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Close calling regulates spacing between foraging competitors in the group-living pied babbler

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Among the wide repertoire of vocalizations produced by social species, perhaps the most frequently heard are the 'close' calls (those of short duration and low amplitude). Despite their prevalence, and the many studies focusing on their function in primate societies, little work has been conducted on close calls in avian species. We used a combination of observations, supplementary feeding and playback experiments to investigate the function of one particular close call, the 'chuck', in group-living pied babblers, *Turdoides bicolor*. There was no evidence that the chuck call is used to recruit conspecifics to a food source or to reduce the likelihood of an individual becoming separated from the group. Instead, there was good evidence that it is used to regulate spacing between potential foraging competitors. Although the chuck call is not used aggressively to deter competitors that attempt to share an individual's foraging patch, it appears to indicate the forager's current position and thus minimize the likelihood of another group member approaching closely in the first place. Foragers increased their call rate in larger groups and when their nearest neighbour was closer (i.e. when foraging competition was potentially higher), and playbacks of chuck calling caused individuals to stay further away from the speaker than did background noise. Maintenance of spacing was beneficial because individuals suffered a decrease in foraging efficiency if they shared a foraging patch. This study represents one of the first experimental tests of the function of avian close calling.

Keywords: conflict resolution; food calls; pied babbler; playback experiments; social birds; spatial separation; *Turdoides bicolor*; vocal communication

It has long been recognized that group-living primates produce a wide variety of calls (Rowell & Hinde 1962; Snowdon 1986), but it is now apparent that social birds possess a similarly complex range of vocalizations (e.g. Kroodsma & Miller 1996; Seddon et al. 2002). For both taxa, a substantial body of data have accumulated on the function of some of the more conspicuous of these, notably alarm calls (e.g. Seyfarth et al. 1980; Zuberbühler et al. 1997; Naguib et al. 1999) and intergroup choruses (e.g. Radford 2003, 2005; Kitchen 2004). However, 'close' calls, which are characteristically of relatively short duration, low amplitude and considerable acoustic variability, are far more frequently heard (Palombit et al. 1999). Snowdon (1988) argued that the use of these vocalizations in mediating intragroup interactions was a major unexplored area in the study of vertebrate communication, and increasing research interest has subsequently focused on the function of close calls in primates (e.g. Boinski & Campbell 1996; Palombit et al. 1999; Uster & Zuberbühler 2001). In contrast, the function of avian close calls has rarely been examined, the few relevant studies tending to investigate either the costs of calling (e.g. Krams 2001) or the extent to which the calls are individually distinct (e.g. Lefevre et al. 2001).

Initially, close calls were assumed to function as a means of maintaining regular contact between group members (Gautier & Gautier 1977). However, the range of circumstances in which such calls are given suggests additional functions (see Boinski & Campbell 1996), of which three dominate the literature. First, close calls may notify conspecifics of food to be shared, conveying information

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about, for example, the location or quality of foraging patches (Radford & Ridley 2006). Second, close calls may regulate spacing between potential foraging competitors, reducing overlap of individual foraging areas. In this context, calls may be used aggressively to deter competitors that approach closely and attempt to share an individual's foraging patch (Marzluff & Heinrich 1991; Radford 2004a), or they may be used to announce a forager's current position, thus minimizing the likelihood of another individual approaching closely in the first place (Radford 2004a). Third, close calls may reduce the likelihood of an individual becoming separated from a group (Caine & Stevens 1990; Boinski 1991). Some close calls are given rarely and it is simply the production of the call that conveys the message (e.g. Radford & Ridley 2006). In other cases, the call is given frequently and it is the variation in call rate which is likely to carry the key information (e.g. Radford 2004a).

The pied babbler, *Turdoides bicolor*, a cooperatively breeding bird species found in southern Africa, provides an ideal opportunity to investigate the function of close calling in avian societies. First, pied babblers live in groups of three to 15 individuals, which defend a territory together throughout the year (Hockey et al. 2005). Group members therefore associate closely with one another for extended periods of time. Second, pied babblers spend much of the day on the ground searching for invertebrates. Individuals usually forage in separate patches, but the whole group is often spread over a relatively small area (Radford & Ridley 2006). It is thus possible to monitor simultaneously the position and movement of all group members. Finally, groups can be habituated to the close presence of observers (see Ridley & Raihani 2007). This not only facilitates clear observations (it is possible, for example, to score accurately the foraging success of individual birds), but enables the use of playback experiments to test call functionality directly, rather than relying solely on correlative data.

Here, we investigate the potential function of one particular avian close call, the 'chuck' (Fig. 1) given by foraging pied babblers. First, we examine whether the chuck call is used to recruit conspecifics to a food source. If this is the function, we predict that an increase in call rate will result in the approach of other individuals and that individuals will produce the call more frequently when their foraging success is high. Second, we investigate whether the chuck call is used to regulate spacing between potential foraging competitors, either by deterring individuals that attempt to share a foraging patch or by announcing a forager's position and minimizing the likelihood of another individual approaching closely in the first place. If the regulation of spacing between foraging competitors is important, we predict that the sharing of a foraging patch will be costly. If the chuck call is used as a direct deterrent, foragers should increase the rate of production when others approach closely and this increase in call rate should result in the approaching individual moving away. If the chuck call is used to announce a forager's position and minimize the close approach of other individuals, it should be given more frequently when the potential foraging conflict is highest, that is in larger groups and when there are other individuals nearby, and its production should cause others to stay further away. Finally, we ask whether the chuck call functions to reduce the likelihood of an individual becoming separated from the group. If the chuck call is used in this way, it should be given more frequently by individuals that are further away from, and out of sight of, other group members.

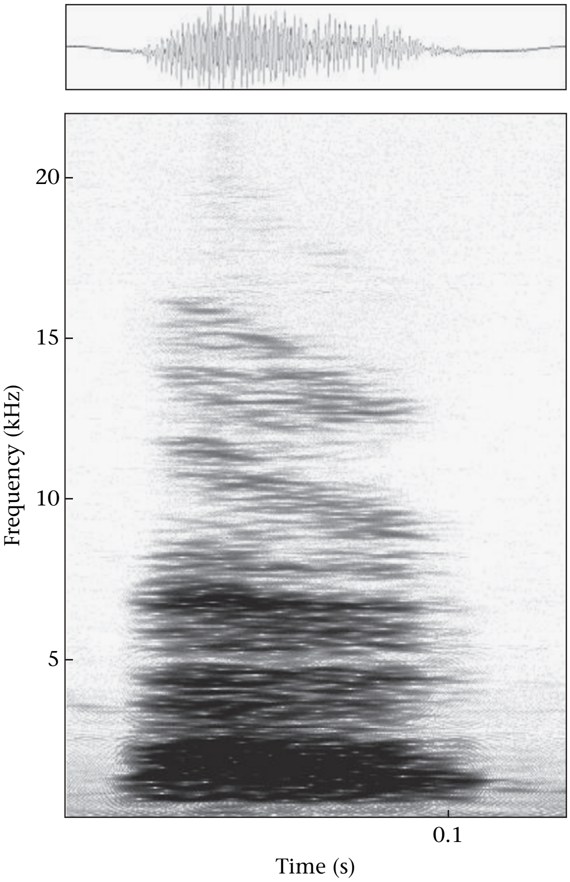

Figure 1. Sonogram of the 'chuck' call produced by pied babblers when foraging.

METHODS

Study Site and Species

Fieldwork was carried out on farmland in the southern Kalahari, close to Vanzyls' Rus (26°58′S, 21°49′E), South Africa. The study area experiences two distinct seasons: a cold, dry season from May to September and a hot, wet season from October to April (Clutton-Brock et al. 1999). Maximum shade temperature (the highest daytime temperature during a 24-h period, in °C) and rainfall (in mm) were measured daily at the study site.

We studied 12 colour-ringed, habituated groups of pied babblers (containing two to eight adults; mean $\pm$ SD $= 4.3 \pm 1.6$). All individuals in the study groups were trained to jump on a scale for an egg yolk reward, allowing regular measures of body weight without the need for capture. Groups varied in size and composition throughout the study, containing varying numbers of dependent fledglings, independent fledglings and adults. Fledglings were defined as ‘independent’ once they obtained 95% of their food from self-feeding; prior to this they were termed ‘dependent’. Adults were defined as individuals greater than 12 months old, and were divided into ‘dominants’ (the putative breeding pair) and ‘subordinates’ (the remainder of the adults). Breeding females always incubate the eggs overnight; breeding males were identified from mid-air courtship chases and copulations with breeding females.

Pied babblers are sexually monomorphic in plumage, so subordinates and fledglings were sexed using a DNA test. Individuals were caught using a walk-in trap, which was placed 20–50 m away from the group to minimize disturbance to other group members. Birds were enticed into the trap using mealworms as bait. Traps were never left unattended and as soon as it was triggered, the trap was covered with a dark blanket to calm the bird. All birds were removed within 5 min of capture, ringed and a blood sample (c. 50 μl) obtained by brachial venipuncture (under Safring licence no. 1263). The ringing process rarely took longer than 5 min. Trapping always occurred during the day, at least 1 h after sunrise or before sunset, when birds were displaying normal foraging behaviour. Trapping never occurred at potentially stressful times, such as during intergroup interactions or predator-mobbing events. There were no adverse effects of the trapping and ringing procedure: birds were promptly released back to their group following completion of ringing and resumed normal foraging behaviour within 10 min of release; birds were not attacked by other group members on their return to the group; and no bird was injured or died during the ringing process. Blood samples were kept cool in the field and then stored at 4°C until DNA extraction and analysis in the laboratory (see Radford & Ridley 2006 for details).

Observational Data Collection

Group members forage together on the ground throughout most of the day, probing beneath the sand or pecking the surface for invertebrate prey. A ‘foraging patch’ was defined as an area in which an individual probed and pecked for food without moving more than 20 cm between attempts (as estimated by the observer). Patches were considered to be either in the ‘open’ (when a bird was clearly visible) or under ‘cover’ (when an individual was, for example, foraging at the base of a bush). Individuals were considered to be foraging ‘separately’ when no other group members were within 20 cm. Foragers were ‘approached closely’ 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’. This distance was chosen because the vast majority of aggressive vocalizations given over food occur when individuals are within 20 cm of one another (A. N. Radford, unpublished data). Moreover, foragers appear to suffer a decrease in foraging efficiency when another individual is within 20 cm, but not when individuals are more widely separated (A. N. Radford, unpublished data).

Observational data were collected from March to June 2004, October to December 2004 and May to June 2005. Observations were made for 4–5 h following dawn and for 4 h before dusk, because this was when the birds were most active. Birds were weighed (to the nearest 0.1 g) at the beginning of each session. We conducted 5-min focal foraging watches on individuals in each group (48 ± 21 watches per adult (mean ± SD), range 11–93, $N = 48$ individuals; 17 ± 6 watches per independent fledgling, range 10–22, $N = 36$ individuals). If the focal individual flew off (e.g. to incubate, to feed at a nest or to take part in an intergroup interaction), the focal watch was abandoned (only data from completed 5-min watches are analysed). During each session, focal watches were conducted opportunistically, although an effort was made to focal watch all individuals equally within a group. At least 1 h was left between watches on the same individual to minimize pseudoreplication. Before each focal watch, we recorded the ‘foraging group size’, thus omitting individuals that were temporarily missing (e.g. incubating).

During focal watches, we recorded on to a dictaphone: (1) each occasion a chuck call was given by the focal individual (confirmed by observing associated bill movements); (2) the habitat (open or cover) of each foraging patch; (3) each foraging attempt (probe or peck); (4) whether each foraging attempt was successful (resulted in the capture of a prey item); (5) the size of each prey item (tiny = barely visible; small = visible in the bill; medium = up to ½ of prey hanging out the side of the bill; large = ½–¾ of prey hanging out the side of the bill; items larger than this were scored as multiples of ‘large’); and (6) each close approach of another individual. If the approaching individual moved away from the focal individual again, we recorded when this occurred. Whenever a focal individual moved to a new foraging patch, we estimated the distance to its nearest neighbour (0–2 m, 2–5 m, 5–10 m, > 10 m). Fifty prey items representative of each size category were weighed and prey sizes were subsequently converted to mean biomass values as follows: tiny = 0.02 g; small = 0.11 g; medium = 0.45 g; large = 0.84 g. ‘Foraging success rate’ was calculated as prey biomass consumed per minute of foraging time. Data from the dictaphone recordings were later transcribed, using a stopwatch to obtain, for example, chuck calling rates and the length of time that patches were shared.

General Playback Protocol

We constructed playback loops using Wavelab, version 2 (Steinberg Media Technologies, Hamburg, Germany) by editing original recordings of calls previously made from members of the study groups. These calls were made using a Sennheiser MKH416T microphone and a Marantz PMD670 hard-drive sound recorder and were digitized (44.1 kHz, 16 bits). No loop was used more than once, thus avoiding pseudoreplication. Trials were conducted in May and June 2005 and in November and December 2006, between 0700 and 1100 hours and between 1500 and 1800 hours, and the order of trial presentation within an experiment was randomized. Only one trial was conducted on a particular group per day, and trials were separated by 1–4 days. All playbacks were from a Sony SRS-A35 speaker placed on the ground and the sound intensity used in each trial matched that of natural close calls (determined using a Tandy sound-level meter). For use in the playbacks, we calculated the 'mean' rate (10 calls/min) and a 'high' rate (90% of the maximum rate heard; 18 calls/min) of chuck calling by analysing natural data collected in 2931 focal watches on 84 individuals.

Data Analysis and Experimental Tests

Rates of calling

To assess the variables influencing the rate of individual chuck calling, we used in Genstat (8th edn, Lawes Agricultural Trust, Rothampstead, U.K.) a Linear Mixed Model (LMM), because this allowed the inclusion of both random and fixed terms. Random terms allow the analysis to take account of repeated measures of the same individual and group. All fixed terms were entered into the LMM and then sequentially dropped until only terms whose elimination would have significantly reduced the explanatory power of the model remained (the minimal model). The significance of eliminated terms was derived by adding them individually to the minimal model. All two-way interactions were tested, but only those that were significant were retained in the minimal model and are presented in the Results. The LMM was based on 2931 focal foraging watches from 84 individuals in 12 groups. We used as the response term the call rate during the first period of a focal foraging watch in which an individual spent at least 30 s in the same habitat type and within the same nearest-neighbour distance category (either within the same patch or in successive patches with the same values). To normalize the data, call rates were natural-log transformed prior to analysis. The following categorical terms were included: sex, status (dominant adult, subordinate adult, independent fledgling), presence of dependent fledglings (yes, no), month, habitat (open, cover) and distance to nearest neighbour (0–2 m, 2–5 m, 5–10 m, >10 m). We also considered the following continuous terms: foraging group size, foraging success rate (biomass/min), body weight (g) at the beginning of the observation session, total rainfall (mm) in the preceding week and maximum daily temperature (°C).

Recruitment

To investigate whether chuck calling results in the recruitment of conspecifics, we considered observational data from any foraging watch where the focal individual was closely approached. We compared the call rate of the focal individual in the 30 s prior to the approach with its call rate when foraging separately in the same habitat type for a randomly selected 30-s period in the same foraging watch. If a focal individual was closely approached more than once in a particular foraging watch, we used the call-rate data from the first occasion. If values from more than one foraging watch were available for the same focal individual, means were used. We also considered the influence of foraging success rate in the call-rate LMM.

To test experimentally whether chuck calling functions to recruit conspecifics, each of the 12 groups was presented with three different playback trials (playback experiment 1). One trial involved the playback of 30 s of mean-rate chuck calling by a dominant individual from the focal group; another involved 30 s of high-rate chuck calling by the same dominant individual; and a third trial consisted of 30 s of background noise (to act as a control). The speaker was placed on the edge of the group, c. 5 m away from the nearest group member, and we recorded if any individuals approached within 20 cm of the speaker within 1 min of the start of playback. All group members were required to be foraging on the ground and within 20 m of one another before playback commenced.

To test experimentally whether foraging success rate influences the rate of chuck calling, the dominant males from 10 groups were presented with supplementary food, consisting of half a boiled egg yolk divided into at least 40 pieces. The food was placed on the ground out of sight of the group and covered with a cloth. When the correct individual was within 2 m, and separated from other group members by at least 5 m, the food was uncovered by removing the cloth. We compared the call rate of the focal individual during the 30-s period before the food was uncovered with its call rate during the first 30 s of feeding on the egg yolk (or the entire period, if shorter).

Regulation of spacing

To investigate whether sharing a foraging patch is costly, we considered observational data from any foraging watch where the focal individual was closely approached. For occasions where a patch was shared, we compared the foraging success rate of the focal individual in the patch before the approach with its foraging success rate in the same patch during the period of sharing. We also compared the time spent by individuals in patches that they shared with the time spent in patches where they were closely approached but where the approaching individual moved away within 10 s.

To investigate whether chuck calling functions to deter individuals that attempt to share a foraging patch, we considered observational data from any foraging watch where the focal individual was closely approached. We compared the call rate of the focal individual in the 30 s prior to approach (i.e. when foraging separately) with its call rate for the first 30 s (or until the approaching individual left again if that was sooner) that the patch was shared. We also compared the call rate of the focal individual on occasions when the approaching individual remained within 20 cm for longer than 10 s ('undeterred') and on occasions when the approaching individual moved away within that time ('deterred'). As for the recruitment analysis, we used only data from the first close approach in a particular foraging watch and used means if data were available for multiple watches on the same focal individual.

To test experimentally whether chuck calling functions to deter group members that attempt to share an individual's foraging patch, 12 subordinate individuals from different groups were presented with three different playback trials (playback experiment 2). One trial involved the playback of 30 s of mean-rate chuck calling by a dominant individual from the subordinate's group; another involved 30 s of high-rate chuck calling by the same dominant individual; and a third trial consisted of 30 s of background noise (to act as a control). The speaker was placed within 20 cm of the focal individual, which was required to be foraging before playback commenced. We monitored whether the focal individual moved more than 20 cm away from the speaker during the playback.

To investigate whether chuck calling functions to announce a forager's position and so minimize the likelihood of another individual approaching closely in the first place, we considered the influence of group size and nearest-neighbour distance in the call-rate LMM. To test experimentally whether individuals adjust their rate of chuck calling depending on the number of potential foraging competitors nearby, 12 individuals from different groups were presented with three different playback trials (playback experiment 3). One trial involved the playback of 1 min of chuck calling by another individual from the focal group, at a rate of 18 calls/min; another involved 1 min of chuck calling by three individuals from the focal group (including the individual from the first trial described), at 6 calls/min each (total = 18 calls/min); and a third trial consisted of 1 min of background noise (to act as a control). The focal subordinate was required to be foraging at least 10 m away from the rest of the group before playback commenced, and the speaker was placed c. 2 m away in the direction of the rest of the group. We noted how many chuck calls were produced by the focal individual during the playback.

To test experimentally whether chuck calling results in individuals staying further away from the caller, eight groups were presented with three different playback trials (playback experiment 4). One trial involved the playback of 3 min of mean-rate chuck calling by a dominant individual from the focal group; another involved 3 min of high-rate chuck calling by the same dominant individual; and a third trial consisted of 3 min of background noise (to act as a control). The speaker was placed on the edge of the group, c. 5 m away from the nearest individual and in the direction in which the group was travelling. We noted the closest distance any individual approached to the speaker during the playback. All group members were required to be foraging on the ground and within 20 m of one another before playback commenced.

Separation from the group

To investigate whether chuck calling functions to reduce the likelihood of an individual becoming separated from the group, we considered the influence of nearest-neighbour distance and foraging-patch habitat in the call-rate LMM. To test experimentally this potential function, we looked at the rate of chuck calling of individuals presented with playbacks of different numbers of group members (see playback experiment 3 above).

RESULTS

Recruitment

There was no evidence that the chuck call functions to recruit conspecifics to a food source. The rate of chuck calling by individuals significantly decreased with an increase in their foraging success rate (Table 1; Fig. 2a). Moreover, there was a nonsignificant trend for foraging individuals presented with supplementary food to decrease, rather than increase, their chuck call rate (before supplementary food = 9.1 ± 0.8 calls/min, with supplementary food = 7.9 ± 1.2 calls/min; paired *t* test: $t_9 = 2.09$, $P = 0.066$). Foragers that were closely approached had not called at a significantly higher rate prior to the approach (9.8 ± 0.5 calls/min) compared with occasions when they were not approached (10.6 ± 0.6 calls/min; paired *t* test: $t_{71} = 1.41$, $P = 0.163$). Furthermore, there was no significant difference in the number of individuals that closely approached playbacks of high-rate chuck calling (2/11), mean-rate chuck calling (1/12) and background noise (2/12; playback experiment 1, two-tailed exact test for 2 × 3 contingency table: $N = 35$, $P = 0.852$).

Regulation of Spacing

Individuals suffered a significant decrease in foraging success rate when they shared a foraging patch (0.19 ± 0.02 g/min) compared with when they were foraging in the patch alone (0.26 ± 0.03 g/min; paired *t* test:

Table 1. Terms affecting the call rate of foraging pied babbler individuals

Full model	*df*	χ^2	*P*
Foraging group size	1	39.95	<0.001
Nearest-neighbour distance (m)	3	26.16	<0.001
Foraging success rate*	1	6.39	0.011
Maximum daily temperature (°C)	1	3.14	0.076
Total rainfall in the preceding week (mm)	1	1.34	0.246
Sex	1	0.39	0.534
Habitat	1	0.36	0.547
Month	5	3.33	0.650
Body weight (g)†	1	0.13	0.721
Status	2	0.20	0.906
Presence of dependent fledglings	1	0.01	0.951

Minimal model		Effect	SE
Constant		2.283	0.017
Foraging group size		0.036	0.006
Nearest-neighbour distance:	0–2 m	0	0
	2–5 m	−0.046	0.014
	5–10 m	−0.117	0.034
	>10 m	−0.122	0.036
Foraging success rate		−0.198	0.078

Results from a Linear Mixed Model based on 2931 focal watches of 84 individuals in 12 groups. Group and individual identity were included as random terms.

*Assessed as prey biomass (g) caught per minute of foraging.

†Determined at the start of an observation session (maximum 5 h in length).

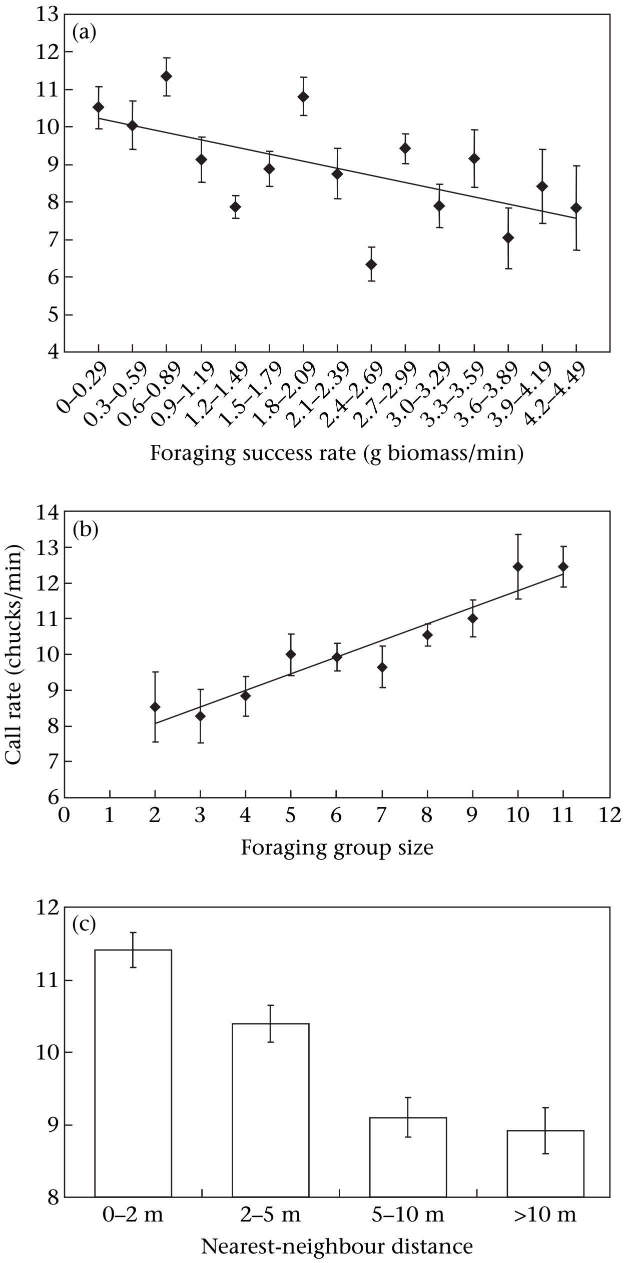

Figure 2. The influence of (a) foraging success rate, (b) foraging group size and (c) nearest-neighbour distance on the rate of chuck calling by 84 foraging pied babblers. Shown are mean ± SE call rates for all individuals that (a) achieved a particular foraging success rate, (b) foraged in groups of a particular size and (c) foraged at each nearest-neighbour distance.

$t_{43} = 6.37$, $P < 0.001$). Moreover, individuals that shared a patch spent significantly less time in the shared patch (25.4 ± 1.8 s) than in patches where they were approached closely but where the approaching individual moved away within 10 s (36.2 ± 2.7 s; paired *t* test: $t_{26} = 5.73$, $P < 0.001$). Hence, individuals benefit by foraging alone in a patch.

There was no evidence that chuck calling functions aggressively to deter individuals that approach closely and attempt to share a foraging patch. There was no significant increase in the call rate of foragers once another group member closely approached (10.2 ± 0.6 calls/min) compared with the preceding period when they had been foraging alone (10.7 ± 0.5 calls/min; paired *t* test: $t_{71} = 0.67$, $P = 0.507$). Following the close approach of another individual, occasions when the approaching bird moved away within 10 s were not prefaced by a significantly higher call rate from the forager (9.8 ± 0.7 calls/min) than occasions when the patch was shared for longer than 10 s (9.1 ± 0.5 calls/min; paired *t* test: $t_{57} = 0.23$, $P = 0.821$). Furthermore, there was no significant difference in the likelihood of individuals moving away from playbacks of high-rate chuck calling (4/12), mean-rate chuck calling (3/11) and background noise (2/10; playback experiment 2, two-tailed exact test for 2 × 3 contingency table: $N = 33$, $P = 0.887$).

There was, however, good evidence that chuck calling functions to announce the position of a forager and thus minimize the likelihood of another individual approaching closely in the first place. The rate of chuck calling by individuals increased significantly in situations where there was likely to be an increase in potential foraging competition, i.e. in groups of larger size (Table 1, Fig. 2b) and when the nearest neighbour was closer (Table 1, Fig. 2c). Furthermore, individuals produced different rates of chuck calling depending on the number of individuals nearby (playback experiment 3, Friedman test: $\chi^2 = 13.32$, $df = 2$, $P = 0.001$): they called at a higher rate in response to playbacks of chuck calling compared with background noise, and they gave significantly more calls in response to three individuals compared with one (Fig. 3). Chuck calling also significantly influenced the likelihood that individuals travelling in that direction kept away from the speaker (playback experiment 4, Friedman test: $\chi^2 = 9.48$, $df = 2$, $P = 0.009$): individuals remained significantly further away from playbacks of chuck calling compared with background noise (Fig. 4).

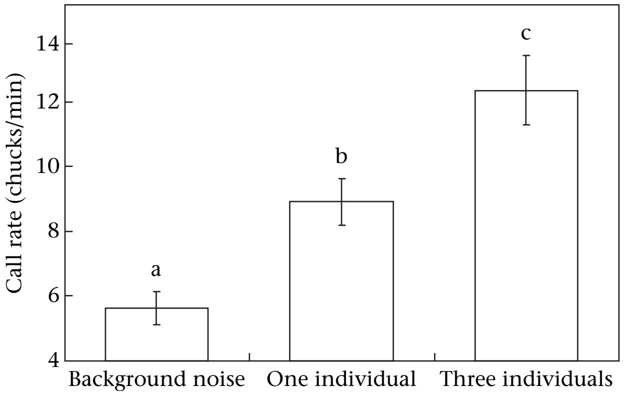

Figure 3. Results of playback experiment 3, testing the chuck calling response of individuals to playbacks of different numbers of group members. Shown are mean ± SE chuck calling rates in response to background noise (no individuals calling, control), one individual calling at 18 calls/min and three individuals calling at 6 calls/min (total = 18 calls/min). Data are from trials on 11 groups because one trial was aborted in one group. Different letters above the bars indicate which trials differed significantly (multiple comparison tests).

Separation from the Group

There was no evidence that chuck calling functions to reduce the likelihood of an individual becoming separated from the group. Individuals called at a lower rate the further they were from their nearest neighbour (Table 1, Fig. 2c) and there was no significant increase in call rate by individuals that were foraging under cover and thus were likely to have obscured lines of sight (Table 1, 'habitat' term). Furthermore, individuals produced more chuck calls in response to playbacks of chuck calling (i.e. when other group members appeared to be nearby) compared with background noise (see results of playback experiment 3 above).

DISCUSSION

There was no evidence that the chuck call of the pied babbler functions to recruit conspecifics to a food source: the relationship between call rate and foraging success rate was negative; individuals presented with supplementary food showed a tendency to decrease their call rate; there was no increase in a forager's call rate prior to the close approach of another group member; and playbacks of chuck calling were no more likely than those of background noise to cause individuals to approach the speaker closely. There was also no evidence that the chuck call functions to reduce the likelihood of an individual becoming separated from the group: individuals called less the further they were from other group members; they showed no increase in call rate when they were foraging under cover and were less likely to be able to see other individuals; and they called more in response to playbacks of other individuals compared with background noise. Instead, the chuck call appears most likely to regulate the spacing of potential foraging competitors. The exact function in this context does not appear to be the aggressive deterrence of conspecifics that attempt to share an individual's current foraging patch: there was no increase in a forager's call rate when another individual approached closely (i.e. within 20 cm of the forager); occasions when an approaching individual moved more than 20 cm away were not prefaced by higher call rates from the forager than occasions when they shared the patch; and playbacks of chuck calling were no more likely than those of background noise to cause an individual to move away from a patch. Rather, the chuck call appears to be used to announce the position of a forager and so minimize the likelihood of another individual approaching closely in the first place: foragers called more frequently in larger groups and when their nearest neighbour was closer (i.e. in situations where foraging competition was likely to be higher); individuals called at higher rates in response to playbacks of more individuals (i.e. when there appeared to be more potential competitors nearby); and individuals stayed further away from playbacks of chuck calling compared with playbacks of background noise.

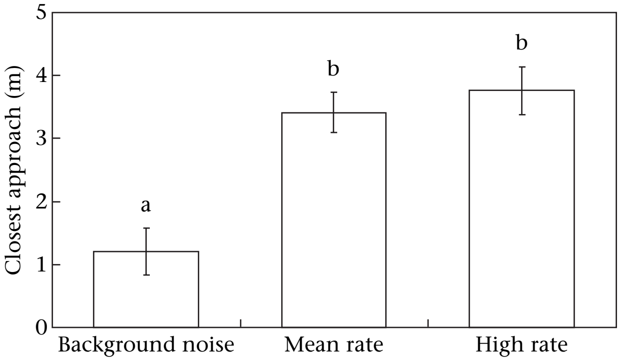

Figure 4. Results of playback experiment 4, testing the effect of chuck calling on the closest approach of foraging individuals that were moving in that direction. Shown are mean ± SE closest distances approached to the speaker in response to background noise (control), mean-rate chuck calling (10 calls/min) and high-rate chuck calling (18 calls/min). Data are from trials on eight groups. Different letters above bars indicate which trials differed significantly (multiple comparison tests).

Close calls have previously been shown to expand between-individual spacing in several primate species (e.g. wedge-capped capuchins, *Cebus nigrivittatus*, Robinson 1982; long-tailed macaques, *Macaca fascicularis*, Palombit 1992; white-faced capuchins, *Cebus capucinus*, Boinski & Campbell 1996), but only one avian species (green woodhoopoes, *Phoeniculus purpureus*, Radford 2004a). The pied babbler chuck call seems primarily to signal a forager's position, perhaps in an attempt to minimize the likelihood of overlap between the foraging areas of different individuals. As in other species (e.g. Robinson 1981; Janson 1990; Radford 2004a), pied babbler foragers appear to benefit by maintaining some spatial separation from other group members, because individuals that did share a patch suffered a reduction in the amount of time spent in the patch (suggesting it was depleted faster). Moreover, individuals sharing a patch suffered a decrease in foraging success rate compared with when they were foraging alone in the patch, although this may also be the consequence of patch depletion over time. Because all foragers are likely to benefit in these ways from foraging alone in a patch, it is not surprising that the mean rate of individual chuck calling was invariant across sex and status classes.

Despite the use of close calls in an effort to minimize the overlap of individual foraging areas, foragers of most species are sometimes approached closely by other group members (e.g. Boinski & Campbell 1996; Radford 2004a; this study). Often, these approaching individuals then receive some form of aggression from the forager; if the close call is ignored, its role as a spacing call is therefore enforced through aggressive behaviour, which is presumably detrimental to the approaching individual. This aggression is often vocal in nature and can take one of two forms. In green woodhoopoes, for example, foragers increase their close-calling rate when a competitor encroaches on their foraging patch, and this often seems to deter the approaching individual (Radford 2004a). In pied babblers, however, there is no change in the close-calling rate; instead, approaching individuals receive a different, obviously aggressive, call and are sometimes physically chased (A. N. Radford, unpublished data).

Occasionally, rather than being deterred, a pied babbler that approaches another foraging group member is allowed to stay and share the patch. Theoretically, foraging in close proximity to others might result in benefits, such as a reduction in time spent being vigilant for predators (Elgar 1986) or increased foraging success from the disturbance of prey (Brown et al. 1991), which would compensate the costs of sharing to some extent. However, a previous study has indicated that these benefits are unlikely to be important in pied babbler groups (Radford & Ridley 2006). Alternatively, foragers might allow another group member to share a patch if, for example, the approaching individual is an inexperienced juvenile that would benefit greatly from access to a valuable food source, or if the costs to sharing a particular patch are outweighed by those involved in aggressively chasing the approaching bird away. These possibilities remain to be explored.

Individuals gave chuck calls more frequently when there were more potential foraging competitors nearby. Theoretically, they could assess the level of threat either visually or vocally. For many species, both primate (e.g. Robinson 1981; Boinski & Campbell 1996; Uster & Zuberbühler 2001) and avian (e.g. Radford 2004a), vocal cues are likely to be most important because lines of sight are usually obscured in the densely foliated, arboreal habitats in which the species moves and forages. In green woodhoopoes, for example, individuals occupy two distinct foraging niches (Radford & du Plessis 2003) and can be distinguished from the pitch of their vocalizations (Radford 2004b), thus giving foragers important information about the potential competition nearby; only individuals of the same foraging niche cause a decrease in foraging success if they forage alongside one another (Radford & du Plessis 2003). Although pied babblers live in an open, desert habitat, where visual cues are less likely to be blocked by vegetation, much of their time is spent foraging with their heads lowered or even in holes. Hence, they may also benefit from vocal cues, because these would save them having to suspend foraging to check for the position of other group members (see also Radford & Ridley 2007). Our playback results suggested that foragers use the chuck calling of others to gauge the number of individuals nearby, and thus the potential foraging competition: individuals called at a higher rate in response to playbacks of more individuals, and this was not due to a simple increase in the overall calling rate. The implication is that the babblers have individually distinct calls, which would not be surprising given the range of circumstances in which such individuality has been previously shown (e.g. Falls 1982; Dhondt & Lambrechts 1992; Komdeur & Hatchwell 1999).

The pied babbler chuck call may, of course, serve additional functions not tested here. For example, similar calls in other species have been shown to initiate group movement to a new area (Radford 2004c), to coordinate group activities such as sentinel behaviour (Manser 1999) and to facilitate group cohesion (Farabaugh & Dooling 1996). However, it seems clear from the results presented that one major role of the chuck call is to announce a forager's position, allowing some maintenance of spacing between foraging competitors and thus the optimization of foraging efficiency. Although the use of close calls is commonplace in avian societies, this is one of the first experimental tests of their function.

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