The role of calling in the social behaviour of silvery-cheeked hornbills

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Abstract

Silvery-cheeked hornbills, *Ceratogymna brevis*, live in social groups whose members communicate with each other by harsh quacking calls. We investigated whether the rate of calling depends on the size of a group, its sex ratio, and what activity the birds are engaged in. We also looked at how the rates of calling and patterns of activity changed throughout the day. Our observations consisted of three-minute focal watches and scanning observations at three different times of day, over six days. We found a significant correlation between group size and calling rate, but no relationship between calling rate and sex ratio. The birds called significantly more in the morning and evening than during midday, a pattern that we attribute to the sharing of information at the roosting site. There was significantly more calling during flight than during other activities such as feeding and preening, and no significant difference between the relative amounts of time the hornbills spent on different activities at different times of day. We conclude that calling is a mechanism of information transfer between group members, for example about food availability and the presence of predators.

INTRODUCTION

Many animals live in social groups of conspecific, usually related, individuals. One advantage of this is that the risk of predation for a group member is lower than it would be for a lone individual. This may be because of the dilution effect, because a group may be able to mob an attacker, or because members of a group give information to each other before all members are seen by a predator. Another advantage of social groups is an increased ability to find food, particularly when it is patchily distributed, like fruit or seeds. This is also achieved by the transfer of information between individuals.

This transfer of information is known as communication (Johnstone, 1997). Members of a social group communicate with each other for a variety of reasons. Firstly, signals may convey semantic information, e.g. about the location of a food source or the arrival of a predator. Secondly, communication is used in sexual selection. This may involve signalling as a form of competition between males, or in male displays to females. Thirdly, communication is used in other group interactions, e.g. between parents and young, or between individuals in different territories.

In this study, we looked at communication within social groups of the silvery-cheeked hornbill, *Ceratogymna brevis*. This species is non-territorial and is often found alone or in pairs during the day, although as many as 100 individuals may congregate at fruiting trees or other food sources, and communal roosting of up to 200 birds is common (Fry *et al*., 1993). Like other Bucerotidae, female silvery-cheeked hornbills seal themselves within their nest-holes from the beginning of the egg-laying period until after the chicks have hatched. The female is therefore completely dependent on provisioning by her mate, which predisposes her to monogamy (Leighton, 1986). The practice of nest sealing is also considered by Leighton (1986) to be the ultimate basis of all hornbills' strategies for maximising fitness, including groupings of males and females.

Silvery-cheeked hornbills communicate with each other via loud braying and quacking calls, as well as softer grunts while feeding (Fry *et al*., 1993); auditory communication is preferable to visual signalling in dense forest (Krebs & Davies, 1993). In this study, we investigated the role of these calls in silvery-cheeked hornbills' social behaviour. We aimed to answer the following questions:

1. Does the rate of calling depend on group size or sex ratio, and does one sex call more than the other?
2. Is the rate of calling different during different activities and at different times of day?
3. Do individuals join or leave a group in response to calls?

In doing this, we also observed how the activity patterns of hornbills change throughout the day, and what the most common group sizes and sex ratios were.

METHODS

This study was carried out in Amani Nature Reserve, East Usambara Mountains, Tanzania (5°06'S, 38°37' E), where we observed silvery-cheeked hornbills between the 17th and 22nd of September, 2005. Each day's observations were split into three time slots: 06.00-09.00, 11.00-14.00 and 16.00-19.00. Within each time slot we observed the birds for approximately 90 minutes. The observations were made in three study areas: Mbomole Hill, the paths around Amani Pond, and the roads around Amani village. Each day we changed the time slot we spent at a particular study area, so we monitored each study area twice in the morning, twice at noon, and twice in the evening.

Our observations were made by carrying out focal watches of particular individuals while simultaneously making scans of others in the same group, which we defined as all the silvery-cheeked hornbills in a single tree. Each observation lasted three minutes if possible, and no less than one minute. We recorded the amount of time each focal individual spent on five activities (feeding, flying, preening, watching, and interacting with other group members), whether it called during these activities and whether other group members were present when it called. When scanning the rest of the group, we noted its size and sex ratio, how many calls were made, and whether calls were associated with birds leaving or joining the group. During our observations, we noticed that we could often hear calls but were unable to see the birds themselves; therefore, for the last three days, we recorded the total number of calls heard during each period of observation. We analysed our data using StatView and Microsoft Excel.

RESULTS

Group size

Out of 127 focal watches, 56 birds were observed alone, and only nine birds were members of groups of more than five individuals (fig. 1). There was a significant correlation between a group's size and the number of calls per minute from its members (regression, $p<0.05$, fig. 2). The groups were highly dynamic, and group size often fluctuated during our scanning observations. Table 1 shows that there was no indication that individuals joining or leaving a group did so in response to calls from the existing group members.

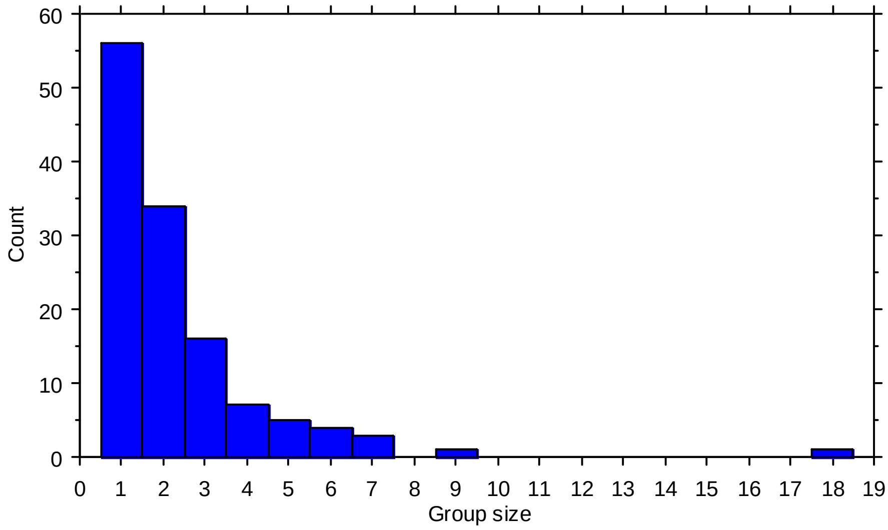

Fig. 1: Frequency distribution of group size

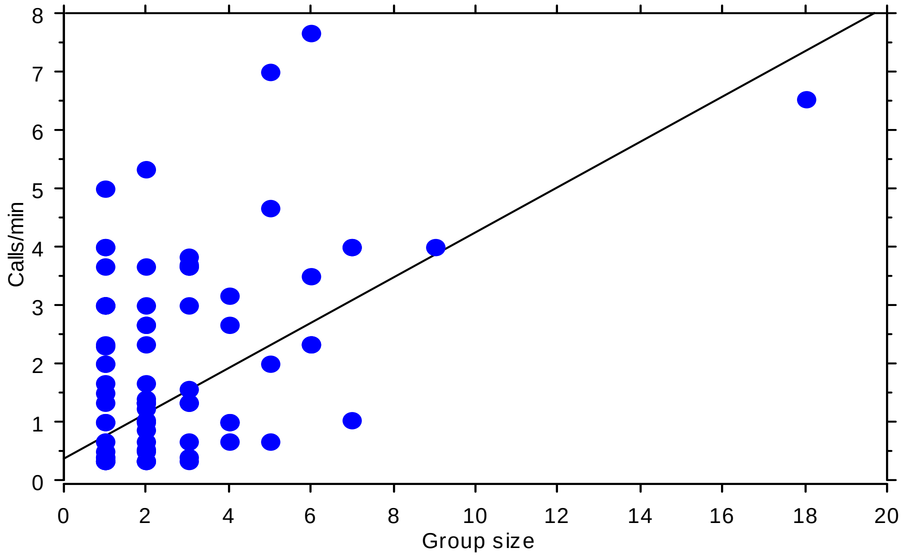

Fig. 2: Relationship between group size and calling rate ($r^2=0.24$, $p<0.05$)

Table 1: Change in group size as a result of calls

Change in group size	**Number of calls**
Arrive	15
Leave	15
No change	392

Sex ratio

43 of the focal individuals were lone males, while 13 were lone females. Most groups consisted of more males than females (fig. 3), in particular two males to one female (11 groups), while there were 23 male-female pairs. Groups with higher proportions of males did not have significantly higher calling rates (regression, $p>0.05$, fig.4). There was no significant difference between the calling rate of males and females from our focal watches (Mann Whitney U, $p>0.05$, fig. 5).

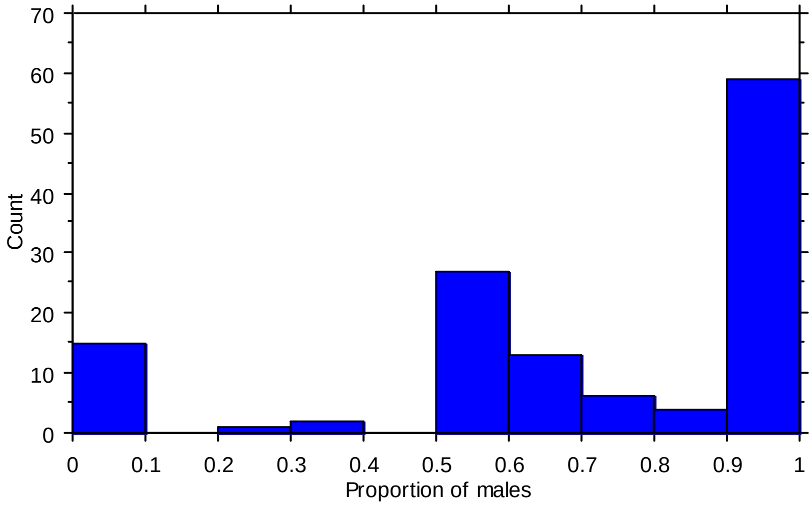

Fig. 3: Frequency distribution of sex ratio (calculated as the proportion of males)

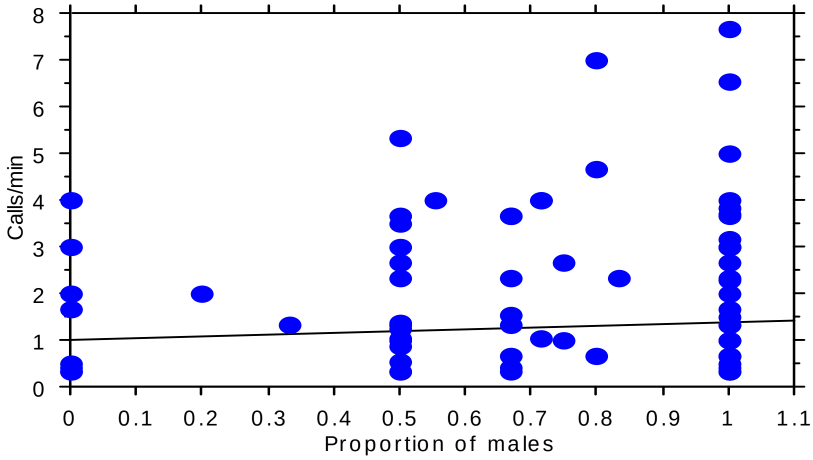

Fig. 4: Relationship between sex ratio (as proportion of males) and calling rate (r^2=0.006, p>0.05)

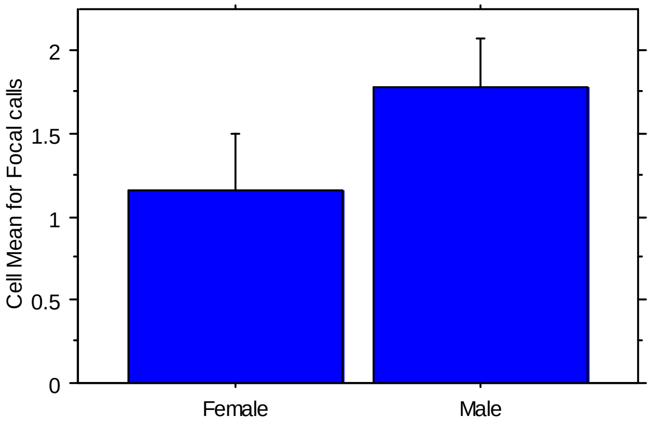

Fig. 5: Sex differences in calling rate of focal individuals (mean ± 1 SE)

Diurnal variation in calling and activity patterns

There was no significant difference in calling rate between morning, noon and evening (Kruskal Wallis, $p>0.05$, fig. 6), although when noon was compared separately to morning and to evening, there was almost a significant difference (Mann Whitney U, $p=0.06$ and 0.052 respectively). There was a significant diurnal variation in the number of calls recorded from birds which we did not see (Kruskal Wallis, $p<0.05$), with many fewer calls heard at noon. There was no significant diurnal variation in the relative time focal individuals spent on different activities, apart from feeding, which was observed significantly more in the evening (Kruskal Wallis, $p= 0.01$, fig. 7). Calling rates varied significantly for different activities (Kruskal Wallis, $p<0.05$, fig. 8): the highest rates of calling were recorded during flying, and the lowest during preening and feeding.

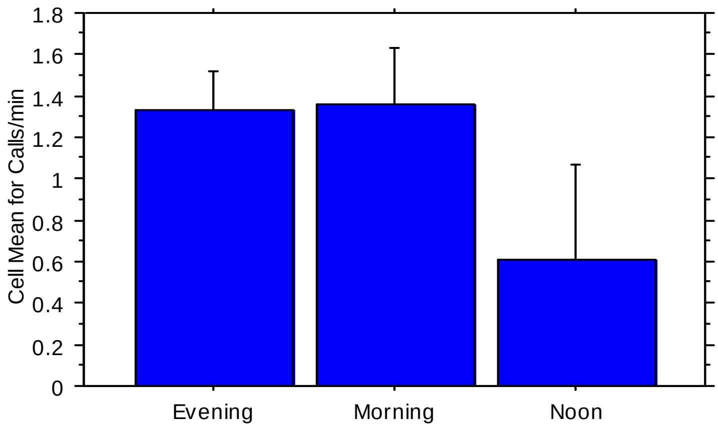

Fig. 6: Diurnal variation in calling rate from observed groups (mean ± 1 SE)

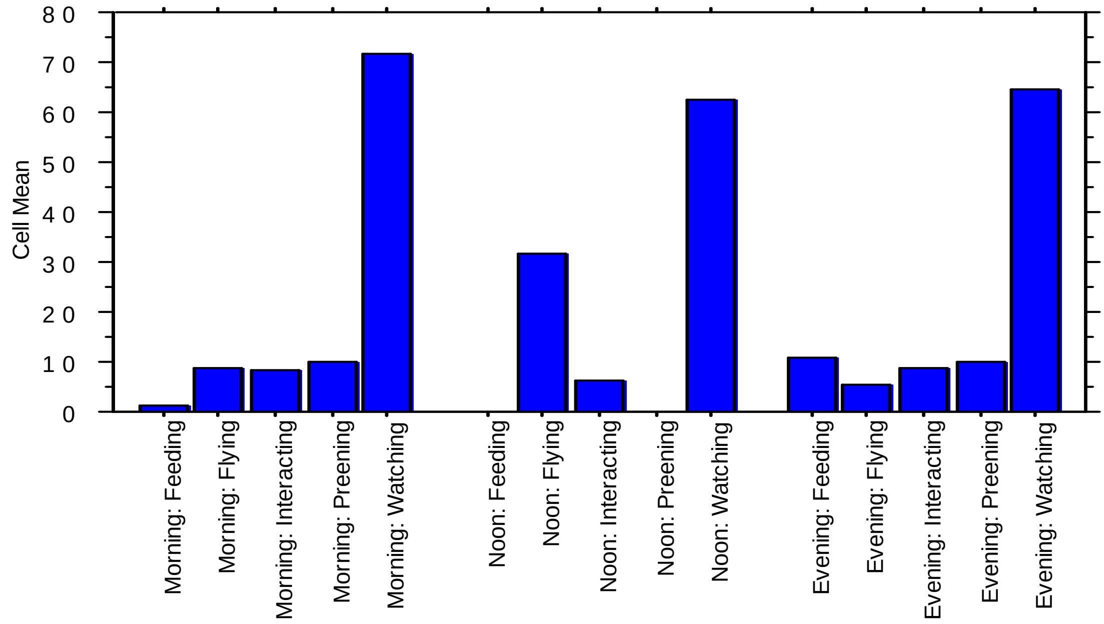

Fig. 7: Percentage time spent on different activities at different times of day

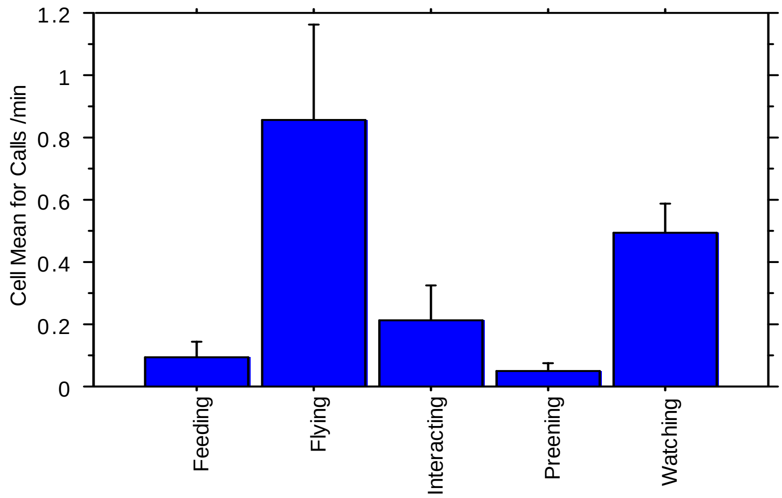

Fig. 8: Calling rate during different activities (mean ± 1 SE)

There was a significant difference in the calling rate of groups observed in the three different study areas (Kruskal Wallis, $p<0.05$), although no significant difference in the number of calls heard from non-observed birds in the different areas (Kruskal Wallis, $p>0.05$). We decided to disregard this significant difference and treat all three study sites as equal in our analysis.

DISCUSSION

Group size and sex ratio

The high proportion of lone males, male-female pairs and groups of two males with one female is likely to be due to hornbills' breeding behaviour. Silvery-cheeked hornbills in Tanzania breed in August and September (Fry *et al.*, 1993): we would therefore expect females to be sealed into nest holes at the time this study took place, which explains the abundance of single males. The male-female pairs are likely to be birds which are delayed in breeding, and the groups of three probably include birds which have not yet paired off. The large groups (more than 5 individuals) that we observed had not congregated at high concentrations of food, as might be expected (Leighton, 1986), although four of them, including the group of 18 individuals, did form in response to birds of prey. The lack of many groups of more than five members could be to do with competition over food, as well as the difficulty and human error of recording the number of individuals in large groups when they are constantly arriving and leaving.

As we expected, group size was significantly positively correlated with calling rate. A simple explanation is that the larger the group, the more likely it is that a call will be produced. In terms of information transfer, e.g. about food sites, the more group members there are, the more information there is that can be transferred. However, the scatter of points on figure 2 suggests that factors other than group size may influence the group's calling rate, for example the time of day or what the birds were doing (see below).

We had hypothesised that hornbill calling would be involved in mating displays, in which case males would be predicted to call more than females, either as an intrasexual dominance signal or as a display to attract a mate. However, we found no correlation between the calling rate and sex ratio of a group and no significant difference between the calling rates of males and females, giving no evidence that calling is involved in hornbill mating behaviour.

Diurnal variation in calling rate

The peaks in calling in the morning and evening which we observed are similar to the calling patterns of other birds, e.g. passerines. This may correspond to basic avian activity patterns. Other reasons for these peaks in calling rate may involve favourable environmental conditions for acoustic signalling (Krebs & Davies, 1993) or low activity of predators at these times of day. We observed four instances of a bird of prey coming into contact with a group of hornbills, which caused the group to call loudly and raucously and for several new individuals to join. This suggests that predators do have an influence on hornbills' calling patterns.

Another reason for the higher rates of calling in the morning and evening may be that these are times when many birds are roosting. Ward & Zahavi's (1993) information centre hypothesis suggests that individuals or groups of birds congregate at roosts in order to obtain information about feeding sites and food availability. This idea is developed by Richner & Heeb's (1996) recruitment centre hypothesis, whereby an individual that has found a food site will return to the roost to recruit helpers, since it will benefit from foraging in a group. The recruitment centre hypothesis accounts for "the aerial displays and calling observed at roosts" (Richner & Heeb, 1996). This corroborates our observations: we recorded a high rate of calling when the hornbills were roosting, and also that hornbills called more during flying than during other activities (see below).

Diurnal variation in activity

There was no significant diurnal variation in the relative amount of time hornbills spent on the activities we recorded, except for feeding, which was greater in the evening. We did not expect this, since we thought roosting sites were usually distinct from feeding sites, with the birds sometimes travelling a number of kilometres between them (Leighton, 1986). Consequently, we had also expected the hornbills to spend a greater proportion of time flying in the morning and evening when they were travelling between roosting and feeding sites. The (not significantly) higher proportion of birds flying at noon is likely to be because flying birds are easier to spot than stationary ones, and it was difficult to spot stationary birds at noon because they were not calling (there was thus a smaller sample size at noon than in the morning or evening). The birds spent a large proportion of time merely sitting on branches and watching; since this was relatively constant throughout the day, it means that the relative proportions of time they spent in other activities were also relatively constant.

Variation of calling rate with activity

The significantly higher calling rates associated with flying may be linked to the recruitment centre hypothesis, as discussed above. The highest rates of calling that we observed were when a bird of prey was present, and this also involved the hornbills taking flight. We did not expect there to be significantly less calling during feeding, as we had hypothesised that one function of hornbill calls was to alert conspecifics to an area rich in food. We had also thought that calls might be involved in the interactions of male-female pairs or in competitive interactions between males; however, the relatively low rate of calling during interactions gives no evidence for this. The overall pattern of calling during different activities (most calling during flying and watching) suggests that the function of calling may be to do with group cohesion – individuals signalling their whereabouts if they are stationary and hidden in the canopy – and transfer of information when flying around the roost site.

Further study

Although extensive work has been carried out on the social behaviour of Bornean and African savannah hornbills (e.g. Leighton, 1986), there is little in the literature on *Ceratogymna* and other African rainforest hornbills. Since different hornbill genera have distinct patterns of behaviour, e.g. territoriality (Fry *et al*., 1993), it would be valuable to carry out a long term study on the social behaviour of this genus. A comparison of social patterns of different genera in different habitats and continents could give valuable information about the evolution of sociality. There is also much in the literature about avian communication, but most of this work has concentrated on passerines. It would therefore be useful to supplement the study of hornbill calling with investigation into the calling behaviour of other non-passerine bird families.

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