



## Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome

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Most studies of asymmetric contests have focused on interactions between individuals. We examined territorial contests between groups of green woodhoopoes, *Phoeniculus purpureus*, which take the form of vocal rallying displays. The distribution of encounter durations was bimodal: interactions were generally either decided within 5 min (short contests) or took longer than 15 min to reach an outcome (extended contests). As short contests progressed, there was an escalation in the length of rallies, and these encounters were longer when the competing groups were more evenly matched in size. Residents won the majority of short contests, whereas the difference in the sizes of the competing groups was not a significant predictor of the outcome. The resident group appeared to match the rally length given by the intruding group, tending to lose the contest when it no longer achieved this. In extended contests, there was no further escalation in rally length after the first 5 min. There was also no resident advantage, but larger groups were more likely to win. These extended contests may be a test of stamina. To achieve a similar length of rallying, individuals in smaller groups must contribute more effort than those in larger groups. We discuss the possibility that physiological constraints prevent smaller groups from sustaining the same level of rallying as larger groups, and that this difference decides the outcome of extended contests. We consider the different possible functions of short and extended contests, and discuss our findings in relation to existing models of agonistic interactions.

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The outcome and duration of an asymmetric contest should be dependent on the nature and strength of the asymmetry (Maynard Smith & Parker 1976), of which there are two fundamental types. First, there are asymmetries in resource-holding potential (RHP), or differences in fighting ability (Parker 1974). Body size is an example of a character that may differ between contestants, thus giving one individual a greater RHP (e.g. Wells 1988; Smith et al. 1994). The number of individuals may similarly affect the RHP of groups (McComb et al. 1994; Radford 2003; Seddon & Tobias 2003). Second, there are payoff asymmetries, or differences in the consequences of winning or losing the contest for the two contestants (Maynard Smith & Parker 1976). Prior residency is one

example of such an asymmetry, since residents may place a higher value on a territory and so have more to gain from winning (Maynard Smith & Parker 1976; Getty 1987).

Contests are often settled by an initial assessment phase, without recourse to escalated fighting. It is during this display phase that contestants gain information on potential asymmetries that might determine contest outcomes were fighting to occur. These display phases may last for a long time. For example, roaring contests between rutting red deer, *Cervus elaphus*, stags extend for up to 40 min (Clutton-Brock & Albon 1979). The exchange of display and attack manoeuvres during staged interactions between male convict fish, *Cichlasoma nigrofasciatum*, may occupy 20 min (Koops & Grant 1993). Even duels of aerobic skill between short-lived damselflies, *Calopteryx maculata*, can continue for almost an hour (Marden & Rollins 1994).

The majority of empirical studies considering such displays have focused on contests between individuals (e.g.

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Riechert 1998 and references therein). However, many interactions in the natural world take place between groups (e.g. Cheney 1986; Stacey & Koenig 1990; McComb et al. 1994). We examined territorial contests between groups of green (or red-billed) woodhoopoes, *Phoeniculus purpureus*. Groups consist of 2–12 individuals that defend year-round, multipurpose territories (Ligon & Ligon 1978). Territorial encounters between neighbouring groups may occur several times per day and are characterized by raucous vocal rallying displays, with all adults rocking back and forth while cackling loudly. On such occasions, competing 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.

Contests between neighbouring woodhoopoe groups do not tend to result in permanent changes in territory size (Radford & du Plessis 2004). However, trespassing is common, with successful intruders examining roost/nest holes and feeding in the neighbouring territory (Ligon & Ligon 1990). There is therefore an incentive to prevent encroachment. In addition, rallying contests may provide information to potential dispersers about breeding vacancies elsewhere (Radford 2003). The longer a contest, the greater the potential level of information transfer. We considered the importance of residency, as well as aspects of group size and composition, in determining the duration and outcome of these contests between woodhoopoe groups.

Several models have been developed with regard to extended antagonistic encounters between animals, but they have generally considered dyadic interactions between individuals (Payne 1998). Only recently have attempts been made to model explicitly the relation between the relative number of animals in two competing groups and the costs and benefits of entering a contest. We discuss our results from the interactions of woodhoopoe groups with reference to Lanchester's theory of combat (Lanchester 1916), which was formulated with human warfare in mind, but which has been shown to be applicable to intergroup contests in other species (e.g. Wilson et al. 2002; Adams & Mesterton-Gibbons 2003).

## METHODS

### Data Collection

Fieldwork was carried out on a colour-ringed population of green woodhoopoes near Morgan's Bay (32°43'S, 28°19'E), Eastern Cape Province, South Africa. In the 33-km<sup>2</sup> study area, riverine forest forms belts along river valleys. Valleys are separated by open grassland, which is not used by the birds. Woodhoopoe territories are arranged linearly along the river courses, and thus each territory borders a maximum of two others. Data were collected from November 1999 to May 2000 and from November 2000 to May 2001.

Green woodhoopoes often produce a resonant cackling 'kek-ek-ek-ek' call, at a rate of approximately 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 chorus is called a 'rally' (Ligon & Ligon 1978). During contests between neighbouring groups of green woodhoopoes, raucous vocal rallying displays were generally given alternately, for up to 45 min ( $\bar{X} \pm \text{SE} = 8.4 \pm 0.4$  min; Results).

We monitored 488 full contests (i.e. interactions in which the start and the finish were observed) between 23 pairs of neighbouring groups ('group-pairs'). By chance, each of these group-pairs consisted of two different-sized groups. In a particular contest, the 'resident' was defined as the group on whose territory the interaction took place, while the group attempting to invade the resident's territory was termed the 'intruder'. Within a group-pair, these roles could be reversed on different occasions (e.g. A sometimes intruded into B's territory, while B intruded into A's territory the rest of the time). Contests were therefore assigned to a particular resident/intruder pair, of which there were two per group-pair. Although it would have been ideal to complete matched comparisons of the same two groups when their roles were reversed, a mean  $\pm$  SE of  $74.7 \pm 2.1\%$  (range 53.5–90.0%) of contests were recorded when one of a particular group-pair was the intruder. Thus, for most group-pairs, the sample size for one of the resident/intruder combinations was prohibitively small. For analyses we therefore used the resident/intruder combination with the largest number of recorded contests from each group-pair. By chance, taking these combinations meant that no group featured more than once in the same role (i.e. as intruder or resident) within an analysis. We have therefore analysed 369 contests from 23 fixed resident/intruder pairs ( $\bar{X} \pm \text{SE}$  number of contests per pair =  $16 \pm 1$ ).

Since group members spent most of their time together, we assumed that the absence of an individual on three consecutive observer visits to a group reflected its death or dispersal to another territory. When one of a group-pair permanently changed in size in this way, no further interaction data were collected from that group-pair. All adult group members generally participated in rallies (Radford 2003), but recently fledged juveniles (<3 months) did not contribute at all (unpublished data). We therefore noted the number and composition (number of males and females) of adults within the competing groups (adults:  $\bar{X} \pm \text{SE} = 3.8 \pm 0.2$ ; juveniles:  $0.7 \pm 0.2$ ). 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).

A contest was considered to have started when a resident group responded within 5 min to a rally given by an intruding group. We timed each rally given by the two groups and recorded how long after the start of a contest it was given. We also noted the time of day (in 2-h periods) and the month. A contest was considered finished once no rally had been given for 5 min. We recorded how long the whole contest lasted, from the start of the first rally to the end of the last one. At the end of a contest, we recorded the outcome. If the intruding group remained on the resident's territory for at least 10 min after the final rally, and the residents moved deeper into their own territory, the contest was 'won' by the intruder. If the intruding

group retreated back to its own territory within 1 min of the final rally, the contest was 'won' by the resident. In 5% of cases, the intruding group remained on the resident's territory for 1–10 min after the end of the rallying or the resident group did not move deeper into its own territory. These cases were discounted from the analyses.

## Statistical Analysis

For each resident/intruder pair, details were available from a number of contests on different days, so we used mean values to avoid pseudoreplication. Each analysis included only resident/intruder pairs for which at least four relevant contests were recorded, and thus sample sizes vary. To enable parametric testing, proportions were arcsine square-root transformed and contest duration was  $\ln$  transformed before analysis. Summary statistics are presented as mean  $\pm$  SE.

When considering the outcome of contests, we used absolute group size differences (i.e. resident group size minus intruding group size). However, when considering contest duration, we ignored the sign of the difference (e.g. '-1' and '1' were both classified as a difference of '1'). Weighted regressions were initially used when analysing the effect of group size difference because there were different numbers of each group size. Because the ratio of group sizes may also be important (Seddon & Tobias 2003), we calculated the 'odds ratio' (number of defenders relative to number of intruders). Since group size difference and odds ratio were significantly correlated (pearson correlation:  $r_{21} = 0.927$ ,  $P < 0.001$ ), they could not both be used as predictors of contest outcome in the same multiple linear regression. We therefore conducted separate weighted regressions for the two predictors, to give an indication of which explained most of the variation in contest outcome.

We used an ANCOVA to assess simultaneously the importance of intruding-group rally length (a covariate) and the relative size of the resident group (either larger or

smaller than the intruding group: a factor) on the rally lengths given by the resident group. When analysing the length of rallies given in each minute of a contest, we used a repeated measures ANOVA because all resident/intruder pairs contributed to each minute of the time scale. To give an indication of how reliably the rally lengths given at the start and the end of the contest reflected group size, we used weighted regressions to examine the scatter (indicated by the  $r^2$  value) in mean rally lengths given by groups of different sizes. Ideally,  $r^2$  values should be calculated for each group separately and then compared. However, each study group was of a fixed size, and so we calculated values after combining the data from all groups.

## RESULTS

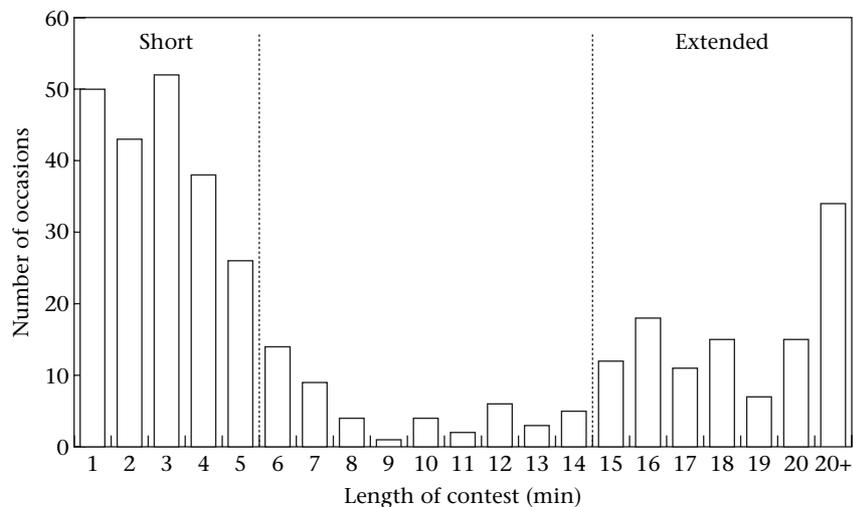
### Contest Occurrence

Contest lengths showed a bimodal distribution (Fig. 1). This was not due to some resident/intruder pairs always resolving contests quickly and others always taking longer, since all resident/intruder pairs had contests of varying duration: there was no significant difference in the mean (ANOVA:  $F_{22,346} = 0.83$ ,  $P = 0.685$ ) or the variance (Levene's test: test statistic = 0.98,  $P = 0.491$ ) of contest lengths of different resident/intruder pairs. For further analysis, we therefore separated the data into interactions that lasted for 5 min or less ('short' contests) and those that continued for 15 min or longer ('extended' contests), since 87% of encounters were decided within these time frames.

### Short Contests

#### Duration of contests

Fifty-seven per cent of all contests were decided in 5 min or less. We analysed 209 short contests between 23 resident/intruder pairs. There was no significant relation between contest length and time of day (ANOVA controlling for



**Figure 1.** Frequency distribution of contest lengths. The bimodal spread of the data resulted in a division into short ( $\leq 5$  min) and extended ( $\geq 15$  min) contests, as indicated by the dotted lines.

resident/intruder pair:  $F_{5,181} = 0.49$ ,  $P = 0.786$ ) or month ( $F_{4,181} = 2.19$ ,  $P = 0.072$ ). Data were therefore combined for each resident/intruder pair.

In a multiple linear regression explaining 47.5% of the variance in mean short-contest duration, group size difference was the only significant predictor (size difference:  $t_{22} = -2.37$ ,  $P = 0.028$ ; resident size:  $t_{22} = -1.02$ ,  $P = 0.323$ ; intruder size:  $t_{22} = -0.16$ ,  $P = 0.879$ , difference in male numbers:  $t_{22} = -0.81$ ,  $P = 0.431$ ; difference in female numbers:  $t_{22} = 0.28$ ,  $P = 0.782$ ). Contest duration decreased significantly with increasing size difference (weighted regression:  $F_{1,21} = 6.11$ ,  $P = 0.022$ ; Fig. 2).

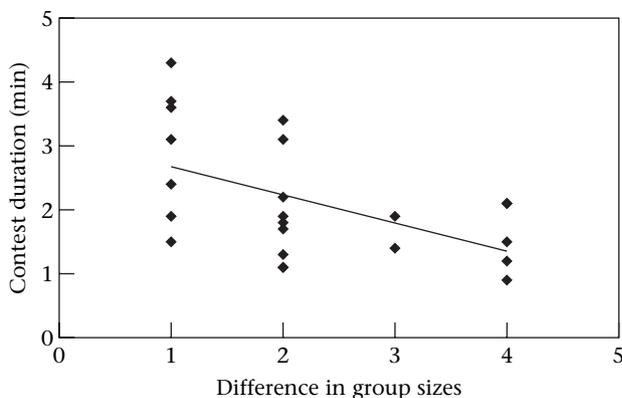
Contests won by resident groups ( $2.0 \pm 0.2$  min) were shorter than those won by intruding groups ( $2.9 \pm 0.1$  min; paired  $t$  test:  $t_{22} = 3.32$ ,  $P = 0.003$ ). Encounter duration was also significantly shorter when the winning group was larger than the losing group (larger winner:  $2.2 \pm 0.2$  min; smaller winner:  $2.7 \pm 0.2$  min;  $t_{22} = 2.29$ ,  $P = 0.032$ ).

#### Outcome of contests

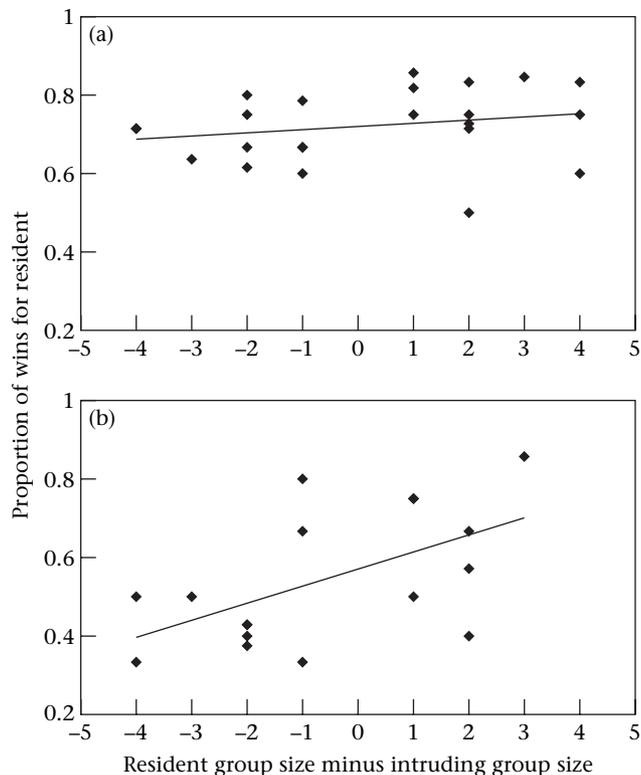
Resident groups won  $72.2 \pm 1.9\%$  of short contests, which was significantly more than would be expected by chance (paired  $t$  test comparing the observed number of wins by a resident group with 50% wins:  $t_{22} = 8.35$ ,  $P < 0.001$ ). However, there was no significant relation between the difference in resident and intruder group size and the proportion of wins for the resident (weighted regression:  $F_{1,21} = 0.48$ ,  $P = 0.497$ ; Fig. 3a). There was also no significant relation between the odds ratio and the proportion of wins for the resident (weighted regression:  $F_{1,21} = 0.19$ ,  $P = 0.663$ ).

#### Details of contests

Short contests were characterized by a significant increase in rally length as the encounter progressed (repeated measures ANOVA examining the mean rally length given by different resident/intruder pairs in each minute of a short contest:  $F_{4,19} = 39.98$ ,  $P < 0.001$ ).



**Figure 2.** Relation between the difference in size of two interacting green woodhoopoe groups and the mean duration of short contests ( $\leq 5$  min) between them. The least-squares regression line is shown:  $Y = -0.44X + 3.12$ .  $N = 23$  resident/intruder pairs.

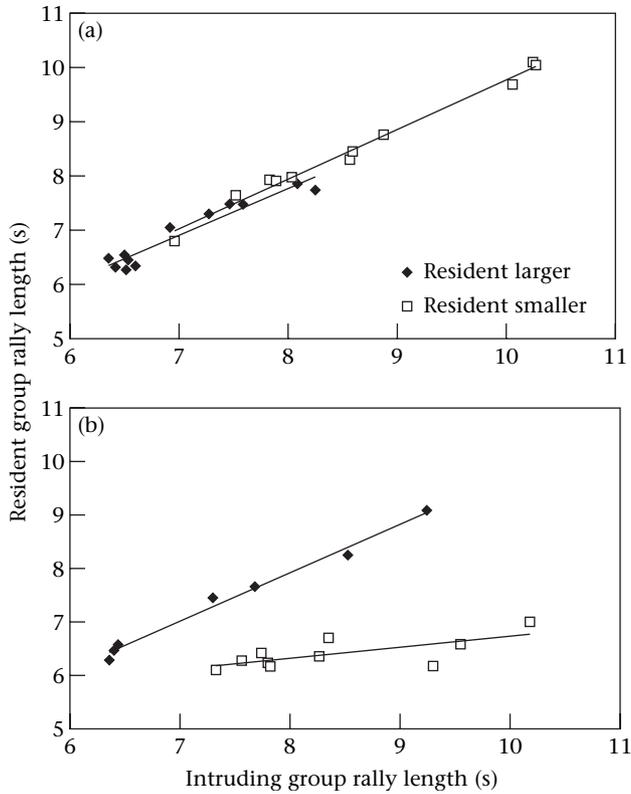


**Figure 3.** The importance of green woodhoopoe group size in determining the likelihood of winning (a) a short ( $\leq 5$  min) or (b) an extended ( $\geq 15$  min) contest. Least-squares regression lines are shown: (a)  $Y = 0.01X + 0.72$ ,  $N = 23$  resident/intruder pairs; (b)  $Y = 0.04X + 0.57$ ,  $N = 17$  resident/intruder pairs.

Considering all rallies given during short contests, there was a highly significant, positive relation between the rally lengths of the intruding group and those of the responding resident group (ANCOVA:  $F_{1,19} = 806.25$ ,  $P < 0.001$ ). In fact, the resident group closely matched the rally lengths given by the intruding group (Fig. 4a). In response to intruding-group rallies of a particular length, all resident groups, whether they were larger or smaller than the intruding group, gave rallies of a similar length (ANCOVA:  $F_{1,19} = 0.62$ ,  $P = 0.441$ ). The relation between resident rally length and intruding rally length was the same for both relative sizes of resident group, throughout the range of intruding rally lengths given (ANCOVA, interaction term:  $F_{1,19} = 0.51$ ,  $P = 0.484$ ).

When the resident group won, the last rally given by the intruding group was not significantly different in length to its penultimate rally, nor to the preceding one given by the resident group (Table 1). However, when the intruding group won, the last rally given by the resident group was significantly shorter than its penultimate one and the preceding one given by the intruding group.

The length of the first rally given in a contest by the resident group did not appear to offer a reliable indication of its size, regardless of whether it won ( $r^2 = 5.6\%$ ) or lost ( $r^2 = 4.4\%$ ). If the resident won the contest, its last rally was also an unreliable indicator of group size ( $r^2 = 7.2\%$ ). However, if the resident lost, its final rally gave a much better indication of its true group size ( $r^2 = 46.4\%$ ).



**Figure 4.** Relation between the mean rally lengths of resident and intruding green woodhoopoe groups during (a) short ( $\leq 5$  min) and (b) extended ( $\geq 15$  min) contests. Each point represents the mean of all rallies given by the relevant group: (a) during entire contests (0–5 min),  $N = 23$  resident/intruder pairs; and (b) from 15 min onwards in contests,  $N = 17$  resident/intruder pairs.

**Extended Contests**

*Duration of contests*

Thirty per cent of contests took 15 min or longer to reach an outcome. We analysed 112 extended contests between 17 resident/intruder pairs. There was no significant relation between contest length and time of day (ANOVA controlling for resident/intruder pair:  $F_{5,79} = 0.62, P = 0.683$ ) or month ( $F_{4,79} = 2.03, P = 0.098$ ). Data were therefore combined for each resident/intruder pair.

A multiple linear regression indicated that none of the predictor variables had a significant influence on the mean duration of extended contests (size difference:  $t_{16} = 1.10,$

**Table 1.** Rally lengths of green woodhoopoe groups at the end of short contests ( $\leq 5$  min)

Winner	Last rally of loser	Penultimate rally of loser	$t$	Preceding rally of winner	$t$
Resident	$7.6 \pm 0.2$	$7.8 \pm 0.3$	1.69	$7.7 \pm 0.2$	0.96
Intruder	$7.6 \pm 0.2$	$8.1 \pm 0.2$	2.43*	$8.2 \pm 0.2$	3.78**

Mean  $\pm$  SE rally lengths (s) from all contests between 23 resident/intruder pairs are shown. Results are from paired  $t$  tests comparing the last rally of the loser with either its penultimate rally or the preceding rally of the winner.

\* $P < 0.05$ ; \*\* $P < 0.01$ .

$P = 0.294$ ; resident size:  $t_{16} = 0.85, P = 0.411$ ; intruder size:  $t_{16} = -0.24, P = 0.818$ ; difference in male numbers:  $t_{16} = -1.67, P = 0.124$ ; difference in female numbers:  $t_{16} = -0.90, P = 0.385$ ).

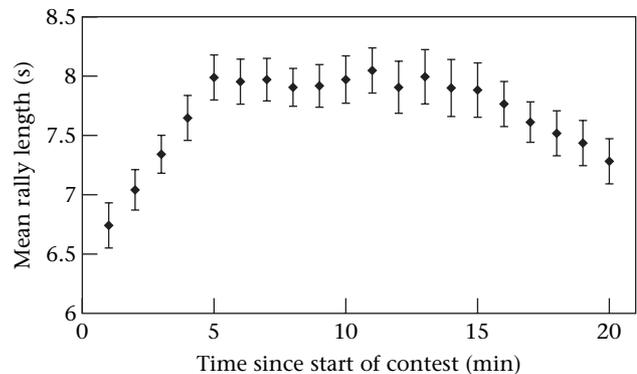
*Outcome of contests*

Resident groups won  $55.5 \pm 4.0\%$  of extended contests, which was not significantly different from that expected by chance (paired  $t$  test comparing the observed number of wins by a resident group with 50% wins:  $t_{16} = 1.38, P = 0.188$ ). However, group size was important in extended contests, with the larger group significantly more likely than the smaller one to win (weighted regression:  $F_{1,15} = 5.18, P = 0.038$ ; Fig. 3b). There was also a non-significant trend for the proportion of wins for the resident to increase with the odds ratio (weighted regression:  $F_{1,15} = 4.04, P = 0.063$ ).

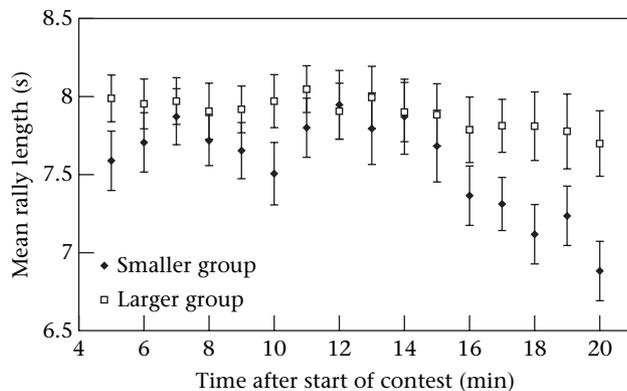
*Details of contests*

The relation between time since the start of an extended contest and average rally length was best explained by a quadratic function ( $r^2 = 0.390, P < 0.001$ ; Fig. 5). It was not possible to conduct a repeated measures ANOVA on the complete data set, since there were insufficient residual degrees of freedom.

As in short contests, there was a highly significant, positive relation between the rally lengths of the intruding group and those of the responding resident group during extended contests (ANCOVA:  $F_{1,13} = 144.06, P < 0.001$ ). However, the relation between the rally lengths of the two groups differed depending on their relative sizes (Fig. 4b). In response to intruding-group rallies of a particular length, resident groups that were larger than the intruding group gave significantly longer rallies than did smaller resident groups (ANCOVA:  $F_{1,13} = 29.17, P < 0.001$ ). This difference became increasingly apparent with increasingly long intruder rally lengths (interaction term, ANCOVA:  $F_{1,19} = 0.51, P = 0.484$ ). In other words, resident groups that were larger than intruding groups matched the rally lengths produced by the intruding group, as in short contests, but resident groups that were smaller than intruding groups failed to sustain this matching.



**Figure 5.** Change in the rally lengths of green woodhoopoe groups during extended ( $\geq 15$  min) contests. Means  $\pm$  SE are shown for 17 groups. For each group, rally lengths were averaged from each minute after the start of all contests in which they were involved.



**Figure 6.** Rally lengths given by competing green woodhoopoe groups at different stages of an extended ( $\geq 15$  min) contest. Means  $\pm$  SE are shown for 17 groups in each category. For each group, rally lengths were averaged from each minute of all contests in which they were involved.

The larger group tended to maintain a consistent rally length after the first 5 min of a contest (repeated measures ANOVA:  $F_{15,2} = 0.18$ ,  $P = 0.983$ ; Fig. 6). However, the smaller group showed a decrease in rally length after 15 min ( $F_{15,2} = 23.81$ ,  $P = 0.041$ ).

## DISCUSSION

### Contest Duration

Vocal rallying contests between the same pair of neighbouring woodhoopoe groups varied greatly in their duration. This variation was not related to either the time of day or month. Theoretically, extended contests might have arisen after changes in group membership. Among songbirds, for example, newly arrived territorial individuals have more fights with their neighbours than do established individuals, and their fights are more intense and escalate to higher levels (Krebs 1982; Eason & Hannon 1994). Experimental work on green woodhoopoes has shown that, after the removal of breeding individuals, groups rally significantly more frequently than undisturbed groups, and groups that contain no replacements rally significantly more frequently than those that do (du Plessis 1989). However, in our study, no data were collected once a group changed in size.

On some occasions, contests might have been cut short by the detection of a predator, thus distracting the groups. Alternatively, short and extended contests may have different functions. Short contests may offer opportunities to assess the composition of neighbouring groups, and thus any potential breeding vacancies (Radford 2003). Extended contests may serve a more aggressive, expansive function, whereby groups are interested in at least temporary invasions of a neighbouring territory.

### Short Contests

#### Duration and outcome

The duration of short contests was inversely related to the degree of asymmetry in group size. The more evenly

matched the contestants, the more costly the behaviour required to assess relative fighting ability. Decreasing contest length with increasing size disparity between competing individuals has been found in velvet swimming crabs, *Necora puber* (Smith et al. 1994), jumping spiders, *Euophrys parvula* (Wells 1988), fiddler crabs, *Uca annulipes* (Jennions & Backwell 1996) and African elephants, *Loxodonta africana* (Poole 1989). Our study is the first to report contest length variation dependent on the relative numbers of individuals in competing groups.

Residents won more encounters and resident advantage had more of an influence than either relative group size or odds ratio on the outcome of short contests. In many cases, intruders may have retreated after simply establishing the presence of the resident group, and its willingness to compete. This hypothesis is supported by the finding that when residents won short contests, the intruding group did not appear to be outcompeted in terms of rally length, but it left the territory anyway. It is possible that some other acoustic measure, such as rallying rate or volume, is being assessed by competitors. Alternatively, residents may have won because of asymmetries in territory ownership, as in iguanas, *Iguana iguana* (Rand & Rand 1976), speckled wood butterflies, *Pararge aegeria* (Davies 1978), great tits, *Parus major* (Krebs 1982) and European robins, *Erithacus rubecula* (Tobias 1997). Owners may place a higher value on a territory and hence have more to gain from winning for several reasons, including familiarity with resources within the territory or established relations with neighbours (Maynard Smith & Parker 1976; Getty 1987).

#### Details of contests

Rallies were sometimes given in isolation, often in the middle of a group's own territory. The length of these unprovoked rallies was positively correlated with group size, making it a potential indicator of group RHP (Radford 2003). However, the initial response rally given by a resident group tended to match the rally length given by the intruding group, making it unreliable as an indicator of group size (Radford 2003; this study). Despite an increase in the length of rallies given as short contests progressed, resident groups continued to match the rally lengths produced by intruding groups. The roaring frequency of a red deer stag is related to the frequency of roars it hears (Clutton-Brock & Albon 1979), while songbird countersinging often involves males matching the song type of their territorial rivals (Krebs et al. 1981; McGregor et al. 1992). Krebs et al. (1981) suggested that by controlling the degree to which they match their rival's song, male songbirds provide information on their willingness to escalate conflicts. Similarly, the more closely a resident woodhoopoe group matches an intruding group's rally length, perhaps the greater its willingness or ability to continue the contest.

On a coarse scale, matching seemed to occur throughout short contests, whether the resident group was larger or smaller than the intruding group. However, in contests won by the intruding group, the final rally given by the losing resident group was shorter than its previous rallies

and shorter than the preceding one given by the intruding group. Once a resident group fails to match the rally length of its opponent, either through reduced motivation or because of physiological constraints, there may be little point in continuing to vocalize, since the contest outcome has effectively been decided. It is at this point that the true size of the resident group becomes apparent, assuming that rally length, rather than rate or volume, is the indicator used.

### Extended Contests

In contrast to short contests, there was no obvious resident advantage in extended contests. Instead, the larger group was more likely to win, and group size difference explained more of the variation in contest outcome than did the odds ratio. Thus, for both short and extended contests, the outcome appeared to depend on a single dominant asymmetry (residency for short contests and relative group size for extended contests), as predicted by Hammerstein (1981). Larger groups defeat smaller ones in many species of primates (Cheney 1986) and larger groups of lions, *Panthera leo*, can successfully repel smaller ones in territorial contests (Packer et al. 1990).

In extended contests between woodhoopoes, the rally lengths of smaller groups tended to tail off, whereas those of larger groups were maintained at a higher level for longer. To produce a particular rally length, individuals from smaller groups must contribute more effort than those in larger groups (Radford 2003). If participation in rallying is energetically costly, which is possible considering the amount of bowing that is involved (personal observation), there may be a physiological constraint on how long groups of different size can sustain a particular length of rallying. Alternatively, individuals in small groups may be less motivated to continue with the contest, even if they are physiologically capable of doing so.

### Comparison with Theoretical Models

Lanchester's (1916) two quantitative models provide predictions about conflicts between groups. The 'square law' states that the ability of a group to win escalated contests is proportional to the square of group size, but rises only linearly with individual fighting abilities, and assumes that members of the more numerous group can concentrate their attacks on members of their less numerous foe. Under the 'linear law', members of the more numerous group are unable to concentrate attacks, and group strength is linearly proportional to both group size and individual fighting ability. The square law has been invoked to explain the behaviour of a number of ant species (e.g. Franks & Partridge 1993; Whitehouse & Jaffe 1996; McGlynn 2000), and may be applicable to chimpanzee, *Pan troglodytes*, battles (Wilson et al. 2002). Although woodhoopoe contests also satisfy some assumptions of the square law, for example participation of all group members in the contests (Radford 2003), no recruitment to the group during contests, and an important

role of group size disparity, we believe Lanchester's laws may be less applicable than in the species described above. This is because, in several thousand intergroup contests viewed over 20 years, only a handful have ever ended in physical attacks, and never has a woodhoopoe been seen to be injured or killed by a conspecific (personal observation). Furthermore, whereas the laws have been successfully used to calculate when a group or individual should enter a contest (Wilson et al. 2002), our study examined only contests that had actually begun. This emphasizes the need for new models that consider additional aspects of group interactions.

It is important to remember that there is a complex interplay of interactions apparent when groups compete. This is because the response of the group to an intruder is the product of decisions made by several different individuals. Radford (2003) showed that individuals of different sex and dominance class respond differently depending on, among other things, the composition of the intruding group. The motives behind territory defence and the assessment of breeding vacancies might differ for different individuals, and the emphasis on one or the other might change with age. It is the resulting responses of individuals that lead to the within-contest patterns seen here. 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).

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