ORIGINAL ARTICLE

Andrew N. Radford

Vocal mediation of foraging competition in the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*)

Abstract Many group-living species produce frequent vocalisations when foraging, but the function of these food-associated calls is often difficult to divine. I investigated the 'kek' call of the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*), a species in which individuals have preferred foraging techniques dependent on their bill size. Individuals called at a greater rate (1) in foraging compared to non-foraging situations, and (2) in groups containing potential foraging competitors (i.e. individuals that foraged using the same preferred techniques). I therefore asked whether the kek call is used to recruit conspecific foragers or whether it acts as a vocal signal of foraging niche and mediates foraging competition. Foragers that were vocalising were no more likely to be approached than those that were silent, and individuals gained no foraging advantage from the close proximity of another group member. Thus, keks are unlikely to be used to recruit conspecifics. Instead, they appear to regulate spacing between potential foraging competitors. Although an individual forager was equally likely to be closely approached by all other group members, it increased its calling rate only in response to potential foraging competitors. This increase in calling rate resulted in the approaching individual moving away, thus maintaining some separation between individuals that forage in the same way. Maintenance of such spacing is important because the success rate of an individual decreased when a foraging competitor was close by.

A. N. Radford (✉)
Department of Zoology,
University of Cambridge,
Downing Street, Cambridge, CB2 3EJ, UK
e-mail: ar255@cam.ac.uk
Tel.: +44-1223-331759
Fax: +44-1223-336676

A. N. Radford
Percy FitzPatrick Institute of African Ornithology,
Department of Zoology,
University of Cape Town,
7701 Rondebosch, South Africa

Introduction

Individuals of many group-living species produce and exchange frequent vocalisations when foraging (e.g. Evans 1982; Benz 1993; Boinski and Campbell 1996). The exact function of this very common social behaviour is often difficult to divine, which is perhaps why many studies have focused on questions about the proximate mechanisms of production, rather than questions about selective benefits (Snowdon 1988). Initially, calls given when foraging were assumed to function as a means of maintaining contact with other group members. While this is surely one use (Gautier and Gautier 1977; Boinski 1991; Palombit 1992), the range of circumstances in which the calls are given is too wide for maintenance of contact to be their sole function. Furthermore, vocalisations are often given at close quarters when animals can see one another (Cheney and Seyfarth 1982; Robinson 1982; Harcourt and Harcourt 1986).

Among the numerous potential functions suggested for food-associated calls (see Boinski and Campbell 1996), two dominate the literature. First, calls may be used to convey information about food locations or quality, and to recruit conspecifics (Dittus 1984; Elgar 1986; Heinrich 1988; Brown et al. 1991). Second, calls may serve to regulate spacing in some way. That is, they may be used to deter competitors when, for example, an individual is defending a food resource (Marzluff and Heinrich 1991), or they may be used to maintain spatial separation of group members (spatial-separation hypothesis) and thereby reduce overlap of individual foraging areas (Robinson 1982; Palombit 1992; Boinski and Campbell 1996).

The green (or red-billed) woodhoopoe (*Phoeniculus purpureus*) is a highly vocal species found in cooperatively breeding groups throughout sub-Saharan Africa (Fry et al. 1988). In South Africa, these groups consist of

2–12 individuals (du Plessis 1991) and inhabit thickly forested riverine valleys (du Plessis 1989). Each group spends much of its time foraging in trees as a close-knit unit. Woodhoopoes use five different foraging techniques to obtain their invertebrate prey, and the techniques preferred by an individual are tightly linked to its bill length (Radford and du Plessis 2003). Recently fledged individuals of both sexes have short, straight bills, which are of a similar length to adult females. These three categories of individual prefer pecking, thus competing for similar foraging sites or resources or both. By contrast, adult males (which have 36% longer bills than adult females; Radford and du Plessis 2003) spend a greater proportion of time end probing and scaling (the removal of loose bark). Approximately 4 months after fledging, a male's bill grows to exceed the length of all female bills in the population, and it begins to compete with adult males for foraging opportunities.

Green woodhoopoe group members generally forage within 15 m of one another, but lines of sight may often be obscured by the dense vegetation. Perhaps as a consequence of this reduction in the possibility of visual assessment, they regularly give 'kek' calls. Adult vocalisations are sexually dimorphic in frequency (Ligon and Ligon 1990; Radford 2004b), but the calls of males and females are similar on fledging: the male voice 'breaks' (i.e. undergoes a sharp decrease in fundamental frequency) at the same stage of development that the extreme bill dimorphism becomes apparent (Radford 2004b). Thus, individuals competing for the same foraging sites produce similarly pitched vocalisations. Here, I investigate the function of the kek call when woodhoopoes forage as a group, and provide one of the first avian studies of the role played by a food-associated vocalisation.

I begin by asking whether group composition and/or the close proximity of other individuals affect the kek calling rate. I then investigate the effect these calls have on the behaviour of other group members. If the kek call is being used to recruit conspecific foragers, there should be an increased likelihood of another individual approaching a vocal forager compared to one which remains silent. If the kek call is being used to maintain a minimum distance between individuals, and thus minimise foraging competition, I predict a change in calling when a potential foraging competitor approaches a forager. Furthermore, any change in calling should result in a change in behaviour (e.g. a movement away from the vocal forager) by the approaching individual.

Methods

Study site and species

Fieldwork was carried out near Morgan's Bay (32°43′S, 28°19′E), Eastern Cape Province, South Africa, from November to May in 1999/2000 and 2000/2001, from November to February in 2001/2002, and in October and November 2003. I focused on 19 colour-ringed groups of woodhoopoes (mean±SE group size: 3.4±0.3; range: 2–6) each of which defended an all-purpose territory throughout the year. I collected data from groups where breeding had failed (10) or young had fledged (9), so all group members were foraging together.

Since green woodhoopoes become physiologically capable of reproducing after one year (M.A. du Plessis, personal communication), birds that had been fledged for at least 11 months (the nestling period lasts for 1 month; Ligon and Ligon 1978) were classified as adults. Adults could be sexed on the basis of bill length (Radford and du Plessis 2003) or vocalisations (Ligon and Ligon 1990; Radford 2004b). Four months after fledging, the bill length of a male exceeds the bill length of all females in the population, and this is when males start foraging using an adult-male strategy, having previously foraged in a fashion similar to adult females (Radford and du Plessis 2003). 'Juvenile' here refers to individuals which had fledged less than 4 months prior to data collection. Juveniles were identifiable from their predominantly black bills (Fry et al. 1988), and could be sexed on the presence (males) or absence (females) of a brown throat patch (Fry et al. 1988).

Due to the timing of field seasons, too few data were collected on the behaviour of individuals aged 4–12 months to enable analysis. This paper therefore focuses on four categories of individual: adult males, adult females, juvenile males and juvenile females. The term 'foraging competitor' refers to an individual which might compete with a forager for the same foraging niche. Thus, adult females and juveniles of both sexes may be foraging competitors, while adult males are considered to compete directly only with other adult males.

Data collection

A 'foraging watch' involved the continuous monitoring of an individual from when it started foraging until it vanished from sight (mean±SE duration: 34±8 s). 'Non-foraging' watches were conducted when birds were preening, resting or perching (mean±SE duration: 54±11 s). Observations were made during clear weather between 0500 and 1000 hours and between 1500 and 1900 hours, since this was when birds were most active (personal observation). On any given day, both foraging and non-foraging data were collected from all group members in an opportunistic fashion. To increase sample independence, only one watch of each type was conducted on a particular individual per day (mean±SE days of watches per individual: 78±14).

While foraging, woodhoopoes often probed repeatedly at the same point, thus any individual more than 1 m away was unlikely to cause any interference. A bird was therefore identified as foraging 'separately' when there were no other individuals within 1 m. A forager was deemed to have been 'closely approached' if another group member came within 1 m. During each foraging watch, I recorded the number of probes and pecks made by an individual in an attempt to find food (see Radford and du Plessis 2003 for more details), and the number of these 'probes + pecks' that were successful (i.e. resulted in the capture of an invertebrate prey item). These data were used to compare the foraging efficiency of individuals foraging separately or in close proximity to either a competitor or a non-competitor.

During both foraging and non-foraging watches, I recorded onto a dictaphone the time of each kek (keks are given at a rate of less than one per second and are easily distinguished from other calls; Radford 2004b). During foraging watches, I also recorded each close approach of another individual to the forager. These data were later transcribed, with exact timings calculated using a stopwatch. From this continuous record, I extracted the following information.

1. The mean calling rate (keks/s) when foraging separately and when not foraging for each of the 49 adults and 15 juveniles in the 19 groups.
2. For each foraging watch, I classified the first 10-s period (or the period until another individual closely approached the forager if this was sooner) as either 'silent' (no keks given) or 'vocal' (at least one kek given). I then calculated the proportion of silent and vocal periods when each forager was closely approached. A

bird is less likely to have remained silent the longer the period considered. However, there was no significant difference in the mean length of periods analysed for individuals from different categories (unpublished data).

3. For each forager, I determined the proportion of occasions that a closely approaching individual stayed within 1 m of the forager for more than 10 s. I also calculated the call rate of the forager on occasions when the approacher remained within 1 m for longer than 10 s ('undeterred') and on occasions when it moved away again within this time ('deterred'). Finally, I calculated the call rates of foragers when closely approached by each category of individual.

To investigate whether an acoustic parameter other than call rate was important during foraging communication, kek calls given during some randomly selected foraging and non-foraging watches were recorded on 60 min TDK tapes, using a Sennheiser MKH416T directional gun microphone (with wind shield) and a WM-D6C Sony Professional Walkman. Recordings were made from within 5–15 m of the focal individual. Although the variation in recording distance may influence the fine structure of sound (e.g. there may be greater attenuation of higher frequencies with increasing distance), there was no systematic bias in recording distances between individuals (unpublished data). Calls were recorded when individuals were not foraging, foraging separately, foraging in close proximity to a competitor, and foraging in close proximity to a non-competitor. Kek calls from all four situations were recorded from 18 adult males and 16 adult females. On average, each individual was recorded on 17±3 separate days (range: 10–24 days), with at least 10 kek calls recorded each time.

Acoustical analysis of kek calls

Using a random-number procedure, five suitable kek calls were selected for each of the four situations from those recorded for each individual. Calls distorted by background noise or by overlap with calling from other members of the group were discarded. To minimise pseudoreplication, no two calls given by an individual in the same situation and the same watch were used. Using Canary version 1.2 (Cornell Laboratory of Ornithology 1993), each call was digitised (sample rate of 44,100 Hz, 16-bit precision) and stored in a computer file. To obtain the frequency profile of a call, sound spectra were generated (based on a fast Fourier transformation of 1,024 points, time resolution of 3 ms, 50% overlap and Hamming window), with a frequency resolution of 43 Hz.

Four vocal parameters of each selected kek call were measured.

1. The fundamental frequency was established from the spectrogram of a particular call (see Fig. 1) using the on-screen cursors that moved in increments of 8 Hz. The cursor was placed on the part of the fundamental which corresponded to the frequency with the greatest amplitude.
2. I used the difference between the minimum and maximum frequency of the fundamental as an indicator of the extent of frequency modulation. To enable more accurate on-screen resolution while calculating these measures, energies which fell 300 Hz above or below the fundamental were filtered out.
3. Peak frequency was taken as the frequency at peak amplitude and was automatically calculated by the software from amplitude spectra.
4. The duration of the call was established from the waveform.

A mean value was calculated for each parameter from the five selected calls of each individual in each situation.

Statistical analysis

Mean values for each forager are used throughout and summary statistics are presented as mean±SE. Proportions were arcsine square-root-transformed prior to parametric analysis, which was
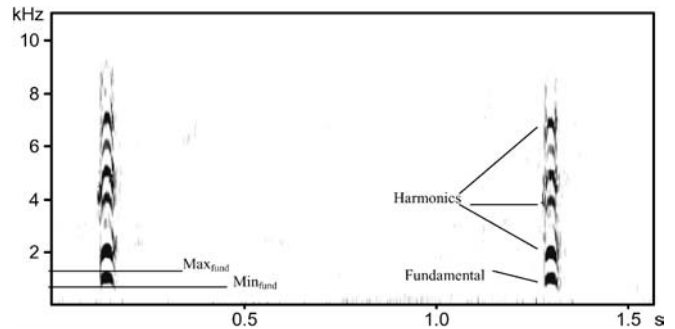

Fig. 1 Spectrogram depicting two 'kek' elements given by an adult female green woodhoopoe (*Phoeniculus purpureus*). Up to 14 harmonics were apparent in some calls, but variability in the sharpness of recordings prevented an accurate assessment of this feature. An indicator of frequency modulation of the fundamental was obtained by taking the difference between the maximum frequency (Max_{fund}) and the minimum frequency (Min_{fund}) of the fundamental. Call duration was measured from the waveform for greater accuracy

completed using SPSS version 11.5. An initial general linear mixed model, examining the overall foraging call rates of different individuals, indicated that the random factor 'group' did not explain significant variation ($P>0.10$). Thus, foragers of the same category from the same group have been treated as independent. After the initial analysis of calling rates in different contexts, I analysed only calls made by adults. This was because juveniles are fed by adult group members for up to 4 months after fledging (unpublished data), and thus juveniles may have been closely approached for this reason. If a juvenile approached an adult to be fed, it generally gave a begging call (personal observation). These occasions have been discounted from the analyses, and I have only included occasions when juveniles closely approached adults without begging. When considering foraging versus non-foraging situations, and the importance of group size, the call rate from a complete foraging watch was used. In other analyses, call rates from specific 10-s periods or until an individual was closely approached or moved away (see above for details) were used.

To assess overall calling rates, I used a repeated-measures ANOVA with context (foraging or non-foraging) as the repeated measure, and category of individual as a random factor. To compare the call rates of adults in groups that either did or did not contain potential competitors, I first controlled for overall group size, and then used 2-sample t-tests.

When considering the likelihood that a forager was closely approached, I used the observed number of approaches and the number of each category of individual within a group to calculate the expected numbers of approaches for each category in each group. I then conducted a chi-squared test on the sum of observed and expected values for all adult males and adult females. Separate ANOVAs were used to assess the call rates of foragers approached by different categories of individual and to examine the likelihood of different individuals moving away again after closely approaching a forager. Paired t-tests were used to compare the call rates of foragers when they successfully deterred another individual and when other individuals remained in close proximity.

To investigate the impact of the close proximity of another individual on a forager's efficiency, I used separate ANOVAs to compare both the rate of probes + pecks made and the success rate of adults when they foraged separately and in close proximity to foraging competitors and non-competitors. Since two different measures were used to examine foraging efficiency, the sequential Bonferroni correction (Rice 1989) was applied, with an initial α-level of 0.025.

Each of the four acoustic parameters measured from the keks given when adults were foraging in different contexts were compared using a separate repeated-measures ANOVA, because each

individual contributed a mean value to each situation. Sequential Bonferroni corrections, with an initial α-level of 0.0125, were applied because the same individuals contributed values to each acoustic-parameter analysis.

Results

Foraging call rates

When foraging, all four categories of individual gave kek calls at a significantly greater rate than when engaged in non-foraging activities (repeated-measures ANOVA: $F_{1,60}=316.53$, $P<0.001$; Fig. 2). There was a significant difference between the four categories of individual in the rate of keks given (repeated-measure ANOVA: $F_{3,60}=3.55$, $P=0.020$; Fig. 2). This was the result of adult males calling at a significantly greater rate than adult females, juvenile males and juvenile females (Tukey's post-hoc test: all $P<0.05$), none of which differed significantly from each other in their call rates (Tukey's test: all $P>0.05$).

The foraging call rate of adults of both sexes was greater, although significantly so only for females, in groups where there was at least one other individual that foraged using the same preferred techniques, compared to groups where there were no potential foraging competitors (males: competitors $=0.24\pm0.02$ keks/s, no competitors $=0.20\pm0.01$ keks/s; 2-sample t-test: $t=2.03$, $df=23$, $P=0.05$; females: competitors $=0.19\pm0.04$ keks/s, no competitors $=0.14\pm0.03$ keks/s; $t=2.32$, $df=22$, $P=0.03$). There was an indication, therefore, that keks might be conveying a message to individuals that foraged in the same way as the caller.

Function of foraging calls

There was no significant difference in the proportion of occasions that silent and vocal foragers were closely ap-
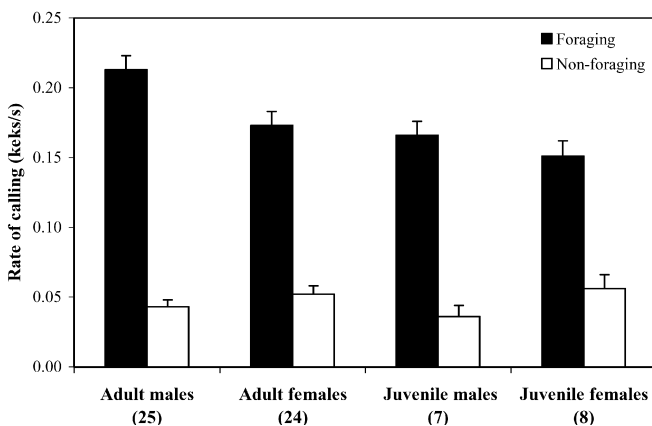

Fig. 2 Rates of kek calling by four categories of green woodhoopoe during foraging and non-foraging situations. Adults were those that had been fledged for more than 11 months, while juvenile refers to individuals that had been fledged for less than 4 months. Shown are the grand means (+SE) of the mean calling rates for the number of individuals given in parentheses
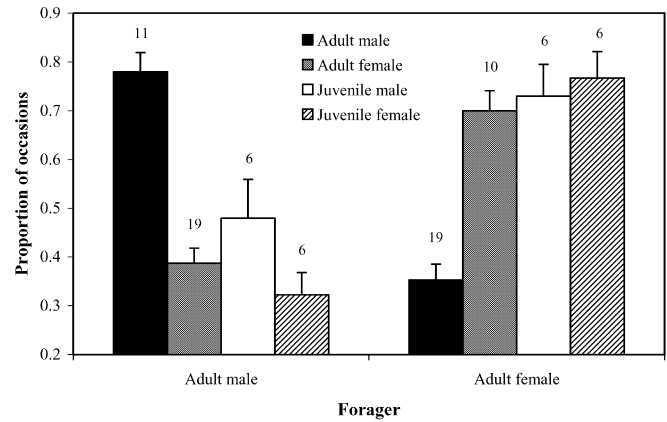

Fig. 3 Proportion of occasions that green woodhoopoes approaching within 1 m of an adult forager moved away again within 10 s. Shown are the mean (+SE) proportions for the number of adult foragers indicated above the *bars*

proached, either by a potential foraging competitor (paired t-test, adult males: $t=0.48$, $df=10$, $P=0.64$; adult females: $t=0.15$, $df=15$, $P=0.88$), or by a non-competitor (paired t-test, adult males: $t=0.08$, $df=24$, $P=0.94$; adult females: $t=0.10$, $df=18$, $P=0.92$).

Although both adult males ($\chi^2=2.43$, $df=3$, $P>0.10$) and adult females ($\chi^2=5.22$, $df=3$, $P>0.10$) were equally likely to be closely approached by individuals of all four categories, there was a significant difference in the proportion of occasions that these individuals moved away within 10 s (ANOVA, adult males: $F_{3,38}=21.80$, $P<0.001$; adult females: $F_{3,37}=24.59$, $P<0.001$; Fig. 3). In the case of adult-male foragers, other adult males were significantly more likely to move away within 10 s than were adult females or juveniles of both sexes (Tukey's post-hoc test: all $P<0.001$), which did not differ in their likelihood (Tukey's test: all $P>0.05$). However, in the case of adult-female foragers, adult males were significantly less likely to move away than were adult females and juveniles of both sexes (Tukey's test: all $P<0.001$), which again did not differ significantly in their likelihood (Tukey's test: all $P>0.05$).

The call rate of a closely approached forager was significantly influenced by the category of individual that was approaching (ANOVA, adult males: $F_{4,62}=48.94$, $P<0.001$; adult females: $F_{4,60}=26.20$, $P<0.001$; Fig. 4). As expected from the spatial-separation hypothesis, there was no significant change in the call rate of foraging adult males when closely approached by an adult female, a juvenile male or a juvenile female, compared to when foraging separately (Tukey's post-hoc test: all $P>0.05$). However, when another adult male (a potential foraging competitor) closely approached, there was a significant increase in the calling rate of foraging adult males (Tukey's test, $P<0.001$). Foraging adult females also significantly increased their call rate when closely approached by a potential competitor (i.e. another adult female, a juvenile female or a juvenile male), compared to when foraging separately (Tukey's test: all $P<0.001$). There was
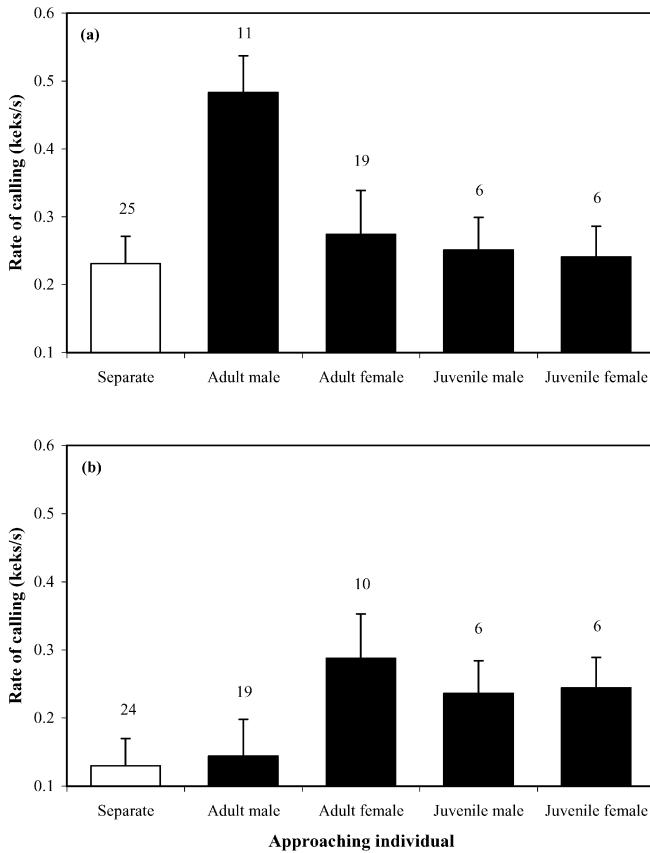
Fig. 4 Vocalisation rates of **a** adult male and **b** adult female green woodhoopoes while foraging separately (no other group member within 1 m) and when closely approached by four categories of individual. Shown are the grand means (+SE) of the mean calling rates for the number of individuals indicated above the *bars*

Fig. 5 Foraging success rates (i.e. the proportion of probes+pecks that resulted in the capture of a prey item) of adult male and adult female green woodhoopoes when foraging separately (no other group member within 1 m), or in close proximity (within 1 m) to either a foraging competitor (a group member that preferentially used the same techniques) or a non-competitor. Shown are the grand means (+SE) of the mean success rates for the number of individuals indicated above the *bars*

no significant change in the call rate of foraging adult females when closely approached by an adult male (Tukey's test, $P>0.05$).

Following close approaches to an adult male, occasions when the approaching bird moved away again within 10 s were preceded by a significantly greater calling rate by the forager (0.34±0.02 keks/s) than occasions when the approaching bird remained within 1 m for longer than 10 s (0.22±0.01 keks/s; paired *t*-test: $t=3.53$, $df=24$, $P=0.002$). Likewise, when individuals closely approached adult females, there was a significantly higher rate of calling by the forager prior to individuals moving away within 10 s (0.26±0.02 keks/s) compared to occasions when the approaching bird remained within 1 m for longer than 10 s (0.14±0.01 keks/s; paired *t*-test: $t=4.45$, $df=23$, $P<0.001$).

Foraging efficiency

Adult males showed a trend, non-significant after Bonferroni correction, for different rates of probing + pecking when foraging in different social situations (ANOVA: $F_{2,58}=3.77$, $P=0.03$). There was an indication of a reduced
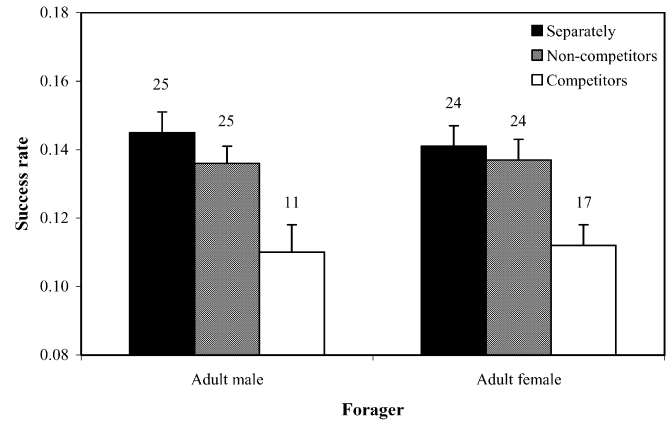
level of probing + pecking when foraging in close proximity to a competitor (0.28±0.02 probes + pecks per s) compared to when foraging separately (0.33±0.01 probes + pecks per s) or in close proximity to a non-competitor (0.34±0.01 probes + pecks per s). Adult females showed no significant difference in their probe + peck rates in different foraging situations ($F_{2,62}=1.37$, $P=0.26$).

The foraging success rates of both adult males (ANOVA: $F_{2,58}=5.87$, $P=0.005$; Fig. 5) and adult females ($F_{2,62}=5.52$, $P=0.006$) differed significantly depending on the foraging situation. For both males and females, there was no significant difference in the success rate of individuals foraging separately and those foraging in close proximity to a non-competitor (Tukey's post-hoc test: $P>0.05$). However, the foraging success of both sexes was significantly reduced when foraging within 1 m of a competitor compared to separately (Tukey's test: $P<0.01$) or in close proximity to a non-competitor (Tukey's test: $P<0.05$).

Acoustic properties of kek calls

Kek calls given in the four situations (not foraging, foraging separately, and foraging in close proximity to a competitor or a non-competitor) did not differ significantly in any of the four measured vocal parameters (repeated-measures ANOVA, adult males: all $F_{3,15}<2.38$, all $P>0.11$; adult females: all $F_{3,13}<1.67$, all $P>0.22$).

Discussion

Green woodhoopoes gave kek calls 3–5 times more frequently when foraging compared to during non-foraging activities. A similar increase in calling during foraging

was found in white-faced capuchins (*Cebus capucinus*; Boinski and Campbell 1996), and wedge-capped capuchins (*C. nigrivittatus*) exhibited increased calling rates during foraging compared to when resting (Robinson 1982). Rarely have such studies been conducted on birds, and thus most comparisons here are with the mammalian literature. The increase in kek calling while foraging, combined with the greater calling rate of woodhoopoes in groups which contained individuals foraging using the same preferred techniques, suggested that kek calls convey some message to other foragers in the group.

The food-associated calls of many social taxa serve to aggregate group members to a food source, albeit sometimes selectively (e.g. Elgar 1986; Hauser and Wrangham 1987). A few previous studies have, however, indicated that individuals producing food-associated calls are never (Clark and Wrangham 1993) or seldom (Chapman and Lefebvre 1990; Boinski and Campbell 1996) joined by group mates. My study also provided little evidence that the keks of green woodhoopoes promote the sharing of food resources within the group: foragers that were calling were no more likely to be closely approached by another individual than those that remained silent. This may be because prey items (invertebrates) of the green woodhoopoe are not easily divisible (cf. Elgar 1986). Furthermore, neither adult males nor adult females benefited from an increased foraging success when foraging within 1 m of a member of the opposite sex, as compared to when foraging separately (this study; Radford and du Plessis 2003). Thus, there would seem to be no foraging advantage to attracting other individuals to a particular site.

Instead, I suggest that the kek call of the green woodhoopoe prompts increases in the spatial separation of group members that would compete for a similar foraging niche (i.e. individuals that forage using the same preferred techniques). The spatial-separation conclusion is supported by two main pieces of evidence. First, woodhoopoes doubled their rate of kek calling when closely approached by a potential foraging competitor. There was no significant increase in kek calling when a non-competitor closely approached. Both white-faced (Boinski and Campbell 1996) and wedge-capped capuchins (Robinson 1982) also increased their rate of calling when approached by another individual, especially when that approach increased competition for resources. Playback experiments are needed to assess whether it is vocalisations of the approaching individual or visual signals that result in an increased calling rate from the forager. Interestingly, however, the vocalisations of juvenile male woodhoopoes are indistinguishable from those of females at fledging; a male's voice only breaks (i.e. undergoes a sharp decrease in fundamental frequency) at approximately the same time that it begins to use an adult-male foraging strategy (Radford 2004b). Thus, the frequency of a woodhoopoe's vocalisations accurately signals its foraging strategy. Theoretically, the increase in calling rate when another individual approaches may be the consequence of intrasexual competition for breeding opportunities. However, adult females increased their kek calling when juvenile males (which present no breeding threat, but are foraging competitors) approached, suggesting that the kek call plays at least some role in mediating foraging competition.

Second, the increase in kek rate when a competitor closely approached tended to result in the competitor moving away once more. Likewise, in both white-faced (Boinski and Campbell 1996) and wedge-capped capuchins (Robinson 1982), calls tended to discourage neighbours from approaching and encouraged them to move away again. The retreat of a competitor would explain why adult woodhoopoes are more likely to be seen foraging in close proximity to an individual of the opposite sex rather than one of their own sex (Radford and du Plessis 2003). The kek call appeared sufficient in itself to instigate the change in position of a competitor, as little overt aggression or other behavioural shifts accompanied the forager's calling. The call rate seemed to be the most likely signal causing a response, since there was no significant difference in the frequency or duration of keks given when an individual was approached by a competitor compared to when foraging alone.

The competitor's retreat may, theoretically, have been based on an individual's visual assessment of the forager, rather than the latter's increased calling. However, occasions when an approaching individual moved away again tended to be preceded by higher rates of calling than occasions when the approacher stayed in close proximity to the forager. Moreover, the dense vegetation may prevent accurate visual assessment on many occasions. Playback experiments would elucidate this further, but they are almost impossible in a species that forages high in the canopy and moves large distances.

Hence, in green woodhoopoes, as in white-faced capuchins (Boinski and Campbell 1996), wedge-capped capuchins (Robinson 1982) and long-tailed macaques (*Macaca fascicularis*; Palombit 1992), there is some evidence that the expansion of between-individual spacing is the primary function of a commonly emitted vocalisation. This maintenance of spatial separation may be advantageous to the vocaliser as both adult males and adult females suffered a decreased success rate when foraging in close proximity to a foraging competitor, and there was also a hint that males made fewer foraging attempts when a competitor was close by. The success of white-faced capuchins foraging for arthropods is also known to increase with increases in nearest-neighbour distances (Robinson 1981; Janson 1990).

The kek call of the green woodhoopoe may, of course, serve additional functions not tested here. For example, similar calls are used in other species to initiate and coordinate group activities, to maintain contact between group members (particularly in dense vegetation where visibility is limited) and to facilitate group cohesion (e.g. Farabaugh and Dooling 1996). In the green woodhoopoe, a mobilisation call based on the kek element is certainly used to initiate group movement (Radford 2004a). I do not have data to test whether the kek acts as a contact call,

but such a function would be useful in the thick forests inhabited by woodhoopoes.

Finally, it is worth noting that adult males gave kek calls at a greater rate than any of the other three categories of individual. This could result from them having generally higher levels of testosterone than other individuals (see Groothuis et al. 1993). Furthermore, in some oscines, the amount of song produced is strongly associated with seasonal or conflict-induced changes in testosterone (Kern and King 1972; Arcese et al. 1988). Since suitable foraging sites for adult male woodhoopoes are scarcer than those for females and, hence, there is more aggression between males than females (Radford and du Plessis 2003), the increased calling of males may also be a consequence of a higher level of foraging conflict. This would provide further indirect evidence for a role played by the woodhoopoe kek call in the mediation of foraging competition.

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