold 1986). If so, females will vocalize at periods of highest nutritional need (egg-laying or incubation), and will be loud enough to be perceived at a distance by the mate or other provisioners. (5) The *offspring need hypothesis* posits that a mother produces loud begging calls to advertise the nutritional needs of her offspring. This might apply if: a) offspring are unable to advertise effectively (e.g. young

chicks), b) a mother can assess offspring nutritional need, and c) either food begging by a female is more productive than foraging on her own, for example if begging can inform multiple allofeeders, or else begging allows the female to provide other nest-focused parental care such as protection from adverse environmental conditions or predators. If so, peak adult begging will coincide with peak offspring need.

The final three hypotheses propose that loud begging functions as a signal of reproductive state rather than nutritional need. (6) The *care potentiation hypothesis* posits that loud begging by breeding females stimulates parental behaviour (as quiet nestling vocalizations may do, see Schoech et al. 1996), especially by group members other than her mate. Thus begging occurs in cooperatively-breeding species, at initiation of breeding or near hatching, and begging is not strongly associated with food-provisioning. (7) The *breeding suppression hypothesis* proposes that loud begging by breeding females serves to reinforce reproductive dominance, and hence suppress breeding by other, subordinate females within a social group. In this case, begging only occurs in groups with more than one potential female breeder, begging occurs at the initiation of breeding, and begging is not strongly associated with food-provisioning. (8) Finally, the *fertility advertisement hypothesis* posits that loud begging by a breeding female advertises fertility and attracts males seeking courtship opportunities. In this case, loud beg calls may aid the female in attaining extra-pair copulations (Montgomerie & Thornhill 1989; Wiley & Poston 1996); help her to assess the competitive ability of current and potential replacement mates (Montgomerie & Thornhill 1989; Wiley & Poston 1996); or constrain her mate to remain nearby and constantly attentive, which may be advantageous to the female in some instances (e.g. prevent him from copulating with an additional female, resulting in divided paternal parental care). Thus begging occurs during the fertile period, begging is not strongly associated with food-provisioning, and female begging is not restricted to groups with more than one potential female breeder.

Although the hypotheses are not necessarily mutually exclusive, each makes distinct predictions about the phenology of begging vocalizations during the breeding cycle, including the functional signal space of the vocalization; the associations between calling rate, nutritional need, and allofeeding rate; and the social context of loud begging vocalizations (Table I). Two studies on passerine birds have provided data consistent with the *breeder need* hypothesis (Tobias & Seddon 2002; Otter et al. 2007), and one of these studies presented data that were also consistent with the *fertility advertisement* hypothesis (Tobias & Seddon 2002). The data of a third study is most consistent with the *appeasement hypothesis* (Heinrich et al. 1993).

In this paper we evaluate each of these eight hypotheses using behavioural observations of a the white-throated magpie-jay *Calocitta formosa*, a group-territorial cooperatively-breeding bird that includes adult loud begging within its vocal repertoire (Skutch 1953; Innes 1992; Langen 1996a). This species is unusual among cooperatively-breeding birds in that females are highly philopatric and typically spend many years caring for offspring of other group members and defending the group territory before attaining breeder status (Innes & Johnston 1996; Langen 1996a; Langen & Vehrencamp 1998; Langen & Vehrencamp 1999). Only one female within a group breeds regularly, but other females occasionally attempt to nest (Langen 1996a). Males disperse from their natal territory at about one year of age and circulate among territories until joining a group as a breeding male; each group has only one breeding male, but other itinerate 'floater' males frequently join the group for brief periods (Langen 1996a; Langen 1996b). During egg-laying, aggression frequently occurs between a group's breeding male and intruding floater males as well as between the breeding female and other females within her group (Langen 1996a). Genetic studies reveal the mating system to be complex; most offspring are sired by the apparent breeding pair, but helpers,

floaters and neighboring breeding males may also achieve parentage within any one nest (Berg 2005).

Adult magpie-jays produce begging vocalizations that are structurally similar to those made by nutritionally-dependent fledglings (Fig. 1). In fledglings, calling rates peak at about 41 days post-hatching, while allofeeding rates peak about 11 days before the peak begging rate (Langen 1996b). After controlling for age, Langen (1996a, b) found that fledgling begging rate and provisioning rate were positively associated, consistent with the hypothesis that begging calls are signals of need, at least in this age class. Here, we review the natural history correlates of loud begging by adult white-throated magpie-jays and examine the phenology of begging and allofeeding, the correlation between the rate of begging and rate of allofeeding, and the relative contributions of different potential recipients of the signal to provisioning effort. Our objective is to evaluate these data in light of the eight hypotheses for the function of adult begging, to infer which hypotheses best account for adult begging in this species.

Methods

Study site

We studied vocal and reproductive behaviour of white-throated magpie-jays at Santa Rosa National Park, a unit of the Guanacaste Conservation Area, in northwest Costa Rica (10°50' N, 85°37' W) during three periods: 1992-1993 (T.A.L.), 1999-2002 (E.C.B.), and 2003-2005 (J.M.S.E.). Between 8 and 14 groups were intensively studied during each period (see Langen 1996a; Langen & Vehrencamp 1998; Langen & Vehrencamp 1999; Berg 2004; Berg 2005; Ellis 2008). Most individuals in each group were trapped and marked with colored metal bands for individual identification. All research protocols were approved by the research director of the Guanacaste Conservation Area. JMSE's protocols were approved by Cornell University IACUC, protocol No. 98-81-04. ECB's field procedures were approved under University of California, Davis Animal Use and Care Protocol No. 8934. Groups were observed mainly during the breeding period (January-July), which spans both the dry and wet seasons. Severe seasonality at this tropical dry forest site results in dramatic changes in food abundance, and hence diet, of the magpie-jays between the dry and early wet seasons (Langen 1996b). Over the 14 year span of this study, both regrowth of former pasture into secondary forest and increases in abundance of some nest predators resulted in changes in group composition and territory boundaries, but some birds that were banded during the initial period were present at the end of the study. Whereas during the first period all breeding groups contained multiple nest helpers, during the last period both groups and pairs bred.

Correlations between begging and provisioning across nest stages

We collected data on allofeeding and begging vocalizations during two of the three study periods, 1992-1993 and 1999-2002 (for methodological details, see Langen and Vehrencamp 1999). In 1992-1993, T.A.L. and assistants made repeated 1-4 h focal observations of nests at least once weekly for six groups, and less frequently for eight additional groups (48 nests, 508 nest watches). During 1999-2002, E.C.B. and assistants conducted 1-4 h focal observations at eight groups (69 nests, 268 nest watches) three times per week throughout the breeding season. During both periods, focal observations were taken during four stages of breeding: (1) *nest building*, when nests were under active construction, (2) *pre-incubation*, when females were laying eggs but had not begun incubating, (3) *incubation*, when the female constantly brooded the clutch, and (4) the *nestling* period, after eggs had hatched but before fledging. During each focal observation, we quantified the number of begging calls given by the focal breeding female, the number of

allofeeds received by her or the offspring during each observation period, and the identity of provisioners and other birds that interacted with the breeders or offspring. During 2003-2005, while performing focal sound recordings of magpie-jays (Ellis 2008), J.M.S.E. and assistants monitored begging vocalizations and breeding behaviour (whether breeding units were nest-building, egg-laying, or incubating eggs or nestlings) in 14 breeding units, including 16 group-breeding attempts and 20 pair-breeding attempts. Units were defined as group-breeding if a non-nesting female shared the home range with a breeding female; in all cases non-nesting females provisioned the breeding female. We also monitored the begging and breeding behaviour of secondary breeding females. Secondary females are group members that normally act as helpers to a primary breeding female but also occasionally attempt to nest (Langen 1996a). In the latter period we classified females as begging if they produced the vocalization for sustained bouts in the absence of the arrival of another jay transporting food.

Statistical analyses

We analysed associations among breeding stage, begging rates, and allofeeding rates using general linear models in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA). The unit of analysis was thus the mean begging rate or allofeeding rate for each combination of group, stage and season. Begging rates and provisioning rates were log transformed to meet parametric requirements of normality. A random intercept model controlled for the effect of group identity. We tested (1) whether nest stage (building, pre-incubation, incubation, nestling), season (wet, dry) or an interaction of season and stage predicted begging rates, and (2) whether begging rates, nest stage and group size were predictors of provisioning rates. Group size (defined as breeders and helpers, but excluding floaters) was included in both models, because individual groups varied in size from year to year. To address the question of how different receiver classes (paired male, helper and floater male) respond to the signal, we compared whether individuals of each class provisioned at different rates, and whether any one class's provisioning rates differed by nesting stage (and thus possibly begging rate). We analysed these non-normal data with non-parametric pair-wise comparisons and controlled for Type I Error using Bonferroni corrections.

Results

Natural history of the loud begging call

White-throated magpie-jays used three vocalizations and associated visual displays that resulted in the caller receiving an allofeeding: a quiet, high-pitched begging chirp produced by nestlings and recently fledged young upon the arrival of a potential provisioner; a moderately loud swallow-call associated with the transfer of a food item to a begging bird, produced by both sexes of all ages; and a loud begging call, produced by fledglings and some adult birds (Langen 1996b; Ellis 2008). The loud begging vocalization often included an associated visual display of bill-gaping, wing-flapping, and a crouching posture with the bill oriented upward.

Among adult magpie-jays, we observed loud begging calls in two contexts. Breeding females produced the vast majority of loud begging calls (Langen 1996a). During the 2003-2005 study period, the loud begging vocalization was broadcast by all primary breeding females (16/16 attempts) and secondary (3/3 attempts) females within cooperatively breeding groups, as well as all pair breeding females (i.e. not cooperatively breeding, 20/20 attempts). In addition, mate-guarding males, helpers, and floaters infrequently produced a few loud begging calls and the associated visual displays upon the arrival of a group member or floater male transporting a food item. We typically observed this behaviour when either breeding females or fledglings were regularly using the same

vocalization. In this context, loud beg calls occasionally resulted in an allofeeding to the caller, but more frequently the caller was bypassed for one of the birds that vocalized more consistently (i.e. fledglings or breeding female).

The begging vocalization used by breeding females appeared to be structurally identical to the loud food-begging vocalization used by fledglings (Fig. 1). As is characteristic of loud, harmonically-rich, low fundamental-frequency vocalizations (Bradbury and Vehrencamp 1998), the caller was easily localizable. The loud begging call was the loudest vocalization in the magpie-jay repertoire (Ellis 2008), and on at least three occasions we heard begging females from over 750 m from the nest (measured using a GPS) at the same time that another observer located the female within 5 m of the nest. Since white-throated magpie-jay territories average 17 ha (Langen & Vehrencamp 1998), territory radius is about 230 m, and receivers have the potential to detect loud begging calls from a distance of approximately two territories beyond the caller's territory.

Females broadcast begging vocalizations repeatedly (a few seconds between notes; see rates below) for hours from exposed perches at the tops of trees or near their nest. During nest-building and pre-incubation, females usually called from open areas within 50 m and in sight of the nest. During these extended bouts, begging appeared to occur independently of the presence of other individuals, suggesting that at least in these cases begging was not being triggered by the arrival of potential allofeeders (see below). During the incubation and nestling stages, begging occurred while the female was on the nest, most frequently when helpers arrived with food.

Associations among begging rate, provisioning rate and breeding stage

Female begging rate peaked during the nest-building and pre-incubation stages of breeding, dropped dramatically in the incubation stage, and was lowest during the nestling stage (Fig. 2a; $F_{3,46} = 50.8$, $P < 0.0001$). The begging rate dropped in a step-function manner between the pre-incubation and incubation stages, and again after the eggs had hatched (Fig. 3). Provisioning to the breeding female was highest in the nestling stage, lower during the nest-building and pre-incubation stages, and lowest during incubation (Fig. 2b, Fig 3; $F_{3,27} = 19.1$, $P < 0.0001$). The ratio of begging calls given to allofeedings received (a measure of begging efficiency, lower ratios being more efficient) was highest in the nest building and pre-incubation stages, much lower for the incubation stage, and lowest at the nestling stage (Fig. 2c, $F_{3,42} = 18.1$, $P < 0.0001$). Within each stage, provisioning rate increased with begging, except during the nestling stage, when provisioning rates remained high even in the absence of loud begging (Fig. 4; Spearman's rank correlation: building $r_s = 0.49$, $P = 0.008$; pre-incubation $r_s = 0.44$, $P < 0.0001$; incubation $r_s = 0.48$, $P < 0.0001$; nestlings $r_s = 0.15$, $P = 0.19$). Correlations between provisioning and begging could occur if the causality is reversed from what we propose (i.e. provisioning, or at least the approach of a group-member bearing food, elicits begging, rather than begging eliciting provisioning). Because we do not have specific temporal data on provisioning events relative to production of begging calls, we cannot methodologically control for this. However, our initial observations indicated that this was only a possibility in the incubation and nestling phase. The ratio of beg calls to provisioning events shows that in the building and pre-incubation phases, a female produces over 150 beg calls per provisioning event, and frequently calls for prolonged periods without receiving a feeding. During all stages, only a small proportion of the adult begs were made during the period immediately preceding a feeding.

After controlling for group identity, neither begging rates nor provisioning rates varied as a function of group size, so we removed group size from the models. Season significantly predicted begging rates, probably because begging rates in the pre-incubation stage of nesting were higher in the dry season (season: $F_{1,46} = 8.5$, $P = 0.006$; season*nest stage:

$F_{3,46} = 3.5$, $P = 0.02$; post-hoc LS means test, pre-incubation stage: $P = 0.01$). Season had no effect on provisioning rates.

For each social class (breeding male, helper, and floater), per capita feeding rates were highest in the nestling stage, when there was virtually no adult loud begging (Fig. 2a), and did not differ between building, pre-incubation and incubation stages (Fig. 5).

Discussion

While non-breeding adult magpie-jays occasionally begged, breeding females begged most frequently and incessantly, primarily from near the nest during the pre-incubation period. The pre-incubation period coincides with three other previously documented increases in behaviour: (1) attendance of the breeding female by many courting floater males (Innes 1992, Langen 1996a); (2) constant mate-guarding by the breeding male of the group, who frequently chases and fights floater males (Langen 1996a); and (3) aggression by breeding females towards female helpers that approach the nest (Langen 1996a). All three of these behaviours decrease with the onset of incubation (Langen 1996a).

We conclude that adult white-throated magpie jays use the loud begging call in two different contexts. When non-breeding adults produce this call, it has the following features necessary for evaluating the functional hypotheses outlined in Table I: (1) the signaller is either sex; (2) the social context is arrival of a bird transporting food; (3) calling occurs when either the breeding female or fledglings are regularly broadcasting loud begging calls and receiving allofeedings; (4) the call is similar in loudness to the begging of other callers (breeding female or fledglings), but is only used for brief bouts; and (5) calling is at least occasionally effective at attracting allofeedings. We infer that in this context adult begging calls are most consistent with the *atavism* or *deceit* hypotheses. To distinguish between these hypotheses, we will need to quantify the relationship between calling and receiving food, make more detailed observations on the identity of callers and context of calling, and collect data on use of the loud-calling vocalization in relation to need.

When the adult loud begging call is broadcast during pre-incubation (the most common context), the call has the following key features: (1) the signaller is a breeding female; (2) the social context is a breeding pair or breeding group; (3) peak calling occurs when the breeding female is fertile, but calling continues during incubation; (4) the call is very loud, and the signal space is far beyond the territory; (5) there is a positive correlation between call rate and food delivery to the breeding female; (6) there is no correlation between call rate and food delivery to nestlings; (7) there is no evidence that calling is effective at suppressing breeding by other female group members; (8) loud calling is used in all nest attempts of a breeding season, before and (most frequently) after non-breeding group members have begun to help in the breeding effort; and (9) high intensity begging during the nest building and pre-incubation stages of breeding is associated with the arrival of courting floater males and constant mate-guarding by the breeding male.

As a consequence of these features, we infer that loud begging by breeding white-throated magpie-jay females is highly inconsistent with the *atavism*, *deceit*, *subordinate appeasement*, *offspring need*, *care potentiation*, and *breeding suppression* hypotheses. Instead, the features associated with begging are most consistent with the non-exclusive *breeder need* and *fertility advertisement* hypotheses. We conclude that the signal has two functions, serving to attract both potential mates and allofeeders.

The fact that provisioning rates increased with begging rates in all stages of nesting except the nestling stage suggests that begging rate signals nutritional or energetic need. Begging rates were higher when insects and other food was scarce (the dry season) (Langen 1996b,

Langen & Vehrencamp 1998). The higher rate of begging during building and pre-incubation suggests that egg production is probably more nutritionally demanding than incubation, if such need is the only factor affecting begging rates. As in black-billed magpies (*Pica hudsonia*, Buitron 1988), elevated begging can begin a week or more before egg-laying begins. Alternatively, the timing might also indicate that costs of begging were prohibitively high during incubation, but we do not see how the energetic costs would differ, and risks of attracting predators to the caller and the caller's nest site should be about equal. Eggs were present in the nest in the final days of pre-incubation, when females were still begging intensely, so predation costs on nests should be equal for both stages. It seems unlikely that costs of begging would rise so dramatically between the pre-incubation and incubation periods that it would account for the observed precipitous drop in begging rates.

Rather than strictly indicating nutritional need, we infer that the high-rates of loud begging during the nest-building and pre-incubation stages of breeding also function to attract males as potential extra-pair mates or as rivals to assess the quality of the breeding male, much like the lovely-loud copulation solicitation calls of female chaffiches (Montgomerie & Thornhill 1989; Sheldon 1994; Wiley & Poston 1996). Extra-group males aggregated near the calling breeding female and attempted to court her. Although breeding males may attempt to prevent courting, breeding females nevertheless mate with some of the extra-group males that they attract, resulting in up to 33% extra-pair paternity (Langen 1996a, Berg 2005). However, we did not observe turnovers in breeding males during this nesting stage, suggesting that the function of the vocalization is mainly to attract extra-pair matings rather than test the quality of the paired male. Playback experiments of female loud-begging calls could be informative about how rapidly and effectively this vocalization attracts males.

Tobias & Seddon (2002) suggested that adult female European robins broadcast loud begging calls (homologous to fledgling begs) during the fertile period to elicit allofeeding by the male. Using mate removal and playback experiments, the authors also revealed that female begging calls attract extra-pair males, and that pair males may therefore be forced to increase their provisioning rate to reduce begging, thus defending against extra-pair fertilizations. These results were interpreted as evidence that female begging calls functioned concurrently as signals of breeder need and fertility advertisement, with the latter function perhaps reinforcing the efficacy of the former. Several of our results suggest that mechanisms by which signals of breeder need and fertility advertisement interact in magpie-jays act are different than in robins. For robins, provisioning reduces begging; in magpie-jays, begging increases provisioning, at least during the fertile period (the building and pre-incubation stages of nesting). Magpie-jay pair males, who have the most to lose if they do not secure paternity, do not appear to “buy” a female's silence with food: they do not feed at a rate higher than other group members (Langen 1996). In addition, Innes (1992) found that floater males were most likely to join groups during the pre-incubation and building phases of nesting. These elements seem to suggest that male magpie-jays are not acting as though ‘blackmailed’ by their mates into feeding more. Instead, they respond by mate-guarding, which seems highly adaptive in a social system in which unpaired floater males regularly visit groups and aggregate during the breeding female's fertile period. A male magpie-jay who left his mate in order to forage for her would probably sacrifice significant paternity, unlike a territorial male robin (Tobias & Seddon 2000). Further data on feeding rates and quantification of mate-guarding behavior might shed more light on whether females actively engage in blackmail, or solicit visits by many floater males (by begging loudly) in an effort to elicit fights and male-male chases, allowing her to either test her mate's quality or escape from her mate-guarding mate.

Interestingly, in the closely related brown jay (*Cyanocorax morio*), breeding females in the pre-incubation period also broadcast a loud begging call near the nest (Skutch 1960, Lawton

and Lawton 1985). Brown jay breeding groups include multiple males: 66% of the offspring are fathered by group-member males other than the social mate, and an additional 17% are fathered by extra-group males (Williams 2004; Williams & Rabenold 2005). There are frequent changes in the social mates between years (Williams 2004). For this species, female loud begging may serve, in part, to incite male-male competition, and thus assess the quality of the social mate versus other candidates within the breeding group as well as outside of it.

It is curious that white-throated magpie-jay females begged so loudly and continuously in close proximity to the nest, particularly given the high nest failure rate due to predation (80% or greater, Langen and Vehrencamp 1999; Berg 2004). Moreover, one of the most common predators is the white-faced capuchin monkey (*Cebus capucinus*), which could plausibly learn to associate begging calls with nests. We believe that adult female magpie-jays are constrained to beg from near the nest by the threat of brood parasitism by their female helpers. Aggression among females near nests and moderate levels of detected brood parasitism (up to 16% of offspring) suggest that brood parasitism represents a significant cost to dominant females. This may explain why females incur the cost of possible predator attention to the nest (predators may be attracted to adults near nests: Skutch 1953, Martin et al. 2000). Like magpie-jays, brown jays have female helpers, produce calls homologous to juvenile begging calls from near the nest, and show high aggression between breeding females and other female group members near the nest (Lawton and Lawton 1985, Williams et al. 1994). However, mixed maternity may be lower (1% in Williams 2004, possibly higher in Lawton and Lawton 1985); it would be informative to analyse the trade-offs between predation and brood parasitism in the two species.

Based on our analysis of the natural history and current putative functions of loud adult begging, we hypothesize the following five-step scenario for its evolution: (1) Loud adult begging originates as an atavism of the loud food-begging vocalization of fledglings. (2) The positive consequences of receiving extra food from begging positively selects for increased food begging in breeding females and for provisioning by mates and group members. Females and their mates benefit directly (e.g. more rapid re-nesting, higher clutch size, more sustained incubation), while group members benefit through increases to inclusive fitness. Two scenarios might generate the necessary conditions: courtship feeding and reproductive division of labor. The latter allows simultaneous fledgling provisioning and initiation of a new breeding attempt, as occurs in cooperatively breeding groups of white-throated magpie-jays (Langen and Vehrencamp 1999), and it is during this period that breeding and the trigger to atavistic calling (food-transporting adults) would overlap. (3) Once loud food-begging becomes established in breeding females, males evolve to use the vocalization as a cue of mating opportunities, as in robins (Tobias & Seddon 2002). (4) If there is an advantage to attracting potential mates or inciting male-male competition, then breeding females might be selected to co-opt the loud food-begging call, amplifying it to be more detectible to ‘eavesdroppers’ during the fertile period (similar to the “blackmail” hypothesis suggested by Tobias and Seddon (2002)).

At Step 2 or Step 4, assuming that the risk of nest predation is not prohibitively high, begging may become limited to the nest site (and potentially increase in amplitude to reach intended receivers) if other females can use begging as a cue that a nest is available for conspecific brood parasitism. This next step is most likely to occur in group-breeding species where the risk of intraspecific nest parasitism is potentially high.

Although loud begging by females is phylogenetically widespread in passerine birds, most examples are known from the Corvidae, including species within the genera *Corvus* (Verbeek & Caffrey 2002), *Pica* (Verbeek 1972, Buitron 1988), *Cyanocorax* (Skutch 1960; Crossin 1967; Hardy 1979; Lawton & Lawton 1985), and *Calocitta* (this study). Indeed,

begging is common in corvids, and we differentiate loud begging from short-range begging performed in the presence of a feeding individual, as shown by ravens (Heinrich et al 1993), jackdaws (de Kort et al 2006) and rooks (Schied et al 2008). Within the monophyletic New World jays (Saunders & Edwards 2000; Bonaccorso & Peterson 2007), prolonged bouts of loud begging by breeding females are characteristic of the *Cyanocorax* clade (see references above), but appears to be reduced or absent among well-studied species in the genera *Aphelocoma*, *Cyanocitta*, and *Gymnorhinus* (Brown 1994; Woolfenden & Fitzpatrick 1996; Greene et al. 1998; Tarvin & Woolfenden 1999; Balda 2002; Curry et al. 2002). We suspect that a phylogenetic approach that focuses on how loud begging is distributed in relation to breeding systems will be quite informative about the evolution and current functions of breeding female loud begging. We predict that nest-centered loud begging by breeding females will be prevalent in systems where there is courtship feeding, incubation exclusively by the breeding female, propensity for mixed paternity due to unforced extra-pair matings or frequent turnover of consorts, and high risk of intraspecific brood parasitism (colonial species or cooperative breeders with female helpers).

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Figure 1.
 (a,b) Begging calls of two adult female white-throated magpie-jays. (c) Food-begging calls of a fledgling magpie-jays. Timing between calls was altered for ease of comparison.

Figure 2.

(a) Mean $\pm$ SE begging rate by breeding female white-throated magpie-jays for each breeding stage and season. (b) Mean $\pm$ SE provisioning rates by group members for each breeding stage and season. (c) Beg to provision ratio mean $\pm$ SE for each breeding stage. Breeding stages with different letters were significantly different from each other ($P < 0.05$). Significant differences between two seasons for a stage are indicated by stars ($* = P < 0.05$, $*** = P < 0.0001$).

Figure 3.

Mean $\pm$ SE rate of food begging at each nesting stage during four consecutive unsuccessful nesting attempts and a final successful attempt by one breeding female white-throated magpie-jay. The numbers above each nesting attempt are the range of Julian dates that observations were made; the rainy season began after Julian day 135. Pr = Pre-incubation, In = Incubation, Ne = Nestlings present, n = number of nest watches.

Figure 4. The relationship between begging rate and provisioning rate during each nest stage. Provisioning was positively related to begging in all but the nestling stage.

Figure 5.

Box plots (medians and quartiles) of provisioning rates for each social class, by nesting stage. Within each social class, provisioning rates were significantly higher ($P < 0.0001$) in the nestling stage, and both helper and social mates fed at higher rates than floaters in that stage ($P < 0.05$).

Table 1
Key features distinguishing eight hypotheses for adult loud begging in birds

	Signaler	Social context	Peak calling	Signal Space	Calling-feeding correlation	Calling-need correlation	Function
Atavism	Any adult	Breeding pair or group	Begging young present	Same as begging young	None	None	Non-functional
Deception	Any adult	Breeding pair or group	Breeding young present	Same as begging young	Low or high	High	Deceive offspring provisioners to feed adult
Subordinate appeasement	Subordinae	Dominance structured group	During altercation	Only to the opponent, quiet	None	None	Inhibit aggression by dominant
Breeder need	Breeding female	Breeding pair or group	Egg laying or incubation	Throughout the territory, loud	High	High	Advertise need for food provisioning to breeder
Offspring need	Breeding female	Breeding pair or group	Soon after hatching	Throughout the territory, loud	High	High	Advertise need for food provisioning to offspring
Care potentiation	Breeding female	Breeding group	Initiation of breeding or near hatching	Throughout the territory, loud	None	Low	Activate alloparental behavior by group members
Breeding suppression	Breeding female	Breeding group	Initiation of breeding	Throughout the territory, loud	None	None	Repress breeding by other group females
Fertility advertisement	Breeding female	Any breeding system	When female is fertile	Beyond the territory, very loud	Low?	None	Attract mates, generate male-male competition