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Adult vocalizations during provisioning: offspring response and postfledging benefits in wild pied babblers

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When provisioning offspring many bird parents give specific calls, which typically stimulate begging. Previous studies have investigated the benefits of food calling during the nestling phase, however, there is a current paucity of data on the use of food calls after young have fledged. This study describes the use of 'purr' calls, given by adult pied babblers, *Turdoides bicolor*, when feeding both nestlings and fledglings. Offspring associated these calls with food delivery: nestlings begged in response to experimental playbacks of purr calls; whereas fledglings, which were no longer confined to the nest, approached calling adults. As well as with feeds, adults also gave purr calls in nonfeeding contexts. Playbacks of purr calls given in feeding and nonfeeding contexts elicited the same responses, suggesting that offspring expected food when they responded to both 'feed' and 'no-feed' purr calls. Adults seemed to use the association between purr calls and food delivery by giving no-feed purr calls to promote fledgling movement, for example when leading young away from predators. Fledglings directly benefited when they approached adults who gave no-feed purr calls, despite not receiving any food. This study raises the possibility that food calling during the fledgling phase is a widespread, but understudied form of parent–offspring communication in birds and may be a more important aspect of avian parental care than is currently realized.

Keywords: begging; communication; fledgling; food call; parental care; playback; pied babbler; postfledging; signalling; *Turdoides bicolor*; vocalization

In many avian species, adults give calls when feeding young at the nest. Such food calls prompt nestlings to begin begging, providing benefits to both parents and nestlings as a result (for a review see Madden et al. 2005). When begging is energetically costly (Leech & Leonard 1996; Kilner 2001; Rodriguez-Girones et al. 2001) nestlings may minimize energy expenditure by only begging when an adult gives a food call, signalling that it is bringing food to the nest. Begging vocalizations attract predators to the nest area (Haskell 1994; Leech & Leonard 1997; Dearborn 1999) so nestlings may benefit from begging only when parents indicate it is safe to do so by giving food calls. There is evidence that parents also benefit from the use of food calls. For example, giving a food call prior to arriving at the nest prepares nestlings for food delivery, increasing the efficiency of feeding visits for adults (Bengtsson & Ryden 1981; Bustamante et al. 1992; Clemmons 1995).

Many bird species continue to provision young after they fledge and there have been some reports of continued use of food calls after young have fledged (Strong 1914; Tinbergen & Perdeck 1950, Norton-Griffiths 1969, Bustamante et al. 1992; Buitron & Nuechterlein 1993; Boersma & Davis 1997). However, there has been little focus on the function of food calls during the fledgling phase. Using food calls to influence fledgling begging may yield similar benefits to those at the nestling phase. However, because they are no longer confined to the nest, fledglings may approach or follow adults who offer food (Strong 1914; Tinbergen & Perdeck 1950; Norton-Griffiths 1969; Horsfall 1984; Bustamante et al. 1992; Boersma & Davis 1997), and postfledging food calls might therefore be used by parents to move mobile offspring around.

Pied babblers, *Turdoides bicolor*, are territorial, cooperatively breeding birds inhabiting the semiarid regions of

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southern Africa. Babblers live in groups, comprising a single breeding pair and nonreproductive helpers of both sexes. All adult babblers contribute to rearing young, who, in common with many cooperative species (Langen 2000), are altricial and require extended periods of parental care (Ridley & Raihani, in press). Adult babblers regularly give a 'purr' call (described in Radford & Ridley 2006) when feeding both nestlings and fledglings. However, after offspring have fledged, adult babblers also give purr calls in nonfeeding contexts. We examine the function of purr calls in this species and ask specifically (1) do offspring associate purr calls with food delivery and (2) how are purr calls used in the fledgling phase?

METHODS

Study Species

We habituated nine babbler groups to close observer presence, allowing detailed and complete behavioural data to be collected, using the ad libitum method (Altmann 1974). All individuals in the population were identified by unique colour ring combinations. Over 615 h of data were collected on 30 broods from the nine habituated groups, each of which was observed for at least three consecutive hours each week, after coming down from roost in the morning, or before going to roost in the evening.

Data were collected from October 2003 to May 2006 in the southern Kalahari, near Van Zyl's Rus (25°8′S; 20°49′E) along the dry bed of the Kuruman river. The study area comprised patches of dry riverbed and sandy, vegetated dunes on either side. There was strong annual variation in rainfall (range 163.8–308.5 mm; mean ± SD = 248 ± 75 mm). Most rain fell in the summer season (October–April) and pied babbler breeding was restricted to these months. Mean babbler group size over the observation period was 4.1 ± 0.9 (range 2–8) adults (defined as any individual aged 12 months or over). Mean brood size over the observation period was 2.3 ± 0.2 (range 1–4) and offspring remained in the nest for an average of 16.1 ± 0.3 (range 14–18) days. Newly fledged babblers had poor motor skills and were often unable to fly for the first week after they left the nest. For the first 2 weeks postfledging, offspring spent most of the day sitting in trees, unlike adults, who spent >95% of foraging time on the ground (N. Raihani, unpublished data). Thereafter, fledglings foraged with the group, but continued to receive food from adults until 40–97 days postfledging (Ridley & Raihani, in press).

During each observation session, we noted when purr calls were given and categorized these as 'feed' or 'no-feed' purr calls (Fig. 1), according to whether the adult was offering a food item while calling. Offspring responses to purr calls were recorded and categorized as 'ignore', 'vocalize' or 'approach'. Purr calls were considered to have been ignored if offspring neither begged nor moved towards the calling adult after the call was given. If offspring begged in response to purr calls, the response was scored as vocalize. Nestlings were considered to have approached if they stood on the edge of the nest, or left the nest in response to a purr call. Fledglings were considered to have approached if they moved towards the adult giving the purr call, and were within 10 cm of the caller after the movement. If offspring approached and vocalized, the response was scored as approach. When fledglings approached calling adults, the latency (s) from the first purr call given until the first movement of the fledgling towards the caller was recorded.

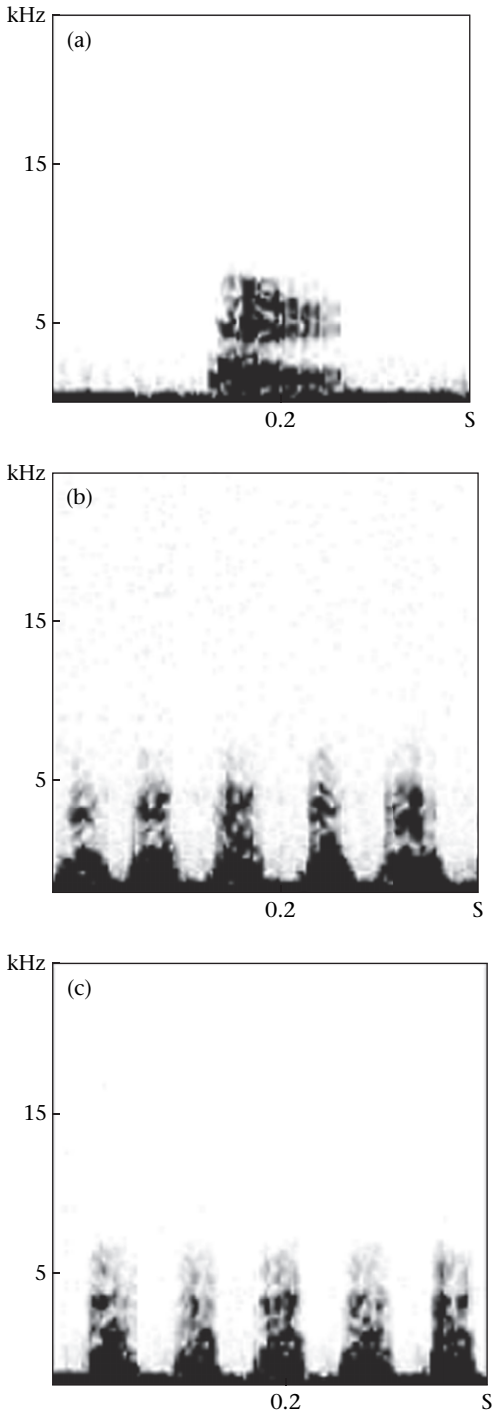

Figure 1. Spectrograms of (a) contact call, (b) no-feed purr call and (c) feed purr call. Spectrograms were created using Avisoft SASLab Light (Avisoft Bioacoustics, Germany), using a bandwidth of 704 Hz, a frequency range of 0–20 kHz, 50% overlap and a time resolution of 2.67 ms.