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Report

Recruitment Calling: A Novel Form of Extended Parental Care in an Altricial Species

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Summary

In many altricial birds, fledglings disperse when they are no longer fed, and this dispersal marks the end of parental care [1, 2]. In some species, however, young remain in close association with their parents after nutritional independence [3–6]. Because juveniles are still inferior foragers at this stage [7, 8], they might benefit from parental assistance in locating good feeding sites, but this possibility remains largely unexplored. Here, we show that parents and helpers in pied babbler (*Turdoides bicolor*) societies use a recruitment call to direct nutritionally independent, but inexperienced, foragers to particular food patches. Observations and a playback experiment indicated that adult babblers use a "purr" call to recruit group members to a foraging patch. Creation of experimental foraging patches supported observations that individuals tend to give the call when they are foraging on abundant, divisible food sources and when their group contains independent fledglings (youngsters who are no longer fed directly). Fledglings responded to calls more often than adults, who frequently encountered aggression from the caller if they did, and the fledglings gained significant foraging benefits. This is the first study to demonstrate that altricial birds may use recruitment calls to extend parental care past the period of direct provisioning.

Results

Production of Purr Calls

A few days prior to the date on which pied babbler nestlings are due to fledge, provisioning adults begin to give a purr call during feeding visits; nestlings associate this call with food and subsequently approach adults that give the call (N. Raihani and A.R., unpublished data). Adults continue to give the purr call when offering food to dependent young that have left the nest, and this reinforces the association. In addition to giving the call while presenting food directly to dependent young, adults sometimes give the purr call (~1 per 100 min of focal observations, n = 48 adults, 193 observation hr) while foraging; fledglings never give the call (n = 36 nutritionally independent fledglings, 51 observation hr). Group members spend much of the day on the ground searching for invertebrates, usually in separate patches, but generally within 20 m of one another, and the purr call is only given by foragers who are alone in a patch (n = 48 adults). Under these circumstances, it appears to function as a "recruitment" call [9, 10], drawing group members to a particular food source. Foraging adults that gave the call were significantly more likely to be approached than silent adults or those giving a contact call (Chi-square test: $\chi^2 = 12.23$, df = 2, and $p < 0.001$). Furthermore, individuals were significantly more likely to approach the playback of a purr call (8/10 trials) than that of a contact call (2/10 trials; Fisher's exact test: $p = 0.023$).

The likelihood that a purr call was given by an adult foraging alone in a patch was significantly influenced by the breeding stage (Table 1); calls were more likely to be given when groups contained independent fledglings than at other times (Figure 1). There was a significant interaction effect between the abundance of food in the patch and the divisibility of the food source (Table 1); purr calls were only given when there was both a great abundance and great divisibility (Figure 2). The importance of food divisibility was confirmed by the creation of artificial foraging patches; individuals were significantly more likely to give a purr call when presented with a crumbled egg yolk, representing a divisible food source, compared with the same amount of yolk as a single piece, representing a nondivisible food source (8/10 versus 2/10 individuals, respectively; Fisher's exact test: $p = 0.023$). The dominance status of the forager also influenced the likelihood of purr calling (Table 1); dominants (the putative breeding pair; 6.6% of focal watches) were more likely than subordinates (other adult group members; 3.8%) to give purr calls. There was no significant effect of sex, foraging group size, month, maximum temperature, body weight, year, or rainfall on the likelihood of purr calling (Table 1).

Response to Purr Calls

In 108 cases when a purr call was given by the focal individual, 82 (76%) resulted in another group member approaching within 20 s. In 20 of the remaining cases, the focal individual gave a second purr call, 16 of which resulted in another group member approaching within 20 s. There were ten occurrences of calls (9%) where no individual approached.

If independent fledglings were present in the group when a purr call was given, they were significantly more likely to respond than adult group members (Chi-square test: $\chi^2 = 19.58$, df = 1, and $p < 0.001$). Moreover, seven out of the eight responders to purr calls in both the playback and artificial-foraging-patch experiments

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Table 1. Variables Affecting Whether a Purr Call Was Given during a 5 Min Focal Watch

Full Model	χ^2	df	p
Breeding stage	49.39	3	<0.001
Patch divisibility[a] × foraging success rate[b]	5.93	1	0.015
Dominance status	4.52	1	0.033
Sex	2.02	1	0.155
Foraging group size	1.98	1	0.160
Month	7.21	6	0.205
Maximum temperature (°C)[c]	1.28	1	0.258
Body weight (g)[d]	0.19	1	0.664
Year	0.11	1	0.737
Daily rainfall (mm)	0.01	1	0.984
Minimal Model	**Effect**	**SE**	
Constant	−2.17	0.42	
Breeding stage:			
Adults only	0	0	
Nest building/incubation	−1.84		
Dependent young	−0.43	0.77 (0.44–1.04)	
Independent fledglings	2.20		
Patch divisibility × foraging success rate	0.42	0.17	
Patch divisibility	0.19	0.02	
Foraging success rate	18.37	1.84	
Dominance status:			
Dominant[e]	0	0	
Subordinate[f]	−0.62	0.32	

Binomial variable: 1 refers to a call, and 0 refers to no call. Results from a GLMM with a binomial error structure and a logit link function based on a sample of 2,319 focal watches on 48 adult pied babblers from 12 groups. If a purr call had been given during the focal watch, we used the values for foraging success rate and patch divisibility from the patch at which the call was given. If no purr call had been given, values from the entire focal watch were used. There was significant repeatability of both individual identity ($p < 0.05$) and group identity ($p < 0.05$).

[a] Assessed as the number of prey items caught per minute.

[b] Assessed as prey biomass caught per minute and used as an indicator of food abundance in a patch.

[c] The highest daytime shade temperature during a period of 24 hr.

[d] Determined at the start of a data session (a maximum 5 hr in length).

[e] The putative breeding pair.

[f] All other adult group members.

were independent fledglings. Fledglings (9.8 ± 0.7 s) also responded significantly more quickly than adults (16.8 ± 1.5 s) to naturally given purr calls (two-sample t test: t = 3.13, df = 79, and p = 0.002). Fledglings responding to a purr call were significantly less likely than adults to receive vocal or physical aggression from the caller (Chi-square test: $\chi^2 = 7.41$, df = 1, and p = 0.006).

Costs and Benefits

Independent fledglings responding to a purr call gained a significant foraging benefit from doing so; they experienced greater foraging success (paired t test: t = 4.39, n = 27, and p < 0.001; Figure 3A) and spent longer (t = 5.51, n = 27, and p < 0.001; Figure 3B) in the patch to which they were recruited compared to their previous patches in that focal watch. In contrast, fledglings that did not respond to a purr call did not show a significant increase in foraging success rate (t = 0.69, n = 13, and p = 0.501; Figure 3A) and did not spend significantly longer (t = 0.41, n = 13, and p = 0.687; Figure 3B) in their

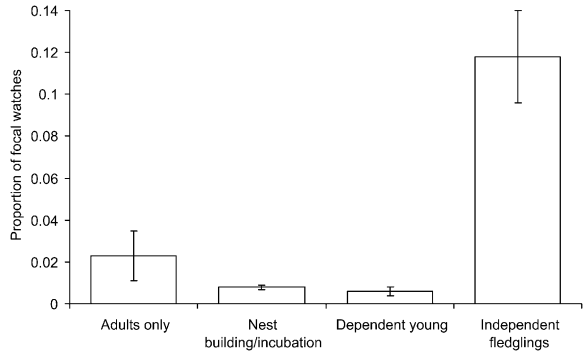

Figure 1. The Importance of Breeding Stage in Determining the Likelihood of an Adult Pied Babbler Giving a Purr Call While Foraging Alone in a Patch

Shown are mean ± SE proportion of focal watches in which a purr call was given (n = 48 adults). "Adults only" refers to occasions when the group contained only adult individuals. "Dependent young" refers to times when there were either nestlings or dependent fledglings present in the group. Independent fledglings are those that obtain 95% of their food from self-feeding.

next patch (i.e., one selected by themselves) than in previous patches. Responding and nonresponding fledglings did not differ significantly in their foraging success rates (two-sample t test: t = 0.49, df = 38, and p = 0.630) or the amount of time spent (t = 0.83, df = 38, and p = 0.414) per patch in the period before a purr call was given by an adult group member. Responding individuals might also potentially gain from having to spend less time being vigilant because the foragers they join are also scanning for predators. However, fledglings did not significantly decrease the proportion of time spent on being vigilant when they were recruited to a new patch (0.12 ± 0.01) compared to previous patches (0.09 ± 0.01; paired t test: t = 1.61, n = 27, and p = 0.118).

The foraging success of calling adults did not change significantly once they were joined by another individual (0.30 ± 0.02 g/min) compared to when they foraged

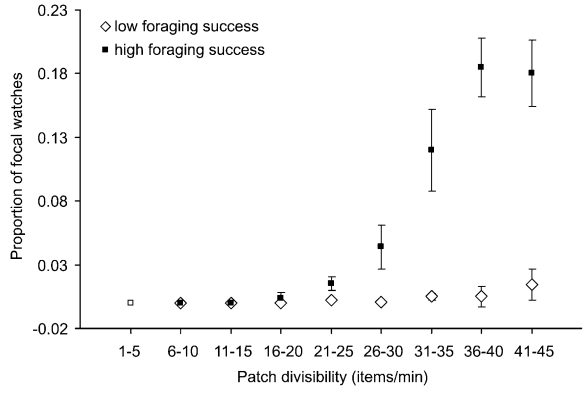

Figure 2. The Importance of Food Abundance and Divisibility in Determining the Likelihood of an Adult Pied Babbler Giving a Purr Call While Foraging Alone in a Patch

Shown are mean ± SE proportion of focal watches in which a purr call was given (n = 48 adults). Divisibility was measured as the rate at which individual prey items were discovered in the patch. Foraging success rate (biomass/min) was used as an indicator of food abundance: "high" refers to values above the median; "low" refers to values below the median.

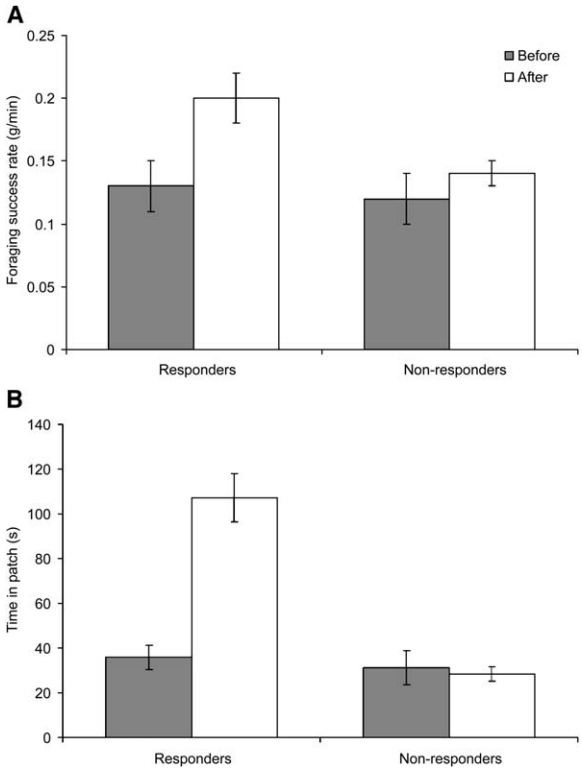

Figure 3. Benefits to be Gained from Responding to a Purr Call in Terms of Foraging Success Rate and Time Spent in a Patch

Shown are mean ± SE (A) success rates and (B) times per patch for independent fledglings that either responded (n = 27) or did not respond (n = 13) to a purr call. For responders, the success rate and time spent in patches before the call and in the patch to which the fledgling was recruited were compared. For nonresponders, the success rate and time spent per patch before and after the call was given were compared.

alone at the same patch (0.32 ± 0.03 g/min; paired t test: t = 1.70, n = 38, and p = 0.098). However, calling adults that were joined by others (98.5 ± 8.6 s) spent significantly less time foraging at a patch than those that were not joined by others (139.6 ± 12.0 s; two-sample t test: t = 2.80, df = 55, and p = 0.007); this finding suggests that patches are depleted more quickly when an additional forager is present. Callers did not reduce the proportion of time spent on being vigilant when they were joined by another individual (0.13 ± 0.02) compared with when they were foraging alone in the same patch (0.11 ± 0.02; paired t test: t = 1.54, n = 38, and p = 0.131).

Discussion

Numerous studies of altricial birds have shown the provisioning of both nestlings and fledglings to be key forms of parental care, with heavier offspring being more likely to survive and subsequently reproduce [11, 12]. However, the possibility of care continuing after nutritional independence has been rarely considered in avian species, even though studies of postweaning care are common in mammals [13, 14]. Our results suggest that foraging pied babblers use a particular vocalization (the purr call) to recruit nutritionally independent fledglings to abundant, divisible food sources and that fledglings benefit by responding to the call. A few studies of precocial avian species have shown that parents may direct offspring to particular foods [15, 16], and there are anecdotal reports that calls may be used by some felids to draw the attention of inexperienced young to prey items [17], but this study is the first to demonstrate that recruitment calling may extend the period of parental care in altricial avian species.

In most measures of foraging performance, juvenile birds tend to be less adept than adults, presumably because proficient foraging requires experience and well-developed muscular, skeletal, and neurological systems [7, 8]. It is often assumed that the transition to nutritional independence marks the end of parental care, but juveniles might still benefit from parental assistance beyond this point. First, they might gain some foraging benefit. Our results demonstrate that, by responding to adult recruitment calls, pied babbler fledglings increased their foraging success rate and were able to spend longer than normal at a patch and thus presumably reduce the amount of time spent searching for food. Second, in species where grouping offers some protection from predators, individuals responding to recruitment calls might benefit from a decreased predation risk or a reduction in the amount of individual vigilance time, or both [9]. However, vigilance benefits appear to be less important to juvenile pied babblers, perhaps because group members usually forage within 20 m of one another and a sentinel (an individual scanning for predators from a raised position above the foraging group) is commonly present [18]. Thus, the extension of care provided by recruitment calling appears to benefit juveniles primarily through increased foraging success. Whether the purr call is used to recruit fledglings that are actually unaware of the food source or to indicate tolerance toward those that might already have some knowledge of its existence remains to be tested.

Adults giving the recruitment call did not suffer a decrease in their foraging success rate when they were joined by others, but there was some evidence that food patches were depleted more quickly when they were shared. This cost does not seem to be offset by a short-term survival benefit to the caller; joined adults did not reduce their time spent on being vigilant [9], and they did not show increased foraging success from prey disturbed by the recruited individual [19]. Instead, by providing post-independence care, adults may gain long-term, inclusive fitness benefits. First, there may be indirect benefits from aiding kin [20, 21]. This might explain why dominants (the putative breeding pair) gave calls more often than subordinates (other adult group members): They are likely to be more closely related to the fledglings they recruit. We used regular weight measurements to rule out the alternative possibility that dominants are heavier and can thus better afford to share food patches. Second, recruitment calling may increase the survival chances of young, and this might aid group augmentation and thus benefit all group members [22, 23]. For example, larger groups may suffer lower predation risks [9] and fare better in intergroup contests if relative group sizes influence the outcome [24]. Third, recruitment calling may accelerate juvenile development. For species (such as pied babblers)

capable of producing multiple broods per year, prolonged postfledging care of one brood may delay the initiation of the next clutch or foreclose the option of another clutch altogether [25]. If recruitment calling reduces the period of direct provisioning, it may allow faster initiation of the next clutch.

The tendency for pied babblers to use the purr call for recruitment only when there are independent fledglings in the group suggests that they mediate their behavior depending on the audience. Some authors have suggested that audience effects are a necessary condition for intentional signaling [10, 26]. Previous studies have demonstrated an audience effect on recruitment calling in a variety of situations. For example, female rhesus macaques (*Macaca mulatto*) give more calls in the presence of kin than nonkin [21], and the calling of male chickens (*Gallus gallus*) is significantly enhanced in the presence of a hen but abolished when another cockerel is around [27]. These results and the current study suggest that recruitment calling is not obligatory and reflexive but is under voluntary control, as in human speech [28].

In addition to the social environment, aspects of the food source itself affected the likelihood of babbler recruitment calling; calls were only given when an individual was foraging at an abundant, divisible food patch. Several previous studies have indicated that the production of recruitment calls is influenced by the quantity [21, 29, 30] or divisibility [9, 31] of food discovered, or both, presumably because these factors greatly affect the relative costs and benefits of sharing. Pied babblers may achieve great foraging success from a variety of different prey types, ranging from single large items, such as snakes and lizards, to many small items, such as termite larvae. The former are not easily divisible, and their capture often results in aggression between competing individuals (unpublished data), demonstrating that a plentiful food source does not necessarily elicit recruitment calling. In contrast, recruitment calls are frequently given at termite nests, where the contents are both abundant and easily shared and so the potential for competitive interactions is lowered. Vocal and physical aggression is still apparent at divisible food sources, however, if another adult tries to join a calling individual. This helps to explain why adults respond to purr calls less often than independent fledglings and emphasizes that the call's primary function in this context is to recruit young, inexperienced foragers to rich foraging sites.

Compared with noncooperative species [8, 32], avian cooperative breeders are known to have unusually long periods of post-fledging offspring dependence. Our results suggest that parental care extends even beyond the point of nutritional independence in at least one cooperatively breeding bird, the pied babbler. Because helpers, as well as breeders, recruit fledglings to foraging patches, recruitment calling can be considered a form of alloparental care, in addition to those behaviors (e.g., incubation, provisioning of young, and territory defense) that have been recognized previously in this regard [6, 22]. Furthermore, the use of recruitment calling as a form of extended parental care need not be confined to cooperative species. It might theoretically occur whenever parents and offspring associate closely after nutritional independence, for example in species where the parents and young leave the breeding area and either roam as a family or join a flock together or in species where the young stay on the parental territory without helping to rear subsequent broods (reviewed in [33]). Thus, the use of recruitment calling in this way may be widespread, and subsequent studies of avian parental care should consider this possibility in more detail.

Experimental Procedures

Study Site and Species

Fieldwork was carried out on farmland near Vanzyls' Rus (26° 58′S, 21° 49′E), in the South African Kalahari [34]. Pied babblers are cooperatively breeding, altricial birds that live in groups of three to 15 individuals [18]. Young are fed by all adult group members for approximately 10 weeks after fledging [18]. On reaching nutritional independence, they are still poor foragers and take several additional months to perfect their foraging skills (our unpublished data). Juveniles remain in their natal group for at least a year after fledging and thus associate with adult group members throughout their foraging development (our unpublished data).

We studied 12 color-ringed, habituated groups of babblers (containing two to eight adults; mean ± SE = 4.3 ± 0.8). Individuals were trained to jump on a scale for an egg-yolk reward. Fledglings were defined as "independent" once they obtained 95% of their food from self-feeding; prior to this, they were termed "dependent." Once fledglings reached 50% of the average foraging success rate for adults in their group, they were classified as "adults." Adults were divided into "dominants" (the putative breeding pair) and "subordinates" (the remainder of the adults). Breeding females incubate the eggs overnight; breeding males were identified from midair courtship chases and copulations with breeding females. Pied babblers are sexually monomorphic in plumage; thus, subordinates and fledglings were sexed with a DNA test (see the Supplemental Experimental Procedures available online).

Observational Data Collection

A "foraging patch" was defined as an area in which an individual probed for food without moving more than 20 cm between attempts. Individuals were considered to be foraging "alone" when no group members were within 20 cm. Foragers were "approached" if another individual came within 20 cm. If the approaching individual stayed and foraged within 20 cm of the original forager, the patch was "shared."

Focal foraging watches involved 5 min of continuous monitoring. Data were collected from March to June 2004, October to December 2004, and May to June 2005 for 4–5 hr after dawn and for 4 hr before dusk. Birds were weighed (to the nearest 0.1 g) at the beginning of each session, during which focal watches were conducted opportunistically, with at least 1 hr between watches on the same individual (48 ± 3 watches per adult (mean ± SE), range 11–93, and n = 48; 17 ± 4 watches per independent fledgling, range 10–22, and n = 36). Before each focal watch, we recorded the date, "breeding stage" (adults only, nest building and incubation, dependent young, and independent fledglings), and "foraging group size" and thus omitted individuals that were temporarily missing (e.g., incubating).

During focal watches, we recorded onto a dictaphone each: (1) foraging attempt, (2) success, (3) prey size (see the Supplemental Experimental Procedures), (4) movement to a new patch, (5) purr call, (6) approach, (7) bout of vigilance, and (8) occurrence of nonforaging behavior (e.g., preening). Foraging success was calculated per minute of foraging time. When another group member approached a focal individual that had given a purr call, we noted its identity, the time taken to respond, and whether there was any aggression (physical or vocal, or both) directed at it by the caller. If another group member gave a purr call, the focal individual's response was noted.

Experimental Data Collection

To test whether the purr call is used to recruit conspecifics, we presented ten groups with two playback trials; one involved a purr call of an individual from the focal group, and the other involved a contact call of the same individual (as a control). Calls were played at least

5 m away from all group members, and we monitored whether any individuals approached the speaker within 20 s. See the Supplemental Experimental Procedures for additional details.

To test the importance of patch divisibility, we presented the dominant males from 10 groups with two artificial foraging patches consisting of half a boiled egg yolk. In the "indivisible food" trial, the yolk half was intact; in the "divisible food" trial, it had been crumbled into at least 40 pieces. In each trial, the food was placed on the ground out of sight of the group and covered by a cloth. When the correct individual was nearby and separated from other group members by at least 5 m, the food was uncovered. We recorded whether any calls were given by the focal bird while it was feeding on the yolk. If a purr call was given, we noted whether any individuals approached.

Statistical Analysis

When possible, we completed matched comparisons of individual behavior. To assess the variables influencing whether an individual gave a purr call in a focal watch, however, we used a generalized linear mixed model (GLMM; see the Supplemental Experimental Procedures). Means ± SE are presented throughout.

Supplemental Data

Supplemental Data include Experimental Procedures and can be found with this article online at http://www.current-biology.com/cgi/content/full/16/17/1700/DC1/.

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