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ARTICLES

Experimental evidence for teaching in wild pied babblers

NICHOLA J. RAIHANI* & AMANDA R. RIDLEY†
*LARG, Department of Zoology, University of Cambridge
†Percy Fitzpatrick Institute of African Ornithology, University of Cape Town

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Giving calls to alert conspecifics to the presence of food is widespread among mammals and birds. Although the circumstances affecting the function of food-associated calls have been well studied, data on how receivers come to associate these calls with food are lacking. Specifically, the possibility that individuals may be actively taught to associate certain vocalizations with food delivery has not been addressed. In pied babblers, *Turdoides bicolor*, adults often give purr calls when feeding young and offspring subsequently associate these calls with food delivery. We investigated how offspring come to associate purr calls with food, specifically addressing the question of whether adults teach nestlings to respond to these calls. Adults use purr calls only in the presence of offspring and purr-calling does not seem to result in immediate, direct benefits to adults. Rather, the function of purr-calling seems to be to promote offspring learning: experimental playbacks show that nestlings learn to respond to purr calls and that purr calls must be reliably paired with food delivery for learning to occur. By giving purr calls during feeding visits at the nest, adults apparently actively condition nestlings to associate these calls with food. This represents a novel form of teaching among nonhuman animals.

Keywords: communication; food call; pied babbler; playback; recruitment call; teaching; *Turdoides bicolor*; vocalization

Pied babbler, *Turdoides bicolor*, adults often give a specific purr call (described in Raihani & Ridley 2007) when they feed offspring. Both nestlings and fledglings associate purr calls with food delivery, but respond differently to these calls: nestlings beg, whereas fledglings beg and approach adults who give purr calls (Raihani & Ridley 2007). There are substantial benefits to fledglings when approaching adults that give purr calls because adults use these calls to cause fledglings to move around the territory or away from potentially dangerous situations (Raihani & Ridley 2007). However, how offspring come to associate purr calls with food delivery or why purr calls are also used during the nestling phase when offspring are immobile is unclear. We investigated the possibility that adults teach offspring to associate purr calls with food by giving these calls during feeding visits at the nest.

Correspondence: N. J. Raihani, LARG, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. (email: njr29@cam.ac.uk). A. R. Ridley is at the DST/NRF Centre of Excellence, Percy Fitzpatrick Institute, Department of Zoology, University of Cape Town, Rondebosch 7701, Western Cape, South Africa.

Teaching occurs when an individual modifies its behaviour, at some cost or at least without immediate benefit to itself, to promote learning in a naïve individual (Caro & Hauser 1992). The facility to accelerate offspring learning through teaching may be advantageous in species with altricial offspring, if it promotes the acquisition of skills or information of critical fitness value to offspring or if it allows parents to shorten the period that offspring are dependent upon them. For an interaction to be classified as teaching, it must fulfil the following three criteria (Caro & Hauser 1992).

(1) The teacher must modify its behaviour only in the presence of a naïve pupil.

(2) The teacher must pay a cost or at least gain no immediate benefit as a result of the behavioural modification.

(3) As a result of the teacher's behaviour, the pupil must acquire knowledge or learn a skill faster than it would otherwise have done.

Caro & Hauser (1992) proposed that teaching in nonhuman animals was likely to be split into two broad categories. The first category, 'opportunity teaching', is

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defined as 'teacher putting pupil in a situation conducive to learning a new skill or acquiring knowledge'. Thus, teachers place pupils in situations where they are able to learn, but pupils learn as a result of their own behaviour or experience in that situation. Two recent examples provide good evidence of opportunity teaching. Adult meerkats, *Suricata suricatta*, gradually introduce pups to live prey, thereby giving pups opportunities to practise hunting skills (Thornton & McAuliffe 2006). Similarly, in tandem-running ants, *Temnothorax albipennis*, knowledgeable individuals provide naïve colony members with opportunities to learn the route to a food source by travelling more slowly to the source and stopping frequently to allow naïve individuals to investigate and memorize distinctive landmarks en route (Franks & Richardson 2006).

The second category of teaching, 'coaching', occurs when 'teacher directly alters the behaviour of pupil by encouragement or punishment' (Caro & Hauser 1992). Coaching is different from opportunity teaching because teachers promote learning by actively reinforcing pupil behaviour. Coaching has been less well documented than opportunity teaching and remains to be empirically proven. Most suggestive reports of coaching concern parental encouragement of infant independent locomotion among nonhuman primates (e.g. Yerkes & Tomlin 1935; Altmann 1980; Whiten 1999). These reports are largely anecdotal, but some quantitative evidence indicates that rhesus, *Macaca mulatta*, and pig-tailed macaque, *Macaca nemestrina*, mothers coach infants by encouraging independent locomotion (Maestripieri 1995, 1996). In these species, mothers frequently break contact with infants and use retrieval signals to encourage the infants to move back towards them. These studies presented data consistent with two of the three criteria for teaching: mothers modified their behaviour by breaking contact with infants and risked the infants being temporarily kidnapped by other group members as a result. However, evidence that infants improved their motor skills as a result of the mothers' behaviour was lacking in both studies, so that neither fulfilled all three criteria necessary to be included as definitive examples of teaching.

Coaching might also be advantageous in species with complex vocal repertoires, where the correct response to a vocalization is of critical survival value. In vervet monkeys, *Chlorocebus aethiops*, for example, there is some evidence that adults play a role in shaping offspring responses to alarm calls. In this species, different alarm calls denote different predators, and the appropriate response to each type of call varies accordingly (Seyfarth et al. 1980). Offspring must learn the relevant contexts for each type of alarm call, and parents reportedly encourage offspring when they give the correct alarm call (Seyfarth & Cheney 1986) and punish them when they make mistakes (Hauser 1987, cited in Caro & Hauser 1992). Although these studies were unable to quantify the effects of encouragement and punishment on offspring learning, they suggested that parental coaching could help offspring learn when to elicit and how to respond to referential alarm calls.

Young may also benefit from being taught how to respond to other types of vocalization or display. For example, a variety of avian and mammalian species use food-associated calls, either to alert offspring to the delivery of food (see Madden et al. 2005 for a review) or to attract offspring and/or other individuals to a food source (e.g. Hauser & Wrangham 1987; Gyger & Marler 1988; Radford & Ridley 2006). In some callitrichid primates, there is evidence to suggest that adults use food-associated calls to encourage offspring to incorporate novel items into their diet (e.g. golden lion tamarins, *Leontopithecus rosalia*; Rapaport 1999) or to produce the appropriate vocalizations to specific food items (e.g. cottontop tamarins, *Saguinus oedipus*; Rousch & Snowdon 2001). In addition, domestic hen, *Gallus gallus*, mothers may use pecking and scratching displays to attract their chicks away from perceived unpalatable food items, thereby encouraging them to forage on food that the mother perceives to be palatable (Nicol & Pope 1996). However, quantitative evidence that individuals are taught to respond appropriately to food-associated vocalizations or, indeed, that they learn anything at all as a result of food calls or other feeding displays is lacking. In this study, our aim was to determine whether adult pied babblers teach offspring to associate purr calls with food according to the accepted definition by Caro & Hauser (1992). First, we asked whether adults modified their behaviour by giving purr calls only in the presence of offspring. Second, we asked whether purr-calling was costly to adults or whether we could rule out the possibility that adults gained immediate, direct benefits from purr-calling. Finally, we used a series of experimental playbacks to determine whether nestlings learned to associate purr calls with food delivery as a result of adult behaviour.

METHODS

Study Site and Species

We collected data between October 2004 and December 2006 from an established population of pied babblers at the Kuruman River Reserve, situated along the dry bed of the Kuruman River in the southern Kalahari, near Van Zyl's Rus (25°8′S; 20°49′E; see Raihani & Ridley 2007, for a detailed description of climate and vegetation). Pied babblers are medium-sized (75–95 g) cooperatively breeding passerines. Babbler groups typically comprise a dominant breeding pair, plus nonbreeding helpers. The dominant pair are thought to produce the vast majority of the offspring (unpublished data). Both breeders and helpers feed offspring, both in the nest and for an extended period postfledging (Ridley & Raihani, in press). We habituated all pied babblers in the population to the close (<2 m) presence of a human observer (see Ridley & Raihani 2007 for a description of the habituation technique) and identified all individuals by using a unique combination of colour rings. Group size ranged from 2 to 13 (3.23 ± 0.2) adults (defined as any individual aged 12 months or over). Brood size ranged from 1 to 4 (2.3 ± 0.2) nestlings. We determined nestling age by checking nests daily to determine hatch dates. We obtained accurate fledging ages by checking nests daily