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Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition

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Group territorial displays are a prominent feature of many avian cooperative-breeding systems. I used natural observations and playback experiments to investigate the territorial vocal rallying display of the green woodhoopoe, *Phoeniculus purpureus*. Rallies, which consisted of all adult group members cackling loudly while bowing up and down, were given both when unprovoked and in response to other groups. Unprovoked rally length correlated positively with group size, making it a potential indicator of group resource-holding potential. However, group members vocalized for longer in response to actual and simulated intrusions by larger groups than by smaller ones. The duration of the initial response rally was therefore strongly influenced by the rally length given by the intruding group, and consequently did not accurately reflect group size. I discuss the implications of this potential deception. Individuals differed in their contributions to response rallies depending on their sex and dominance status, and on the composition of the intruding group. Although males and females contributed equally overall, each sex expended more effort responding to intruders of its own sex, which might have been viewed as a greater threat. Individuals also approached playbacks of the opposite sex more closely than those of their own sex. Subordinates tended to cackle for longer than dominants, perhaps because they had more to lose from the increased foraging competition following the inclusion of additional group members.

Cooperation in territorial defence is frequently cited as one way in which helpers collaborate with breeders while remaining in their natal group (e.g. Heinsohn et al. 1990; Cockburn 1998). Group territorial displays are therefore a prominent feature of many avian cooperative-breeding systems (e.g. yellow-billed shrikes, *Corvinella corvina*: Grimes 1980; yellow-rumped caciques, *Cacicus cela*: Robinson 1985; grey-backed fiscal shrikes, *Lanius excubitorius*: Zack 1986; laughing kookaburras, *Dacelo novaeguineae*: Reyer & Schmidl 1988; Galápagos mockingbirds, *Nesomimus parvulus*: Curry & Grant 1990; Australian magpies, *Gymnorhina tibicen*: Brown & Farabaugh 1991; white-browed sparrow-weavers, *Plocepasser mahali*: Wingfield & Lewis 1993; and subdesert mesites, *Monias benschi*: Seddon & Tobias 2003). However, only Seddon & Tobias (2003) have studied group displays in detail.

The green (or red-billed) woodhoopoe, *Phoeniculus purpureus*, is an excellent species in which to examine group defence because territorial contests involve obvious vocal rallying displays, with all individuals rocking back and forth while cackling loudly. In South Africa, groups of 2–12 birds combine to defend exclusive areas of riverine forest throughout the year (du Plessis 1989). Disputes between neighbouring groups occur when one trespasses into the territory of another, or when members of the two groups meet along their common territory border. Although these territorial interactions do not tend to result in permanent changes in territory size (Radford 2002), trespassing is common. Groups successfully entering a neighbouring territory do so to feed and to examine roost and nest holes (Ligon & Ligon 1990). Larger groups are more successful at temporarily invading neighbouring territories and resisting intrusions (Ligon & Ligon 1978; du Plessis 1989). Assessing relative group size may therefore be an important component of rallying contests.

Game-theoretical models predict that where fighting is costly, contestants should assess the value of the resource and the resource-holding potential (RHP) of their opponent, and withdraw without escalation if they would be unlikely to win an ensuing fight (Parker 1974; Maynard Smith 1982). Most studies of assessment in animal contests have concentrated on disputes between single individuals, where the outcome is often determined by differences in body size and stamina (Riechert 1998 and references therein). However, where groups compete as units, differences in the number of individuals per group might outweigh interindividual differences

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in determining the outcome (McComb 1992; McComb et al. 1994; Seddon & Tobias 2003). Efficient assessors might therefore be expected to adjust their agonistic behaviour on the basis of the groups' relative sizes (e.g. Sekulic 1982; McComb et al. 1994). Playback experiments have shown that a variety of birds and mammals assess opponents through acoustic displays (e.g. Krebs et al. 1978; Clutton-Brock & Albon 1979). During territorial contests, competing woodhoopoe groups may be up to 30 m apart and obscured from one another by thick vegetation. Thus, acoustic cues are likely to provide more useful information than visual cues. By testing whether their response differs depending on the number of potential intruders, I investigated whether green woodhoopoes assess group size and hence RHP on the basis of vocal rallying displays.

In theory, rallying contests may also provide information to potential dispersers about breeding vacancies elsewhere. If correct assessment of breeding opportunities in their own and neighbouring groups is a critical component of reproductive success, helpers should evaluate their options frequently (Emlen 1997). Forays into other groups are believed to be the main mechanism by which animals obtain such information, but information exchanged during territorial displays may aid both potential dispersers and queuing individuals in evaluating breeding options (Wiley & Rabenold 1984). Breeding vacancies are filled rapidly in cooperative species (e.g. Ligon & Ligon 1978; Koenig 1981; Komdeur 1992), presumably because regular encounters and signals advertise the presence or absence of individuals in a given group. After experimental removal of breeding individuals, green woodhoopoe groups rallied more frequently than undisturbed groups (du Plessis 1989). Furthermore, manipulated groups that contained no replacements rallied more frequently than did those containing replacements (du Plessis 1989). Since green woodhoopoes produce sex-specific vocal syllables (Ligon & Ligon 1978), communal vocalizations contain information about both the number and sex of group members. Hence, I investigated whether the responses of male and female green woodhoopoes depend on the sex of the intruder.

Contests between groups of green woodhoopoes usually involve multiple rallies. To gain an insight into the importance of group size and composition, I focused on the first response rally in a contest. Within a group, individuals may differ consistently in the extent of their participation in intergroup conflicts (Heinsohn & Packer 1995), perhaps according to differences in the potential costs and benefits of investment in territorial defence (e.g. Milinski & Parker 1991; Pusey & Packer 1997). I therefore examined factors influencing the contribution of individuals of different sex and social status in intergroup encounters, as well as the response of the group as a whole.

METHODS

Nonexperimental Data Collection

Fieldwork was carried out in the Morgan's Bay region (32°43′S, 28°19′E) of the Eastern Cape Province, South Africa. Green woodhoopoes often produce a resonant cackling 'kek-ek-ek-ek' call, at a rate of about 12 keks/s, while bowing up and down. 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). A rally was strictly defined as the period starting when at least two birds were cackling together, continuing until all but one had ceased calling. Intergroup interactions ('contests') occurred several times per day and were characterized by particularly raucous rallying displays, when groups were separated by 5–30 m. A rally given on a territory boundary usually evoked a response from the neighbouring group: these were termed 'response' rallies. Rallies were also given in isolation, often in the middle of a group's own territory (mean ± SE territory size=23.5 ± 1.7 ha; Radford 2002). These tended to elicit no immediate response and were termed 'unprovoked' rallies.

Using a Sennheiser MKH416T microphone and a WM-D6C Sony Professional walkman, I recorded unprovoked rallies and the first response rally in contests between 24 colour-ringed groups of green woodhoopoes. Calls were recorded throughout the territory, although most response rallies were heard on territory boundaries. I also timed rallies when recording equipment was not available. Using a Tandy sound-level meter, at a distance of 20 m, I established unprovoked rally volume from groups of different size. During each rallying event, I randomly selected one individual and watched its bill movements to establish the duration of its cackling. Whenever possible, I recorded the number of individuals contributing to a particular rally, and the size and composition of the other group involved in response rallies. All adult group members (those older than 12 months) generally participated in rallies, but recently fledged juveniles never did so (personal observation): group sizes given throughout this paper refer to the number of adults in a group. Juveniles were easily identified by their predominantly black bills (Ligon & Ligon 1978). Adults could be sexed on the basis of bill length (Radford & du Plessis 2003) or vocalizations (Ligon & Ligon 1978). Only one pair of individuals in a group breeds, and they are typically the members of each sex that have been in the group the longest (unpublished data). When this information was unknown, I established breeding status by watching copulation attempts and displacement activity during group foraging (when breeding individuals dominate nonbreeding helpers; Radford & du Plessis 2003). Breeders were referred to as 'dominants', while 'subordinate' encompassed all adult helpers.

General Playback Protocol

Playback experiments were used to generate controlled artificial contests between groups of woodhoopoes. I conducted trials from March (after the breeding season was complete, when all group members tended to move around their territory together) to May, in 2000 and 2001. Trials took place from 0600 to 1100 hours and from 1500 to 1900 hours, when the birds were most active (personal observation). Playbacks to the same group were always separated by 7–14 days to minimize habituation, and the order of trial presentation was randomized. All trials within an experiment were conducted in the same, central part of a group's territory at about the same time of day. Each playback rally was from an unfamiliar group (at least three territories away from the focal group), to prevent individuals recognizing opponents and associating them with some prior measure of RHP (see McComb 1992).

I constructed playback loops using Cool Edit 96 (Syntrillium Software Corporation, Scottsdale, U.S.A.) by editing original recordings of unprovoked rallies from 24 groups. Each rally was digitized (sample rate of 44 100 Hz, 16-bit precision) and cut to the relevant length, as determined from the regression equation of unprovoked data given in the legend to Fig. 1. No loop was used more than once, thus avoiding pseudoreplication. Since the mean volume of unprovoked vocalizations increased with group size, albeit not significantly (weighted regression: $F_{1,19}=1.27$, $P=0.274$), I adjusted sound intensity using the volume control on the walkman according to the size of the playback group (volume (dB)=63.2+0.65 × group size). Playback groups numbering three or more varied in their male/female composition, which affected the response of individuals (see Results). However, playback groups were randomly selected and there was no systematic bias in the composition of groups used between trials to different groups (unpublished data). A single rally was played from a Sony SRS-A35 loudspeaker placed about 20 m from the trial group. Only one speaker was used, despite sometimes large group sizes, since woodhoopoes tended to rally from within 1 m of one another (personal observation). Groups were required to be foraging and silent (except for contact calls) for at least 5 min before the start of playback. I detailed all behavioural responses on a dictaphone, and recorded the initial response rally as described earlier. Since woodhoopoes generally responded quickly or not at all, I abandoned the trial if no rally had been given after 90 s.

I recorded variables assumed to reflect aggression by the subjects, namely: (1) response latency (from the end of the playback to the start of a rally); (2) duration of the first response rally; (3) closest approach distance of the group to the speaker before and during the first response rally; (4) rally rate (average number of syllables/s in the first response rally); (5) the number of group members contributing to the initial response rally; and (6) identity of the individual initiating the vocal response. I measured the parameters of the first response rally only, as subsequent vocalizations are likely to be influenced by within- and between-group dynamics.

Numerical Assessment Playbacks

I performed two playback experiments to test whether the size of the intruding group influenced the response of the territory-holding group.

Experiment 1

In 2000, 25 groups each received three trials. A trial consisted of playing a single rally from a group one smaller in size, the same size or one larger in size than the focal group. Since no 'smaller group' trial could be conducted for pairs, I presented them with two 'same size' trials, which provided a test for any habituation in response. In addition to the six variables described above, I noted the position of the defending group when responding: either 'hidden' (deep in the vegetation and so not clearly visible from 20 m) or 'exposed' (e.g. at the top of a tree or perched on bare branches).

Experiment 2

In 2001, 22 groups each received three trials. A trial consisted of playing a single rally from a group one, two or three larger in size than the focal group.

Group Composition Playbacks

I performed two playback experiments to test whether the composition of the intruding group influenced the response of the territory-holding group.

Experiment 1

In 2001, 12 groups of two woodhoopoes (each consisting of one male and one female) each received two trials: a lone male call and a lone female call. As green woodhoopoe vocalizations are sexually dimorphic (Ligon & Ligon 1978), I could ascertain the cackle duration and rate of both the male and female from the recording of the response rally. I also estimated the closest approach distance of both individuals to the speaker, and noted which sex was the last to stop vocalizing.

Experiment 2

In 2001, 12 groups of woodhoopoes containing three or four adults (three groups with 1M:2F, two 2M:1F, four 2M:2F, two 3M:1F, one 1M:3F, where M=male, F=female) each received two trials. A trial consisted of a single rally from either a male-biased or a female-biased group of the same total size as the focal group. I monitored the response of the whole group and determined the duration of cackling by the dominant female and the dominant male. If the focal group contained only one member of a particular sex, the duration of cackling by this individual was ascertained from the recording of the response rally, while the other dominant was watched in the field (using bill movements to determine when it was calling). If the focal group included two individuals of both sexes, the dominant male was watched in the field, and no data were collected for the dominant female. For statistical testing, I combined results from groups of both sizes.

Statistical Analysis

The coefficient of variation (CV) was used as an indicator of variability in certain measures. For parametric testing, proportions were arcsine square-root transformed before analysis. Sequential Bonferroni corrections were applied for multiple comparisons with the same data (Rice 1989). When analysing the effect of group size, I weighted regressions according to the number of groups of each size. For nonparametric tests of small samples, *P* values were obtained from statistical tables, rather than a software package (Mundry & Fischer 1998). Summary statistics are presented as mean ± SE.

Nonexperimental data

When analysing group responses, I used only groups from which a minimum of 10 nonexperimental rallies were timed. To test whether some individuals invested more effort than others, I examined: (1) the duration of cackling by an individual within a rally; and (2) the proportion of occasions on which an individual started a rally, corrected for group size. Only individuals for which there were at least five recorded cackles were included in the analysis. To avoid variability inherent in different-sized groups, I used paired *t* tests to compare males and females within groups and dominants and subordinates of the same sex.

Experimental data

Principal component analysis (PCA) has been recommended as a method of quantifying responses to playback that is complementary to a many measures approach (McGregor 1992). This method, however, requires that the recorded responses are correlated. Since a correlation matrix for each experimental data set showed that the variables were never strongly correlated (coefficient=0.10 ± 0.04, range 0.01–0.21), I did not use PCA and I analysed individual response parameters separately. In experiments with three trials, I used Friedman tests to investigate the effects of these treatments on continuous response measures (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. When only two trials were presented, Wilcoxon signed-ranks tests were used to examine continuous variables. A binary logistic regression for each data set showed no significant influence of group size or composition on the identity of the response initiator (all scores <3.00, *df*=1, all $P>0.085$). *G* tests were therefore performed for each experimental trial, to test for differences between the sexes and between dominance classes. Similarly, a *G* test was used to assess which sex was left vocalizing when pairs responded to lone playbacks.

RESULTS

Nonexperimental Rallying

Unprovoked rallying

There was a significant positive relation between group size and unprovoked rally length (weighted regression: R^2=29.3%, $F_{1,20}$=8.27, P=0.009; Fig. 1). When a group changed in size within a season, there was a significant change in its average unprovoked rally length in the same direction as the size change (paired *t* test: t_{11}=4.20, P=0.001). There was no significant difference between groups of different size in the proportion of times that all group members participated (ANOVA: $F_{5,16}$=0.80, P=0.563). Furthermore, there was no significant relation between the average duration of cackling by an individual and the size of its group (weighted regression: R^2=0.1%, $F_{1,36}$=0.01, P=0.959).

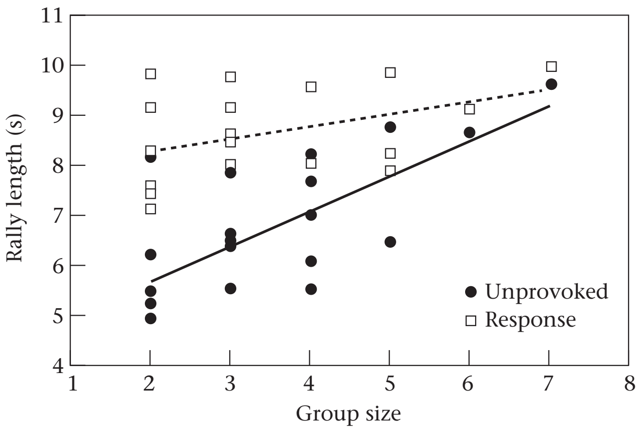

Figure 1. Mean length of rallies given by green woodhoopoe groups in unprovoked situations (*N*=22) and when initially responding to other groups (*N*=19). Each data point represents a mean of at least 10 rallies for one group. Least-squares regression lines are shown for unprovoked rallies (——; $Y=0.69X+4.31$) and response rallies (– – –; $Y=0.25X+7.74$).

During unprovoked rallying, there was no significant difference in the duration of cackling by males and females (paired *t* test: t_{11}=0.24, P=0.818) or dominants and subordinates (t_6=0.32, P=0.758) of the same group. Similarly, there was no significant difference in the proportion of rallies started by males and females (t_{11}=0.44, P=0.668) or by dominants and subordinates (t_6=2.05, P=0.087).

Response rallying

There was no significant relation between resident group size and the initial response rally length (weighted regression: R^2=9.9%, $F_{1,17}$=1.88, P=0.188; Fig. 1). Response rallies were significantly longer (paired *t* test: t_{11}=5.21, $P<0.001$; Fig. 1), but more variable in duration (unprovoked CV: 33.0 ± 1.0%; response CV: 35.9 ± 1.0%; t_{11}=2.70, P=0.021) than unprovoked rallies. Response rallies were significantly longer when a resident group was challenged by a larger group rather than one the same size or smaller (t_9=2.69, P=0.025; Fig. 2). This was not because more of the group responded when they were outnumbered by the intruding group (t_9=0.34, P=0.745).

Individuals cackled for longer in response rallies than unprovoked rallies (unprovoked: 5.9 ± 0.1 s; response: 6.7 ± 0.1 s; paired *t* test: t_{22}=8.96, $P<0.001$). The increase was greatest when responding to larger intruding groups (t_{10}=2.43, P=0.035; Fig. 2). There was also greater variability in the cackle lengths of individuals in response rallies than in unprovoked rallies (unprovoked CV: 19.7 ± 1.2%; response CV: 20.5 ± 1.3%; t_{22}=2.16, P=0.042). In contrast to unprovoked rallies, there was a significant negative relation between resident group size and the average duration of cackling by individuals during response rallies (weighted regression: R^2=17.6%,

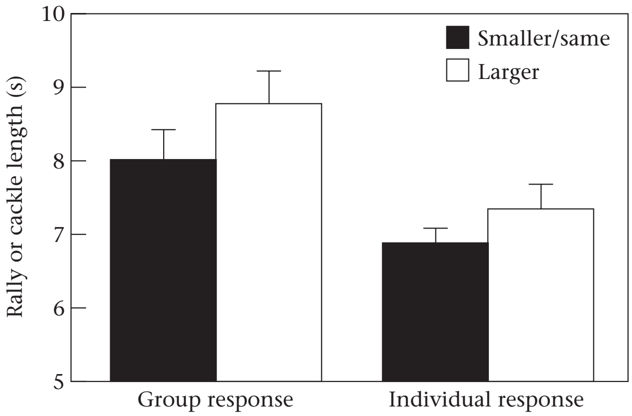

Figure 2. Mean+SE length of the initial rally given by 10 green woodhoopoe groups and the cackle contribution of 11 individuals in response to another group, either smaller/same size or larger than their own.

$F_{1,21}=4.47$, $P=0.047$). Thus, in response to a rally of the same length, individuals in larger groups contributed a shorter cackle than those in smaller groups.

When all initial response rallies were considered together, males and females from the same group did not differ significantly in their cackle length (paired *t* test: $t_6=0.34$, $P=0.749$) or in the proportion of response rallies initiated ($t_6=0.27$, $P=0.796$). However, when the intruding group contained more adults of their own sex, individuals tended to cackle for longer (same sex: 6.8 ± 0.2 s; opposite sex: 6.6 ± 0.2 s; paired *t* test: $t_{10}=2.16$, $P=0.056$) and to initiate more rallies than expected from the group size ($t_9=2.15$, $P=0.060$). Subordinates showed a trend towards longer cackling than dominants of the same sex in the same group (dominants: 7.0 ± 0.4 s, subordinates: 7.8 ± 0.2 s; $t_6=2.31$, $P=0.060$). Subordinates also tended to initiate more response rallies than expected from the group composition ($t_6=2.34$, $P=0.058$).

Numerical Assessment Playbacks

Experiment 1

There were no significant habituation effects ($P>0.30$ for all variables), nor any significant differences in the distance from the speaker and in the rallying rate in response to groups of different size (Table 1). However, groups responded significantly more rapidly to larger playback groups than to those smaller than their own. They also rallied for significantly longer when responding to the simulated intrusion of larger groups than to those of the same size or smaller, but this was not the result of an increase in the proportion of group members contributing.

The length of the initial response rally was significantly related to that of the playback rally (ANCOVA: $F_{1,44}=30.49$, $P<0.001$; Fig. 3), with no significant difference between the three trials ($F_{2,44}=0.92$, $P=0.405$). The size of the responding group did not influence the length of the initial response rally to simulated intrusions by groups of three (ANOVA: $F_{2,14}=0.91$, $P=0.426$) or four ($F_{2,12}=1.48$, $P=0.266$) individuals.

Groups tended to remain hidden from view when responding to larger groups (hidden in 11/16 cases), but rallied from more exposed positions in the other trials (cases in which hidden: 'smaller': 4/16; 'same': 7/16; $G_2=6.15$, $N=16$, $P<0.05$). There was no significant difference between the sexes ($G_1<1.00$, $P>0.10$ for all three trials) nor between dominants and subordinates ($G_1<0.25$, $P>0.50$) in the likelihood of initiating a response rally.

Experiment 2

There were no significant differences in latency, rallying rate or closest approach distance in response to playback groups of increasing size (Table 2). However, there was a significant increase in the length of the response rally with increasing intruder numbers, even though the proportion of the group responding did not increase.

The sexes did not differ in their likelihood of initiating a response rally in any of the three trials ($G_1<1.30$, $P>0.10$). There was also no difference between individuals of different dominance class in the 'one larger' and 'two larger' trials ($G_1<0.70$, $P>0.10$). However, subordinates were significantly more likely than dominants to initiate a response rally in the 'three larger' trial (subordinates: 10/13; dominants: 3/13; $G_1=3.84$, $P=0.05$).

Group Composition Playbacks

Experiment 1

Individuals of the same sex as the playback individual were significantly more likely to respond first (same sex: 18/24; opposite sex: 6/24; $G_1=6.12$, $P<0.025$). There was no significant difference in the latency of the pair's response to male or female playbacks (Table 3), nor in the male or female rate of cackling in response to either a male or a female playback. However, both males and females cackled for significantly longer in response to a playback of their own sex. In addition, females approached male playbacks significantly more closely than playbacks of their own sex. Similarly, there was a trend for males to approach playbacks of the opposite sex more closely, although the difference was not significant after Bonferroni correction. Individuals of the same sex as the playback individual were not more likely to be the last left calling (same sex: 14/24; opposite sex: 10/24; $G_1=0.66$, $P>0.10$).

Experiment 2

Individuals of the sex to which the playback group was biased were significantly more likely to initiate the response rally (same sex: 17/24; opposite sex: 7/24; $G_1=4.21$, $P<0.05$). There was no difference in the latency, rally length or closest approach distance of the group to male-biased and female-biased playback groups (Table 4).

There was no difference in the latency (Wilcoxon test: $T=4.0$, $N=8$, $P=0.059$) or closest approach distance ($T=15.5$, $N=8$, $P=0.779$) of the group to playbacks of groups with a sex bias in the same or the opposite

Table 1. Results of a playback experiment testing the initial response of green woodhoopoe groups to a simulated intrusion (a single rally) by groups of different size

	Playback group size			
Response variable	One smaller	Same	One larger	χ^2_2
Latency (s)	34.9 ± 3.0^{a}	$29.9\pm1.9^{a,b}$	20.2 ± 1.7^{b}	8.97*
Rally length (s)	8.3 ± 0.5^{a}	8.1 ± 0.4^{a}	9.4 ± 0.4^{b}	9.50*
Rate (syllables/s)	12.8±0.2	12.8±0.3	12.9±0.2	1.62
Closest distance (m)	12.8±1.8	15.6±1.6	11.5±1.3	1.03
Proportion contributing	0.94±0.03	0.94±0.03	0.94±0.03	0.01

Only 16 of 25 groups were suitable for inclusion in the analysis. Means are shown ±SE. χ^2 values are from a Friedman test; *$P<0.05$, with sequential Bonferroni corrections. Superscripts indicate in which trials the responses differed significantly (multiple comparison tests).

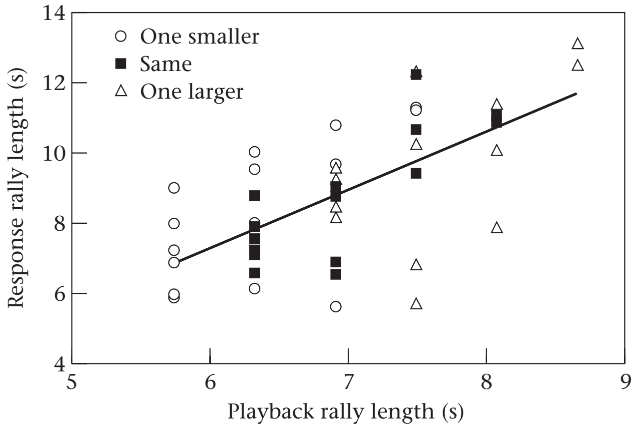

Figure 3. Relation between the length of a playback rally (simulating an intruding group) and the first response rally of a resident green woodhoopoe group. The response rallies of the same 16 groups from three trials are shown, with a least-squares regression line through all the points: $Y=1.67X-2.71$.

direction. However, there was a tendency (although nonsignificant after Bonferroni correction) for the group's first rally to be longer in response to groups with the same sex bias as their own (same: 8.4 ± 0.3 s; opposite: 7.7 ± 0.2 s; $T=35.0$, $N=8$, $P=0.021$).

Considering individual responses, dominant males cackled for significantly longer in response to male-biased groups (Table 4). Dominant females also showed a strong, but nonsignificant, trend to cackle for longer in response to female-biased groups.

DISCUSSION

Territorial Defence and Group Size

In the green woodhoopoe, unprovoked rally length correlated positively with group size. Since individual contributions did not vary with group size, and all adults participated most of the time, the longer rallies of larger groups probably resulted from a lack of coordination between birds when calling. Unlike white-browed sparrow-weavers, which each gives a specific call as part of the overall group chorus (Wingfield & Lewis 1993), woodhoopoes all cackled in a similar fashion and showed no synchronization of vocalizations when rallying (personal observation). Consequently, although rallies by a pair ended as soon as one individual stopped cackling, rallies by larger groups might have been extended as a result of different individuals staggering their calling.

In contests between single competitors, relative RHP is usually straightforward to assess on the basis of body size, weight or weaponry (Riechert 1998). In contests between cooperative groups, however, it is assumed that participants should base their assessment of RHP on the number of competitors they expect to encounter. Roaring in lions, *Panthera leo*, provides a reliable indication of the number of individuals present, at least for groups of up to three (McComb et al. 1994). The relation between woodhoopoe group size and unprovoked rally length suggested that this vocalization may offer a similar means of assessing RHP. However, there was no significant relation between a group's size and its initial response rally length. Natural data indicated that this was at least partially the result of an increase in rally length in response to larger groups. The numerical assessment playbacks elucidated this further: in response to groups larger than their own, woodhoopoes responded more rapidly and gave a longer initial response rally. The greater variability in response rally length, which indicated a less consistent response than in unprovoked rallying, may therefore result from groups responding in a different fashion to intrusions by groups of different sizes.

Although territories are vigorously defended and boundaries are well known, trespassing is common. Large groups are more successful than small ones at temporarily invading neighbouring territories and in resisting intrusions (Ligon & Ligon 1978; du Plessis 1989). By giving an initial response rally that was longer than expected from a group of their size, smaller groups might therefore have been attempting to disguise their true size to larger groups. In short contests, this initial increase in rally length may be sufficient to prevent encroachment by larger neighbouring groups (Radford 2002). Since visual cues may sometimes play a role in naturally occurring contests, smaller groups might have remained hidden while delivering the response to enhance the likelihood of a successful deception. Alternatively, small groups may have hidden to reduce attacks from intruders. The approach distance of a group might be expected to

Table 2. Results of a playback experiment testing the initial response of green woodhoopoe groups to a simulated intrusion (a single rally) by groups of increasing size

	Playback group size			
Response variable	One larger	Two larger	Three larger	χ^2_2
Latency (s)	19.6±3.2	18.9±2.3	19.1±2.5	0.42
Rally length (s)	8.9±0.4^a	9.2±0.4^a	9.8±0.4^b	10.21*
Rate (syllables/s)	12.7±0.3	13.1±0.3	12.9±0.3	0.19
Closest distance (m)	13.2±1.5	14.2±1.5	14.2±1.7	0.48
Proportion contributing	0.93±0.03	0.96±0.02	0.98±0.02	1.56

Only 19 of 22 groups were suitable for inclusion in the analysis. Means are shown ±SE. χ^2 values are from a Friedman test; *$P<0.05$, with sequential Bonferroni corrections. Superscripts indicate in which trials the responses differed significantly (multiple comparison tests).

Table 3. Results of a playback experiment testing the response of 12 green woodhoopoe pairs to a simulated intrusion by either a lone male or a lone female

	Playback trial		
Response variable	Male call	Female call	*T*
Latency (s)	34.5±3.3	43.3±5.1	57.0
Male cackle length (s)	7.8±0.2	6.7±0.5	67.0*
Male cackle rate (syllables/s)	13.2±0.2	12.9±0.2	30.0
Male approach distance (m)	16.7±1.9	13.5±2.3	16.0
Female cackle length (s)	6.5±0.4	7.7±0.3	69.0*
Female cackle rate (syllables/s)	13.0±0.2	12.8±0.1	14.0
Female approach distance (m)	9.2±2.2	17.5±1.6	65.0*

Means are shown ±SE. *T* values are from a Wilcoxon test; *$P<0.05$, with sequential Bonferroni corrections.

Table 4. Results of a playback experiment testing the response of 12 green woodhoopoe groups of three or four individuals to a simulated intrusion by either a male-biased or a female-biased group of the same size

	Playback trial		
Response variable	Male-biased	Female-biased	*T* (*N*)
Group response			
Latency (s)	31.1±3.7	34.8±4.4	29.0 (12)
Rally length (s)	7.9±0.2	8.2±0.2	24.0 (12)
Closest distance (m)	15.4±1.9	13.8±2.5	44.0 (12)
Individual response			
Male cackle length (s)	7.1±0.2	6.6±0.2	72.0 (12)*
Female cackle length (s)	6.8±0.3	7.3±0.2	4.0 (8)

Means are shown ±SE. *T* values are from a Wilcoxon test; *$P<0.05$, with sequential Bonferroni corrections. Sample sizes vary since not all data were available for every group.

give some indication of its willingness to risk confrontation, but the size of the playback group did not significantly affect this variable. However, as interactions last for up to 45 min and involve multiple rallies, approach distance may become more important as contests develop.

Maynard Smith & Parker (1976, page 169) claimed that the essential feature of a bluffed display is that 'it should increase apparent size (or whatever feature is being used to settle conflicts without fighting) without altering RHP in an escalated contest'. As a behavioural response during simulated territorial contests, initial response rallying of woodhoopoes possessed the essential feature of an exaggerated signal of group size: the matching of a larger intruding group's rally length led to an increase in apparent size. Despite the expected rarity of dishonest signalling (Dawkins & Krebs 1978; Grafen 1990) and the limited empirical evidence of its occurrence (Steger & Caldwell 1983; Bee et al. 2000), several models have been developed to show that a low frequency of dishonest signals can be stable in a population (e.g. Bond 1989; Johnstone & Grafen 1993; Adams & Mesterton-Gibbons 1995). Two of these models predict the use of dishonest signals by members of the population that are the most vulnerable in escalated contests (Bond 1989; Adams & Mesterton-Gibbons 1995), as may be the case for initial response rallying in green woodhoopoes. Honesty based on rally length does, however, enter the system during prolonged contests, when larger groups are increasingly likely to win (Radford 2002).

Other aspects of the rally, such as signal intensity (McComb et al. 1994) or some level of overlap in calling between individuals, may provide more reliable cues to group size, thus reducing the potential for dishonest signalling. A further experiment could factor out the effects of rally length versus group size on response rallies, using short playback rallies by simulated 'larger' groups and long playback rallies by simulated 'smaller' groups. Volume is unlikely to offer a reliable indicator of group size, because of the attenuation of sound with distance and intervening vegetation.

The increased rally length in response to larger intruding groups resulted not from more group members joining in, but from an increase in the cackle contribution of individuals. To produce a particular rally length, individuals from smaller groups must therefore contribute relatively more effort than those in larger groups. Although individual rallies are short, contests lasting for 45 min may include well over 100 rallies. The energetic cost of cackling will therefore accumulate over this time. The decrease in per capita input to defence with increasing group size may be one benefit gained by breeders in cooperative groups (Farabaugh et al. 1992). Individuals did not increase their cackle contribution to the same extent on each occasion. The greater variability in response cackle lengths, compared with those in unprovoked rallies, suggests that each individual tailored its response to the threat it perceived.

Assessment of Threat and Opportunities

By individuals of different dominance status

Although all adult group members participated in territorial defence, subordinate green woodhoopoes tended to expend more effort. Compared with dominants, they might have more to lose from the addition of new group members. Since extrapair copulations do not seem to occur within this species (unpublished data), additional males should not adversely affect group males in this way. Furthermore, an extra individual should not theoretically alter the likelihood of an existing member gaining breeding status in the group, as a consequence of the strict queuing system that operates in this species (unpublished data). Extra members of the same sex will, however, compete for the same food resources as existing subordinates, because of the specialization of the sexes for different niches (Radford & du Plessis 2003). Rallying may provide additional benefits to helpers when neighbours are considered not only as competitors, but also as potential mates. By participating in intergroup interactions, a helper's quality may be witnessed not only by groupmates, but also by individuals in neighbouring groups (Lotem et al. 1999).

By individuals of different sex

Although both males and females contributed to all rallies, responses differed according to the sex of the intruders. During naturally occurring rallies, each sex responded more vigorously to intruding groups containing more members of its own sex. In response to lone-call playbacks, individuals initiated more responses and cackled for longer in response to their own sex. Similarly, individuals responded more strongly to playback groups with several members of their own sex. Since green woodhoopoe vocalizations are sexually dimorphic (Ligon & Ligon 1978), assessment of group composition may take place during territorial encounters. It seems likely that individuals were treating same-sex intruders as a threat, whether to breeding or foraging opportunities, and hence were more aggressive towards them.

Greater aggression towards same-sex intruders has been reported in a number of pair-forming species (e.g. eastern bluebirds, *Sialia sialis*: Gowaty 1981; song sparrows, *Melospiza melodia*: Arcese 1989; kestrels, *Falco tinnunculus*: Wiklund & Village 1992). There are also examples of sexual biases in the territorial behaviour of species living in groups. Stonechat, *Saxicola torquata*, males are more aggressive than females when defending the winter group territory, and most aggression is intrasexual (Gwinner et al. 1994). Male and female Australian magpie adults participate equally in the defence of the group territory (Farabaugh et al. 1992), and male Tasmanian native hens, *Gallinula mortierii*, expend more effort in territorial defence than females do (Putland & Goldizen 1998). In the green woodhoopoe, there was no intersexual difference in the overall level of defence investment. This might be expected, given that both sexes remain on the territory to help, and competing groups often consist of multiple members of both sexes. Since each sex showed a stronger response to intruders of its own sex, there was unlikely to be an overall difference between the sexes.

Intergroup interactions may also provide an opportunity to view potential mates in neighbouring territories. This would explain why individuals approached the lone playback of the opposite sex more closely than playback of a member of their own sex. Experimental removal of breeding individuals resulted in increased rallying from the remaining group members, particularly when no replacements were present (du Plessis 1989). These results support the theory that the display functions, at least in part, to advertise the presence or absence of breeding vacancies. In theory, males and females may differ in the function of their calling and in their strategies of mate acquisition and assessment. Playback experiments on bay wrens, *Thryothorus nigricapillus*, for example, showed that female song is used in territory defence against other females, whereas male song functions in mate guarding (Levin 1996a, b). However, a mate-guarding role seems unlikely in the green woodhoopoe, since males and females in groups of two were equally likely to be the last to finish cackling in response to lone playbacks of either sex.

Apparent numerical assessment

The increased vocal response of individuals to members of the same sex could theoretically explain the increased response to larger groups, and the resultant matching of the intruder's rally length. Thus, there may be no numerical assessment of the group as a whole, but perhaps simple assessment of same-sex intruders. To test this, it would be necessary to present a series of playbacks in which the number of one sex remained the same, while the number of the other sex increased. If individuals are truly assessing only members of their own sex, their response to each of these playbacks should be the same. If, however, there is assessment of the intruding group as a whole, there should be an increased response with increasing group size.

Group composition, in terms of the number of adult males and females, seems a vital component in the territorial interactions of the green woodhoopoe. The response of the group is made up of the responses of its individual members. Their interests will differ depending on a variety of factors, some of which (dominance status and sex) have been considered here, while others (e.g. age and motivation) have not. As a consequence, the relationship between neighbouring groups is a dynamic one, perhaps explaining the frequency with which the rallying contests occur.

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