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Group-specific vocal signatures and neighbour–stranger discrimination in the cooperatively breeding green woodhoopoe

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Group displays involving vocal choruses are a prominent feature of many avian cooperative-breeding systems. The existence of group-specific vocal signatures within these choruses could assist territory owners when assessing the threat posed by different intruding groups. To investigate the possible presence of such signatures, I examined the choruses ('rallies') given by 22 green woodhoopoe, *Phoeniculus purpureus*, groups over two consecutive seasons. A rally involved the combined cackling of adult group members. Statistical analysis of midrally vocalizations, when all group members were calling, revealed that samples from the same group clustered in principal coordinate space, and the group clusters segregated from each other to a significant degree. This segregation might theoretically arise from differences in group size and sex ratio, especially since the vocalizations are sexually dimorphic. However, groups containing the same numbers of males and females had rallies that were significantly different acoustically. Groups that maintained the same composition of individuals produced acoustically similar rallies across seasons, while those that changed membership produced significantly different rallies. The group signature is therefore most likely to result from group members producing their own individual vocal programmes, but participating in a similar way for every rally. In a playback experiment, groups responded significantly more rapidly to strangers and to neighbours on the wrong boundary than to neighbours in their expected place. Woodhoopoes therefore appeared capable of distinguishing between groups on the basis of their vocal signatures, representing the first evidence of the 'dear-enemy' phenomenon in a group-living species.

Individuals of many species respond more aggressively to territorial intrusions by nonneighbours (strangers) than to those by their territorial neighbours (Temeles 1994). This 'dear-enemy' phenomenon (as defined by Fisher 1954) has been suggested to occur either because (1) owners stand to lose more to strangers (e.g. both their territory and their mate) than to neighbours (e.g. just their mate; Getty 1987; Temeles 1994), or because (2) owners are more familiar with their neighbours, and hence are less likely to make role mistakes in contests (Ydenberg et al. 1988) and/or have little to learn about their opponent (Getty 1989). A comparative study indicated that hypotheses based upon the relative threat posed by neighbours and strangers have better explanatory value (Temeles 1994). Theoretically, group-living territorial species would also benefit from the discrimination of neighbouring and strange groups that present different threats, but this possibility has never been investigated.

Successful discrimination of neighbours and strangers requires the existence of a reliable indicator of identity (Stoddard 1996). Many bird species use acoustic cues to distinguish between individuals (Falls 1982; Halpin 1991; Dhondt & Lambrechts 1992; Komdeur & Hatchwell 1999), and several studies have shown that individuals in temporary (e.g. Mammen & Nowicki 1981) and permanent (e.g. Brown et al. 1991) groups have similar vocalizations, providing an indicator of group membership. Among avian cooperative breeders, there are also many examples of group-territorial displays involving the combined chorusing of several individuals (e.g. Robinson 1985; Reyer & Schmidl 1988; Curry & Grant

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1990; Brown & Farabaugh 1991; Wingfield & Lewis 1993; Seddon & Tobias 2003). Preliminary evidence suggests that such choruses may themselves include a group-specific vocal signature (Baker 2004), providing a potential way of distinguishing between groups. However, this possibility has not yet been tested in detail.

The green woodhoopoe, *Phoeniculus purpureus*, is an excellent species in which to investigate the potential existence of group-specific vocal signatures and neighbour–stranger discrimination: territorial contests occur several times per day and involve obvious vocal chorusing displays (Radford 2003), or 'rallies' (as defined by Ligon & Ligon 1978). All adults in one group cackle loudly together, while rocking back and forth, and then the opposing group responds in similar fashion (Ligon & Ligon 1978; Radford 2003). Contests may last for up to 45 min, with groups giving rallies alternately (Radford & du Plessis 2004a). Rallies carry important information about group size and composition (Radford 2003), and information about group identity and location would assist in the assessment of rival groups during territorial conflicts. The first question addressed in this study was therefore whether the vocal rallies of green woodhoopoes contain a group-specific signature.

In South Africa, groups of 2–12 woodhoopoes defend exclusive areas of riverine forest throughout the year (Radford & du Plessis 2004b). Each group roosts communally in a cavity every night (Ligon & Ligon 1990), and roost holes are probably the critical resource in determining the spacing of groups (du Plessis 1992). Since roost holes provide vital thermoregulatory benefits (du Plessis & Williams 1994) and/or antipredator benefits (Ligon & Ligon 1978), territory defence from potential usurpers is likely to be crucial for survival. Disputes between groups occur when one trespasses into the territory of another, or when two neighbouring groups meet along their common border. When a group intrudes on to a neighbouring territory and wins the ensuing vocal contest, it forages and examines roost holes for up to an hour (Radford & du Plessis 2004a). However, the intruding group then returns to its own territory and there are no permanent changes in the territory boundaries (Radford & du Plessis 2004b). In contrast, groups have been known to lose their territories permanently to strangers from further afield (Ligon & Ligon 1990). Thus, neighbouring and strange groups present different threats in terms of potential territory loss. The second question addressed in this study was therefore whether woodhoopoes distinguish between groups on the basis of vocal cues and thus respond differently to neighbours and strangers. This is the first test of the dear-enemy phenomenon in a group-living species.

METHODS

Study Site and Species

Field work was carried out near Morgan's Bay (32°43′S, 28°19′E), Eastern Cape Province, South Africa, from November to May in both 1999–2000 and 2000–2001. Green woodhoopoes often produce a resonant cackling 'kek-ek-ek-ek' call, at a rate of ca. 12 keks/s. This call may be given by a single individual, but as soon as one bird starts, other group members often join in. The resulting assembly is termed a 'rally' (Ligon & Ligon 1978). All adult group members (> 11 months since fledging; nestling period lasts 1 month; Ligon & Ligon 1978) generally participate in rallies, but recently fledged juveniles (within 3 months of fledging) do not contribute at all (Radford 2003). In the present study, group sizes therefore refer to the number of adult group members (range 2–6, $N = 26$ groups of colour-ringed woodhoopoes). Juveniles were identified by their predominantly black bills (Ligon & Ligon 1978). Adults could be sexed from their bill length (Radford & du Plessis 2003) and vocalizations (Radford 2004).

Woodhoopoe territories at the study site are generally arranged linearly along river courses, where the forests are concentrated (Radford & du Plessis 2004b). Forested areas are separated by open grassland, which is rarely used by the birds. Thus, each territory tends to border only two others directly. Competing groups may be up to 30 m apart and obscured from one another by thick vegetation, making acoustic cues more useful than visual ones.

Sound Recordings

I recorded rallies from each study group opportunistically on 60-min TDK tapes, using a Sennheiser MKH416T microphone (with windshield) and a WM-D6C Sony Professional Walkman. Recordings were made within 5–15 m of the group, from 0600 to 1000 hours and from 1500 to 1900 hours, when the birds were most vocally active (personal observation). Any rallies distorted by background noise or by overlap with the rallying of another group were discarded. I randomly selected five suitable rallies from each group in each season for analysis. Selected rallies from a particular season had been recorded 3–4 weeks apart.

Rallies varied in duration from 4 to 19 s (Radford 2003). It is impossible to determine from spectrograms the contribution of individual woodhoopoes, so analyses focused on the calling of the group as a whole. I selected the central 1-s segment from each rally because this was when all adult group members were vocalizing (when I recorded rallies, I could identify vocalizing individuals from their bill movements). I created digital sound files from the tapes by sampling at 44.1 kHz with 16-bit accuracy, and the 1-s segments were high-pass filtered at a 300-Hz cutoff. Spectrograms (Fig. 1) were generated (fast Fourier transformation of 1024 points, time resolution of 3 ms, 50% overlap and Hamming window) with CANARY version 1.2 (Charif et al. 1995). The use of a 1024-point fast Fourier transform length resulted in the expected time–frequency features, as judged through visual inspection, and produced the level of spectrogram structure most suitable for call comparison (Cortopassi & Bradbury 2000).

Samples were compared by spectrographic cross-correlation (SPCC) on normalized amplitude values (Clark et al. 1987). This method cross-correlates two spectrograms frame by frame in the time–frequency domains,

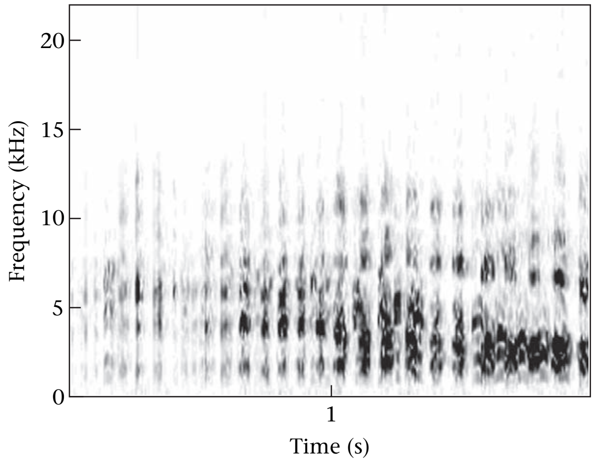

Figure 1. Spectrogram depicting the midrally segment of a group of four green woodhoopoes (two males and two females).

comparing them as matrices (time × frequency) of amplitude measurements. Thus, a matrix of amplitude values from one spectrogram is incrementally overlapped along the time axis with the matrix from another spectrogram. SPCC calculates a correlation coefficient at each increment of overlap and records a peak value where the two matrices are most similar, which represents the best match between the two sounds. The aim of SPCC analysis is to consider all measurable spectrographic features rather than confining the comparison to a preselected and potentially incomplete set of variables.

Batch processing in CANARY produces a triangular matrix of correlation coefficients between all pairs of sound spectrograms. This SPCC matrix of similarity (S) values was converted to a matrix of distance (D) coefficients by the transformation $D = (1 - S)^{0.5}$ (Legendre & Legendre 1998). The correlation matrix of distance values was evaluated by principal coordinates analysis (PCoA; Legendre & Legendre 1998), using R-Package software, version 4 (Casgrain & Legendre 2001). PCoA ordinates the distance values in multidimensional space, providing coordinate values (eigenvectors) that position the sound in reduced space. SPCC combined with PCoA provides not only visual groupings of sounds, but also a set of independent measures against which the association of extrinsic contextual variables (such as group identity) can be measured. The combination of SPCC and PCoA is robust in its ability to separate the effects of shared time–frequency patterns from those of duration, noise and harmonic variation (Cortopassi & Bradbury 2000), and the general approach used here mirrors that of previous studies for the comparative analysis of complex broadband sounds (e.g. Cortopassi & Bradbury 2000; Baker 2004).

Initial analysis, to assess quantitatively the vocal similarity of rallies recorded from each woodhoopoe group and those from different groups, focused on the five rallies recorded from each of the 22 groups that retained the same composition of adult individuals throughout the 1999–2000 season. I performed a stepwise discriminant function analysis (DFA) on the first five eigenvalues from PCoA. DFA provides a classification procedure that assigns each rally to its appropriate group (correct assignment) or another (incorrect assignment) by comparing the multivariate pattern resulting from any interaction of the variables. To illustrate the acoustic clustering pattern visually, in two dimensions, I plotted the first two discriminant functions. The discriminant functions are essentially linear transformations of the principal coordinates, with similar calls being maximally clustered. Intergroup differences may arise from differences in group size and/or sex ratio, especially since green woodhoopoes have sexually dimorphic vocalizations (Radford 2004). To control for this, I ran another DFA on the five rallies recorded from each of six groups having the same size and sex ratio (two males and one female).

I then investigated the effect of a change in group composition on rally acoustic structure. Analysis focused on the 10 groups that retained the same composition of adult individuals between the two field seasons and the 10 that altered composition by one member (i.e. gained or lost one member, or had one member replaced). In both cases, I used a DFA to assess how many of the five rallies recorded from each group in 2000–2001 could be correctly assigned to groups on the basis of their rallies from 1999–2000. I compared the number of correct and incorrect assignments from the two group types (unchanged and changed membership) using a chi-square test.

Playback Experiment

To investigate the possibility of neighbour–stranger discrimination on the basis of acoustic cues, I used a playback experiment to generate controlled artificial contests between groups of woodhoopoes. I constructed playback loops by editing recordings of rallies using Cool Edit 96 (Syntrillium Software Corporation, Scottsdale, AZ, U.S.A.). No loop was used more than once, thus avoiding pseudoreplication. Twenty groups having at least one adjoining neighbouring group were each presented with three trials. One trial consisted of a rally from a neighbouring group on the expected territory boundary. Another trial used a rally from the same neighbouring group, but played on the opposite ('wrong') boundary. Territory boundaries were established from the frequent plotting of groups' positions and activities (Radford & du Plessis 2004b). A third trial consisted of a rally from an unfamiliar group (one from at least three territories away from the focal group), of the same size and sex ratio as the neighbouring group featured in the other two trials, and played on the same boundary as the first trial. All playback trials to a particular group were of the same duration ($\overline{X} \pm SD = 6.8 \pm 1.1$ s, range 5.7–9.8 s; Radford 2003). Trials were conducted from March to May in 2000. By this period, the breeding season had finished and all group members tended to move around their territory together. The same group was presented with all trials at approximately the same time of day. The order of trial presentation was randomized, and playbacks to the same group were always separated by 7–14 days to minimize habituation. The observer was not blind to the trial being conducted.

In each trial, a single rally was played from a Sony SRS-A35 loudspeaker placed 2 m high in a tree about 20 m from the trial group. Only one speaker was used because group members tend to rally from within 1 m of one another. Groups were required to be foraging and silent (except for contact calls) for at least 5 min before the start of playback. Since woodhoopoes generally respond either within 90 s (83% of natural observations, $N = 587$) or not at all (12% of observations) to the rallying of another group on their territory boundary, I abandoned the trial if no rally had been given after 90 s. All behavioural responses were recorded on a dictaphone, and the initial response rally was recorded as described above.

I measured the following variables assumed to reflect aggression by the subjects: (1) response latency (time until a response rally was given); (2) duration of the first response rally; (3) rally rate (average number of syllables/s within the first response rally); and (4) number of individuals contributing to the group's first response rally. I also estimated the closest approach distance of the group to the speaker. I measured only parameters from the first response rally, because subsequent vocalizations are likely to be influenced by within- and between-group dynamics (Radford & du Plessis 2004a).

Principal component analysis has been recommended as a method of quantifying responses to playback that is complementary to a many-measures approach (McGregor 1992). However, because the variables were not strongly correlated (coefficient = 0.12 ± 0.03, range 0.03–0.22), I used individual Friedman tests to investigate the effects of playback trial on each response measure separately. Only groups that responded to all three trials were included in the analysis. Multiple comparison tests were then used to ascertain whether there were significant differences between pairs of trials. Sequential Bonferroni corrections, with an initial alpha value of 0.01, were applied because multiple comparisons were made with the same data set (Rice 1989). Analyses were performed using SPSS version 11.5 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Group Signatures

Following SPCC, a Shephard plot of the values of all pairwise comparisons showed that the representation of the data in reduced space retained the Euclidean relationships of the initial multidimensional space (Legendre & Legendre 1998). None of the eigenvalues extracted by PCoA were negative, so no correction was needed. The first five eigenvalues explained 64.4% of the variance in the data. There was distinct separation of the rallies produced by the 22 woodhoopoe groups in 1999–2000 (DFA: Wilk's lambda = 0.002, $F_{42,174} = 102.01$, $P < 0.001$); 84.5% (93 of 110) were correctly assigned to the group from which they were recorded. Rallies from the same group tended to cluster in principal coordinate space (Fig. 2). When considering only the six groups with the same size and sex ratio, there was still a significant separation in terms of their rallies (DFA: Wilk's lambda = 0.028, $F_{5,24} = 166.62$, $P < 0.001$; Fig. 3); 86.7% (26 of 30) were assigned to the correct groups.

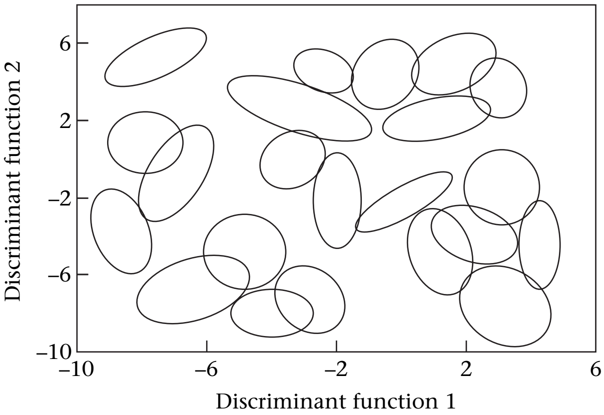

Figure 2. Comparison of rallies produced by 22 green woodhoopoe groups. Each ellipse represents the spread of values obtained from the five rallies analysed for each group. Values of discriminant functions 1 and 2 were derived from discriminant function analysis of five eigenvectors generated by principal coordinates analysis of spectrogram cross-correlation values.

There was a significant difference in the likelihood that rallies recorded in 2000–2001 would be correctly assigned to groups on the basis of the 1999–2000 rallies, depending on whether the group's membership had changed (chi-square test: $\chi^2_1 = 36.95$, $P < 0.001$). For groups retaining the same composition between seasons, 44 of 50 rallies (88%) were correctly assigned to the 1999–2000 groupings. However, only 14 of 50 rallies (28%) recorded in 2000–2001 from groups that had changed in composition by one group member were correctly assigned.

Playback Experiment

The latency to a vocal response differed significantly depending on the playback trial (Table 1, Fig. 4). Groups

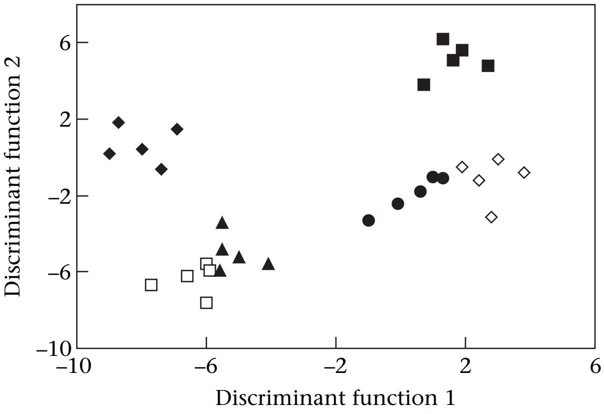

Figure 3. Scatterplot of samples from five rallies given by each of six green woodhoopoe groups of the same size and sex ratio (two males and one female). Values of discriminant functions 1 and 2 were derived from discriminant function analysis of five eigenvectors generated by principal coordinates analysis of spectrogram cross-correlation values. Each symbol represents a different group.

Table 1. Results of a playback experiment testing the response of green woodhoopoe groups to a simulated intrusion by neighbouring and strange groups ($N = 18$ groups)

	Playback group				
Response variable	Neighbour correct boundary	Neighbour wrong boundary	Stranger	χ^2_2	*P*
Latency (s)	42.8±4.5	33.2±2.1	27.3±2.1	10.11	**0.006**
Closest distance (m)	15.0±1.7	8.5±1.8	9.8±1.7	7.52	0.023
Rate (syllables/s)	12.6±0.3	12.3±0.2	12.7±0.3	4.33	0.115
Rally length (s)	8.2±0.5	8.0±0.5	8.2±0.4	0.78	0.678
Proportion of group contributing	0.93±0.03	0.96±0.04	0.95±0.03	0.63	0.729

Means are shown ±SE. χ^2 values are from Friedman tests. *P* value in bold was significant after sequential Bonferroni correction.

responded significantly less rapidly to neighbouring groups on the expected boundary than to neighbours on the wrong boundary (multiple comparison test: $P < 0.05$) and strangers ($P < 0.05$). There was no significant difference in response time to neighbours in the wrong place and strangers.

There was also a strong trend for a closer approach distance to neighbours on the wrong boundary and strangers than to neighbours on the expected boundary, although the difference was not significant after Bonferroni correction (Table 1). Following the playback of a neighbour on the correct boundary, the group usually rallied from their current position (16/18 occasions). This result differed significantly from the response to either a neighbour on the wrong boundary (9/18) or a strange group (7/18; *G* test: $G_2 = 6.92$, $P < 0.05$), when the focal group often flew over the speaker before rallying. There was no significant difference in group rally duration, rally rate or the proportion of group members participating in response to the three playback trials (Table 1).

DISCUSSION

Group-specific Signatures

The results indicate that the rallying calls of different woodhoopoe groups are acoustically distinct. Furthermore, the acoustic nature of a particular group's rallying seemed highly consistent across time, providing the group retained the same composition of individuals. Some of the variation between groups may result from differences in size and sex ratio (Radford 2003). However, groups having the same size and sex ratio were still acoustically distinct, suggesting that rallies include a group-specific vocal signature independent of these factors. Although much research has been conducted on individual and kin recognition in birds (reviewed in Komdeur & Hatchwell 1999), only recently has there been any evidence of a vocal signature within the combined chorusing of a cooperatively breeding species (the laughing kookaburra, *Dacelo novaeguineae*; Baker 2004). Baker (2004) offered only preliminary evidence, however; calls were recorded on 2 consecutive days from eight different groups, and no account was taken of differences in group size or sex ratio. The current study provides a more comprehensive analysis of the evidence for group-specific vocal signatures.

There are several ways in which a group might produce an acoustically unique vocal signature. First, developmentally fixed vocal patterns may be inherited from the parent breeders, which differ genetically from group to group. In the case of the laughing kookaburra, nonbreeding group members are retained offspring (Legge & Cockburn 2000), so if genetic variation causes vocal variation, group differences in acoustic features could simply be heritable differences. This is unlikely to be the whole explanation in the green woodhoopoe, however, because up to 10% of helpers are unrelated to other group members, having immigrated into a new group even when no breeding vacancy was available (Ligon & Ligon 1990).

Second, groups could maintain distinct signatures if there was convergence on the vocal characteristics of a particular individual in the group, and the vocal pattern of these individuals differed between groups, or if group members converged on a common call that differed between groups. In some oscines and parrots, for example, members of stable flocks of nonrelatives develop group-specific contact calls and discriminate these calls from those of other flocks (Mammen & Nowicki 1981; Farabaugh & Dooling 1996). In these cases, the ability to

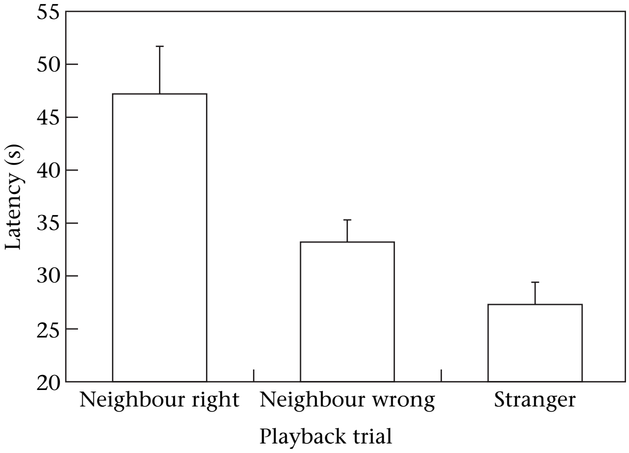

Figure 4. Mean ± SE latency (s) to vocal response of 18 green woodhoopoe groups presented with playbacks of a single rally from a neighbouring group on the expected territory boundary (neighbour right), the same neighbouring group on the opposite boundary (neighbour wrong) and a strange group of the same size and composition as the neighbour (stranger).

distinguish flock members from nonmembers could facilitate territory defence and help maintain a cohesive flock structure. Imitation may also serve as a mechanism for integrating new members into the flock. Such possibilities are also likely in cooperatively breeding species with long-term associations between individuals. A substantial share of laugh choruses in kookaburra groups are initiated by the dominant breeding pair (Higgins 1999), which raises the possibility of convergence by the group towards the vocalizations of these individuals. Furthermore, kookaburras seem to receive 'laughing lessons'; fledglings imitate adult group members and improve over a period of 2 weeks (Baker 2004). In woodhoopoes, however, the situation is less clear. Although adults cackle directly at nestlings in the final few days before fledging (personal observation), perhaps teaching them the group's call structure, fledglings do not themselves start cackling until at least 2 weeks later (unpublished data). Thus, fledglings are likely to have heard other groups in addition to their own before producing the relevant vocalization for the first time. Furthermore, because different individuals lead the rallying on different occasions (Radford 2003), there is no consistent model from which to learn. Finally, when group membership changes, the acoustic nature of the rallying also changes, suggesting a lack of convergence by individuals.

Third, birds in the group could each produce their own individual vocal programmes, but participate in a similar way for each chorus. This is perhaps the most likely explanation in woodhoopoes, given the significant change in a group's vocal signature following a change in group composition. All adult group members certainly participate in the vast majority (94%) of rallies (Radford 2003), but without video analysis it is impossible to know for sure whether they are contributing in the same way each time. It would be interesting to compare the changes that occur when groups gain or lose a member with those that occur when an individual is replaced. However, sample sizes were too small for such an analysis in the current study.

From spectrograms alone, it is impossible to determine the individual contributions of even two woodhoopoes of the same sex (see also Reyer & Schmidl 1988). The technological problem of sorting out vocal contributions of three or more group members remains formidable. This study could not, therefore, distinguish between the alternative explanations for the production of group-specific vocal signatures, but the combined calling of the group does appear to be important.

Neighbour–Stranger Discrimination

Experimental playback provided some evidence for the dear-enemy phenomenon (Fisher 1954) in the green woodhoopoe: groups responded more rapidly to simulated intrusions by strangers than to neighbours. This result implies that discrimination between groups is possible on the basis of acoustic cues, although the specific features used remain unknown. There was also evidence that the relatively less intense response to a neighbour's vocalizations occurs only when the calls originate near the shared boundary. The same neighbour's calls played from another boundary elicited a speed of response similar to that of the response to the calls of a strange group. This result suggests that the spatial position of threatening groups is also important. Previous studies of the dear-enemy phenomenon have concentrated on the discrimination of individuals (Temeles 1994), so the results presented here provide the first illustration that groups may be distinguished in a similar fashion.

Why might there be a different response to neighbouring and strange groups? One proximate explanation involves variation in the level of familiarity with different groups. Habituation has long been suggested as a psychological mechanism underlying reduced aggression between territorial neighbours (Wiley & Wiley 1977; Peeke 1984; Shettleworth 1998; Bee & Gerhardt 2001). As a form of perceptual learning, habituation could allow territorial residents to learn about the idiosyncratic characteristics of their neighbours or their communication signals as a result of repeated exposure across shared territorial boundaries. Researchers have also suggested that territorial residents might become habituated to the direction or location in which their neighbours are usually found (Falls 1969; Falls & Brooks 1975; Wiley & Wiley 1977). In woodhoopoes, interactions with neighbours may occur several times per day, whereas strangers are rarely encountered (unpublished data). Increasing familiarity with neighbours may therefore result in a decreased response to their intrusions.

Although variation in familiarity may alone be sufficient to explain the different responses to neighbours and strangers, an ultimate reason for the distinction may be that different groups present different threats to territory holders. When a woodhoopoe group wins a rallying contest with a neighbour it invades the loser's territory, but only temporarily (Radford & du Plessis 2004a). For up to an hour, the winners forage and examine roost holes, before returning to their own territory. No permanent changes in territory boundaries result (Radford & du Plessis 2004b). The stakes may be higher, however, when a resident group is challenged by a group from further afield. Ligon & Ligon (1990) found in their Kenyan study population that a strange group, if successful in a contest, may take over the owner's territory permanently. This possibility remains to be confirmed in the South African population of green woodhoopoes, but, if true, neighbours might be viewed as less of a threat than strangers. If territory owners can learn to recognize and respect each other's territorial boundaries, they can reduce the energy expended in territorial defence and more successfully focus their defence against potentially permanent usurpers. Similar distinctions in threat between neighbours and strangers have been reported in a number of other studies (Temeles 1994), but this is the first such consideration of a group-territorial species.

Finally, a word of caution is necessary because there is a complex interplay of interactions when groups compete. The response of a group to intruders is the product of decisions made by several individuals, each of which may have a different motive for territory defence. For example, individual woodhoopoes of different sex and dominance class responded differently depending on, among other things, the composition of the intruding group (Radford 2003). Future work on agonistic interactions between groups must therefore consider both the behaviour of individuals and the response of the group as a whole (see also Adams & Mesterton-Gibbons 2003). Furthermore, contests in the green woodhoopoe can last for up to 45 min and include many rallies from both groups (Radford & du Plessis 2004a). Territory owners might not only respond faster to strangers, but contests between strangers might last for longer or escalate more rapidly than those between neighbours. Such predictions can be tested only with an interactive playback design. In the meantime, my results suggest that information about group identity is available to woodhoopoes in the rallying call, and that they are able to use these differences to discriminate between different groups.

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