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Vocal Coordination of Group Movement by Green Woodhoopoes (*Phoeniculus purpureus*)

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Abstract

Communication signals are used by many species to maintain group cohesion when moving over larger areas. Groups of green woodhoopoes (*Phoeniculus purpureus*) generally move around their territory as a close-knit unit. Dominant individuals were more likely than subordinates to initiate movement to a new foraging site, but there was no intersexual difference. Dominants were also more likely than subordinates to be followed immediately. Vocalizations were shown to play an important role in mobilization: in the thick forests inhabited by woodhoopoes, visual cues to coordinate movement are likely to be less successful. When responding to the rallying call of a neighboring group, dominants and subordinates were equally likely to lead, as were males and females. As other group members followed immediately on most of these occasions, vocalizations were less important in this context than when moving to a new foraging site.

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Introduction

There are many advantages to living in a group (Alexander 1974; Krause & Ruxton 2002), but they generally accrue only when group members remain in close proximity. When groups are not tied to a specific location, such as a nesting colony, but are forced by predation risks or foraging requirements to move over large areas, mechanisms for maintaining group cohesion are required (Bradbury & Vehrencamp 1998). Flocks of birds and mammals feeding on scattered food resources, for example, face the difficulty of continually staying together while individuals hunt for food items. Group members are usually somewhat spread out and hidden by vegetation. Communication signals are needed to steer the direction of travel towards known food patches and prevent stragglers from getting lost. The exact signals used to coordinate group movement vary, depending on the reason for grouping, the precision of

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movement required and the mode of locomotion (Powell 1979; Black 1988; Boinski et al. 1994). In a wide variety of species, there is a specific initiation call used to lead group movements in a particular direction (Milton 1980; Boinski 1991; Boinski et al. 1994).

Depending on the species and the context, individuals of different sex and dominance status have been shown to initiate group movement. In ungulates, for example, a relationship between leadership and dominance status has been found in some studies (e.g. Squires & Daws 1975; Stine et al. 1982), but not in others (e.g. Beilharz & Melrea 1963; Reinhardt 1983). In several primates, leaders belong exclusively to one particular social class (e.g. adult males or adult females) and are usually high ranking (e.g. Kummer 1968; Rowell 1972; Dunbar 1983; Norton 1986). However, differences may exist within species. For example, in one population of white-faced capuchins (*Cebus capucinus*), no specific age-sex class appeared pre-eminent in coordinating or determining travel (Boinski & Campbell 1995), while in another area, adult females were more likely than males to initiate troop movement (Boinski 1993). Attempts to coordinate group movement are not always successful (Boinski 1991, 1993; Boinski et al. 1994): among white-faced capuchins, for example, there was a perfect concordance of relative rank and the number and rate of successful attempts to direct troop movement (Boinski 1993), with even alpha males failing to initiate a response on some occasions (Boinski & Campbell 1995).

Many studies of signalling and coordinated group movement have looked at flocking birds and their pre-flight behavior (Raveling 1969; Black 1988). Among social species, most of the current information on mechanisms of travel coordination comes from primates (e.g. Boinski 1993). The highly vocal green (or red-billed) woodhoopoe (*Phoeniculus purpureus*) offers an excellent opportunity to investigate these issues in a cooperatively breeding bird species. Groups contain a single breeding pair and up to 10 non-breeding helpers that participate in all group activities (Ligon & Ligon 1978). Each group tends to forage as a close-knit unit (Radford & du Plessis 2003) and all individuals are present during territorial interactions with other groups (Radford in press). Group members, therefore, tend to spend the majority of their time moving around their territory together. Both sexes may remain on their natal territory to help (Ligon & Ligon 1978), and the strict queuing system for breeding positions results in a linear dominance hierarchy, with breeders dominating non-breeding helpers. Consequently, several individuals of the same sex, but different dominance status, are often present in the same group and available to lead it.

I studied the initiation of group movement in two situations. First, when groups moved from one foraging area to another and, secondly, when a group moved towards its territory boundary in response to the calling of a neighboring group. I investigated: (1) whether particular categories of individual always instigated movement; (2) the importance of vocalizations; and (3) the response of individuals that were not immediately followed.

Methods

Data Collection

I conducted the study in a 33-km^2 area near Morgan's Bay (32°43′S, 28°19′E), Eastern Cape Province, South Africa, between November 1999 and March 2002. Green woodhoopoes in this area inhabit riverine forest, which forms belts along river valleys (Du Plessis 1989a). Territories (mean ± SE size: 23.5 ± 1.7 ha) (Radford & du Plessis in press) are linearly arranged along the river courses. All breeding and roosting, together with the majority of foraging, occurs within a group's territory.

Birds were caught in nets placed over roost holes before dawn, and marked with an individual combination of color rings and an aluminum SAFRING ring bearing a unique number. Individuals could be sexed on the basis of bill length (Radford & du Plessis 2003) or vocalizations (Ligon & Ligon 1990). Breeders tend to be those individuals of each sex that have been in the group the longest (own data). When this information was not known, breeding status was established by watching displacement activity during group foraging, when breeding individuals dominate non-breeding helpers (Radford & du Plessis 2003). Here, I refer to breeders as 'dominants', while 'subordinate' encompasses all non-breeding adult helpers.

I collected data on movements around the territory during the non-breeding season, when all group members were present and there was no complication due to males following females for mating opportunities or mate guarding (Birkhead 1982; Davies 1985). When a group was foraging, I noted the sex and dominance status of the first individual to move at least 30 m in one flight (which was further than the normal sphere of a foraging group, pers. obs.) and whether or not it gave a cackling call. Green woodhoopoes make a variety of calls, but most are based on a simple 'kek' element (Radford 2002). This kek element is often produced at a rate of $< 1/s$, when its likely function is as a contact call during group foraging. However, the kek also forms the basis of cackling calls (when keks are given at approx. 12/s). Cackles given while perched tend to function as alarm calls or form the basis of displays to other groups, while those given in flight are probably used to attract the attention of members of the same group.

An 'immediate response' was recorded if at least one other group member followed the leaving bird within 5 s. On 92% of these occasions (own data), all remaining group members left within 5 s of the second bird to leave. As this paper is concerned with the coordination of group movement, I do not consider the 8% of occasions when some of the group remained behind. If the leaving bird was not followed immediately, I noted whether it continued alone or returned to the rest of the group, and whether it did so silently or while cackling. Birds that did not return to the group within 3 min of leaving were classified as having continued alone.

Green woodhoopoes often produce a vocal rallying display, when all individuals in a group cackle loudly together (Ligon & Ligon 1978). These rallies may be given in isolation or as part of territorial interactions (Radford in press) and can be heard up to 1 km away (pers. obs.). If a neighboring group had been heard rallying in the preceding minute, and the first individual to leave flew towards that neighbor's territory, the movement was classed as 'territory defense'. If no rallying had been heard, the movement of the leaving individual was classed as 'foraging'. I discounted situations where the rally of a neighboring group was heard, but the leaving individual moved in a different direction. I collected no data in the hour before dusk, when birds were likely to be moving towards roost cavities (pers. obs.). To minimize non-independence of observations, I recorded only one movement per group per day.

Statistical Analysis

Data were available from a total of 82 individuals in 26 groups (group size: 2–8), although sample sizes vary for different analyses depending on the number of individuals of the relevant category. As the proportion of times a particular individual led the group is influenced by group size, these proportions were multiplied by group size before analysis. All other proportional data were arcsine square-root transformed to enable parametric testing. A residual maximum-likelihood (REML) analysis showed no significant effect of the random factor 'group' on the sex or dominance status of the first individual to leave a group. Consequently, it was possible to use an ANOVA to assess their importance. A weighted regression was used when analyzing the effect of group size because there were different numbers of groups of each size. Statistical tests were two-tailed and significance was established at $p < 0.05$.

Results

Movement to a New Foraging Site

Dominant individuals were significantly more likely than subordinates to instigate movement to a new foraging site (ANOVA on converted proportions: $F_{1,79} = 167.50$, $p < 0.001$), but there was no significant difference between the sexes ($F_{1,79} = 0.05$, $p = 0.819$).

In larger groups, there was a greater chance that another individual would follow the first bird to leave (weighted regression: $F_{1,76} = 4.63$, $p = 0.035$). After controlling for this group-size effect, dominants were significantly more likely than subordinates to be followed (ANOVA: $F_{1,70} = 49.71$, $p < 0.001$) (Fig. 1), as were males compared with females ($F_{1,70} = 8.83$, $p = 0.004$).

An individual leaving the group was significantly more likely to be followed if it vocalized, rather than remained silent (paired t-test for dominants: $t_{25} = 4.98$, $p < 0.001$; subordinates: $t_{16} = 4.52$, $p < 0.001$) (Fig. 2). Considering only those occasions when individuals vocalized on leaving, there was no significant difference in the likelihood of dominants and subordinates being followed (two-sample t-test: $t_{41} = 1.03$, $p = 0.310$) (Fig. 2). Dominant individuals were no more likely than subordinates to produce a vocalization when leaving the group (two-sample t-test: $t_{74} = 0.14$, $p = 0.890$). Consequently, dominants were more likely than subordinates to be followed immediately because they were more likely

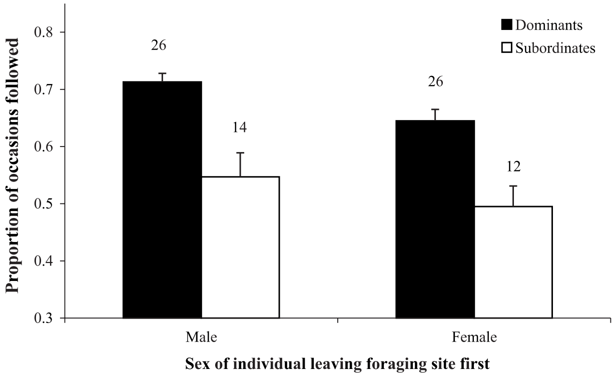

Fig. 1: Likelihood that the first individual leaving a foraging group was immediately (within 5 s) followed by another group member. Shown are means + SE, with sample sizes above the bars

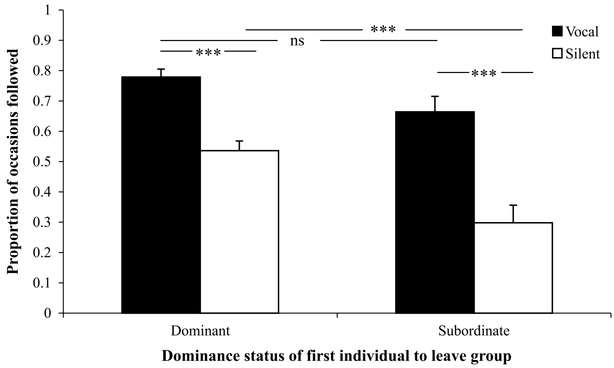

Fig. 2: Influence of vocalizations on the likelihood that an individual leaving a foraging group was immediately (within 5 s) followed by another member of the group. Shown are means + SE. n = dominant individuals from 26 groups, subordinates from 17 groups. ns = not significant, ***$p < 0.001$ (for details see text)

to be followed when leaving silently (two-sample t-test: $t_{41} = 3.56$, $p < 0.001$) (Fig. 2).

If an individual left a foraging group and was not followed, it had four choices: to proceed to the next foraging site alone, either silently or while vocalizing, or to return to the foraging group, again either silently or while vocalizing. In the majority of cases (87%), however, individuals either continued silently or returned and vocalized. The following analysis therefore concentrates on these two options. When dominant individuals were not followed, they were significantly more likely to return and vocalize than to continue silently alone, irrespective of whether they had initially called (binomial test: $Z = 7.60$, $p < 0.001$) (Fig. 3) or not ($Z = 4.24$, $p < 0.001$). Subordinates that called on first leaving were also significantly more likely to return and vocalize again

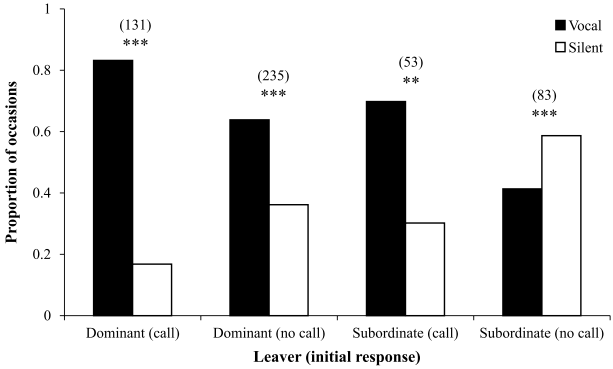

Fig. 3: Response of individuals to leaving a foraging group and not being immediately (within 5 s) followed: either returning and vocalizing (vocal) or continuing silently and alone (silent). n = dominant individuals from 26 groups, subordinates from 20 groups. Shown are overall proportions for each category, with the total number of events shown in parentheses. **$p < 0.01$, ***$p < 0.001$ (for details see text)

(binomial test: $Z = 2.83$, $p < 0.01$). However, if a subordinate left without calling and was not followed, it was significantly more likely to continue alone and silently, rather than return to the group (binomial test: $Z = 4.56$, $p < 0.001$).

Movement Towards a Neighboring Group

There was no significant difference between the sexes (ANOVA on converted proportions: $F_{1,60} = 1.29$, $p = 0.260$) or between individuals of different dominance status ($F_{1,60} = 0.43$, $p = 0.515$) in the proportion of times that they led the group towards a vocalizing neighboring group. Subordinate individuals led a greater proportion of the time in this situation than when moving to a new foraging site (paired t-test: $t_{20} = 3.88$, $p < 0.001$), whereas dominants led less often (paired t-test: $t_{41} = 2.85$, $p = 0.007$).

After controlling for group size, there was no significant difference between the sexes (ANOVA: $F_{1,55} = 2.13$, $p = 0.150$) or between individuals of different dominance status ($F_{1,55} = 0.20$, $p = 0.657$) in the proportion of times they were followed, perhaps because overall the leaver was followed on 90% of occasions. Calling and silent leavers did not differ significantly in their likelihood of being followed (paired t-test: $t_{50} = 1.31$, $p = 0.197$).

Discussion

Foraging Movements

Green woodhoopoes often vocalized when leaving a group for a new foraging site, thus advertising their departure and attracting the attention of other group members. Calling is an efficient signal for the coordination of group movement within a dense, forest habitat, where members of the group may be separated by several meters while foraging. Initiation movements or other visual displays found in some terrestrial species (Kummer 1968; Rowell 1972) are unlikely to be reliable cues when lines of sight are obscured. Vocalizing individuals were more likely than silent leavers to be followed immediately, presumably because their intentions were known to the rest of the group. Evans (1982) found that the contact call performed by black-billed gulls (*Larus bulleri*) was effective in attracting flock members to follow, and that birds initiating departure produced more calls than followers.

Vocal advertisement suggests that the leader derives some net benefit from having others present when leaving, since presumably it would be easy to forego calling if recruiting others were not advantageous. This benefit may involve reduced individual predation risk (Hamilton 1971; Bednekoff & Lima 1998) or there may be territorial-defense benefits to moving as a cohesive unit (Radford 2002). However, the potential gains will differ between individuals. Dominant birds are expected to benefit from being in a group, as they still gain the best feeding sites (Radford & du Plessis 2003), while presumably experiencing a decreased predation risk. It is unsurprising, therefore, that on occasions when they were not immediately followed, they tended to return to the group and attempt once more to initiate its movement. For subordinates, however, there may be a trade-off between predation risk and foraging efficiency. While in a group, predation may be reduced, but foraging success is lowered, and hence subordinates benefit from foraging alone on some occasions (Radford & du Plessis 2003). Thus, when they left the group silently and were not immediately followed, they foraged alone for a while, without interference from dominant members of the group. If the subordinate individual was not attempting to lead the group but to temporarily ‘escape’ from it, this would explain the lack of calling. As the group always reunited, it must either follow well-known routes or, perhaps more likely, the subordinate must have relocated the remainder of the group by listening for its vocalizations.

Dominant green woodhoopoes led the group more frequently than subordinates, as was also found by Du Plessis (1989b). Given the sequential queuing system for breeding vacancies that operates in this species, with queue position determined by the length of time spent in the group, individuals reaching breeding status have usually been in the territory longer than other group members. Dominant birds may, therefore, have the greatest knowledge of the territory and its most profitable foraging areas. It would be interesting to investigate which individuals lead most often when a breeding vacancy is filled from outside the group: perhaps the new breeder does not lead until it has learnt the characteristics of the territory. Among primates, higher-ranking individuals also tend to lead the group more frequently than subordinates (Boinski 1993). However, in some of these cases, the temporal integrity of the unit is dependent on active herding by the male (e.g. Kummer 1968), which is not seen here.

In some species, one sex may initiate group movement far more frequently than the other. In gelada baboons (*Theropithecus gelada*), for example, individual females exert a considerable degree of control over the spatial integration of the troop (Dunbar 1983). In the green woodhoopoe, however, males and females led groups on a similar proportion of occasions. This may be because, unlike in many cooperatively breeding bird species where one sex disperses and the other stays behind to help (Stacey & Koenig 1990), both male and female woodhoopoes may remain in their natal territory (Ligon & Ligon 1990).

Defensive Movements

Territorial vocal-rallying contests may occur several times a day between the same two neighboring groups of green woodhoopoes (Radford in press). These contests may serve to inform rival groups of potential breeding vacancies or they may be the prelude to a temporary territorial intrusion (Radford 2002). Thus, if a neighboring group is heard near the shared territory boundary, the resident group often flies in that direction to try and prevent an intrusion. In many cooperatively breeding species, including the Tasmanian native hen (*Gallinula mortierii*) (Putland & Goldizen 1998) and the white-browed sparrow-weaver (*Plocepasser mahali*) (Wingfield & Lewis 1993), territorial behavior is led by the dominant pair, with helpers providing support. In the green woodhoopoe, however, there is a tendency for subordinates to expend more effort than dominants in defense (Radford in press), perhaps because they would have more to lose as a result of foraging competition were extra group members added (Radford & du Plessis 2003). This might explain why subordinates led more frequently in this situation than when the group moved to a new foraging site. Alternatively, all individuals may have been responding directly to the neighboring group's rally and it was simply a matter of chance which bird flew first. Certainly, in most cases, the first leaver was followed almost immediately by all other group members, thus explaining the reduced importance of vocalizations compared with when heading for a new foraging site.

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