

# Bill dimorphism and foraging niche partitioning in the green woodhoopoe

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## Summary

1. Cooperatively breeding green woodhoopoes, *Phoeniculus purpureus*, forage mainly as close-knit groups, creating opportunities for intrasexual and intersexual foraging competition.

2. Adult males foraged on wider branches than adult females, probably as a consequence of their larger body size (5–8%). Moreover, adult males spent more time scaling bark and probing the ends of broken branches, while adult females preferred pecking. There was no intersexual difference in the use of hole probing or surface gleaning.

3. Intersexual differences in foraging technique probably resulted from morphological differences: adult male bills were 36% longer than those of females, with no overlap between the sexes. In support of the specialization hypothesis: (a) birds were more likely to forage in close proximity to a member of the opposite sex; (b) there was more intrasexual than intersexual aggression during foraging; (c) lone females did not change their foraging behaviour from when in close proximity to a male; (d) the niche breadth of both sexes was similar; and (e) juveniles foraged in ways predicted from their bill lengths. On fledging, bills of juvenile males and females were the same length as those of adult females, and all juveniles fed like adult females. After 4 months, the bills of juvenile males exceeded those of adult females, and they began to forage like adult males.

4. Adult males brought different invertebrate taxa and heavier prey to the nest than females. These differences were a consequence of the different foraging techniques used, because both sexes collected the same types of prey when using the same technique.

5. When all group members foraged together, dominant adults spent more time hole probing than subordinates of the same sex. This intrasexual difference probably resulted from interference competition, as dominants and subordinates did not differ in bill length, and dominants excluded subordinates from prime feeding areas.

6. To compensate, subordinate adults did not increase their foraging time or collect larger prey items than dominants, but more often left the group to forage alone. When alone, subordinates spent more time hole probing and experienced higher foraging success than when in a group.

*Key-words:* interference competition, *Phoeniculus purpureus*, sexual differences, social dominance, specialization hypothesis.

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## Introduction

Individuals within a population may vary considerably in the way they exploit available food resources, thus broadening the species' niche width and reducing intraspecific competition (Selander 1966; Hogstad

1978; Grant 1986). Individual differences in feeding behaviour can be related to age (Partridge & Green 1985), social dominance (Schneider 1984) and sex (Morse 1980). Sex-specific niche segregation and consequent resource partitioning may arise through sexual dimorphism, where males and females specialize on different resources (specialization hypothesis, e.g. Selander 1966; Aulén & Lundberg 1991). Foraging differences therefore represent different preferences for each sex and foraging behaviour should not change in

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**Table 1.** Predictions concerning foraging niche partitioning in the green woodhoopoe

Behaviour	Intersexual conflict (specialization hypothesis)	Intrasexual conflict (interference hypothesis)
Foraging proximity	Individuals of the opposite sex should be more likely than those of the same sex to forage together	Individuals of the same sex should not be found foraging in close proximity
Aggression	There should be little intersexual aggression	Intrasexual aggression is expected to be more common
Foraging alone	Individuals should exhibit no change in behaviour when foraging alone compared to when in the presence of the other sex	Subordinate behaviour is expected to change in the absence of dominant individuals of the same sex
Niche breadth	Expected to be similar in the two sexes	Should be larger in subordinates
Success rate	Overall success rate should be similar. However, success might vary when the sexes are using the same technique, as a result of specialization by one of them for that particular method of foraging	Subordinates should experience a decreased success rate if they are pushed into inferior feeding areas

the presence of the other sex. Probably the most dramatic case of covariation in anatomy and foraging behaviour was provided by the extinct New Zealand huia, *Heteralocha acutirostris*. Males used their short, straight bills to hammer beetle larvae out of decaying wood, while females probed crevices and tunnels with their slender, decurved bills (Buller 1888). Alternatively, foraging opportunities could be restricted by the behaviour of others (interference hypothesis, e.g. Ligon 1968; Hogstad 1976, 1978; Peters & Grubb 1983; Schneider 1984). The larger sex may exclude the smaller from the best sites, leading to a niche shift (Desrochers 1989). In this case, subordinates should alter their behaviour in the absence of dominants, but not vice versa.

The green woodhoopoe, *Phoeniculus purpureus* (also called the red-billed woodhoopoe), a cooperatively breeding, territorial bird, provides an excellent opportunity to study foraging niche partitioning. Each group consists of a single breeding pair and up to 10 non-breeding helpers (du Plessis 1991), and spends much of its time feeding as a close-knit unit, creating opportunities for both intersexual and intrasexual conflict over foraging resources. Here, we begin by demonstrating remarkable sexual dimorphism in bill length: males have 36% longer bills than females, with no overlap between adult males and females. We then show intersexual and intrasexual differences in the type of prey brought to the nest and the preferred foraging technique. Foraging differences between males and females may be related to sexual dimorphism in bill length, whereas intrasexual differences may be the result of dominance hierarchies within the group. A number of predictions can therefore be made (Table 1).

To test these predictions, we analyse data from naturally foraging groups of green woodhoopoes. Because juvenile bills continue to grow for some time after fledging, we compare the foraging behaviour of juveniles of different ages with that of adults, to gain further insight into the importance of bill morphology. Finally, we ask how subordinates compensate for reduced foraging success when feeding in a group with dominant individuals.

## Methods

### MORPHOMETRIC DATA

Green woodhoopoes were caught between 1981 and 2001 around Morgan's Bay (32°43' S, 28°19' E) in the Eastern Cape Province, South Africa, using nets placed over roost holes before dawn. To avoid sampling biases, only the first set of measurements from any given individual was included in the analysis. Five measurements were taken: (a) mass (in grams) using a 100-g Pesola balance; (b) flattened wing chord, i.e. distance from the carpal joint to the tip of the longest primary; (c) tarsus length, along the anterior surface between the articulation with the middle toe and the tibiotarsal joint; (d) bill length, i.e. the chord between the tip of the bill and the anterior edge of the cere; and (e) tail length. Wing and tail lengths were measured to the nearest millimetre with a stopped ruler. Bill and tarsus lengths were determined to the nearest 0.1 mm with dial callipers. Each bird was marked with an individual combination of colour rings and a uniquely numbered aluminium ring. Because green woodhoopoes become physiologically capable of reproducing after 1 year (unpublished data), birds older than this were classified as adults. Male bill length exceeded that of females 4 months after fledging, so individuals aged 4–12 months were referred to as 'full-grown' juveniles. Those under 4 months old were called 'growing' juveniles. Adults could be sexed by vocalizations, while juvenile males have a brown throat patch not found in females (Ligon & Ligon 1990).

### PREY DELIVERY TO THE NEST

Data were collected in 1986/1987 (10 nests), 1999/2000 (six nests) and 2000/2001 (12 nests). Nest sites were located by following birds returning with food. Nest watches were conducted from 20 to 35 m away using binoculars, and lasted for an hour after the first feed. Groups usually resumed normal activities around the nest within 10–15 min of the observer's arrival. The

time, the individual's identity and, where possible, the type and size of the prey were noted each time a bird returned with food. Prey size was expressed as the ratio of prey length to bill length of a female woodhoopoe (taken as 46 mm). When males fed nestlings directly, prey size relative to bill length was adjusted by a factor of 1.3 to correct for the difference in mean bill lengths between the sexes. Prey biomass was calculated from the formula of Rogers, Hinds & Buschbom (1976):

$$B = (0.0305 L)^{2.62}$$

where  $B$  is the dry biomass in mg and  $L$  is the body length in mm.

#### FORAGING BEHAVIOUR

Data were collected from 81 colour-ringed individuals in 30 groups (mean  $\pm$  SE size:  $3.7 \pm 0.3$ , range: 2–8), from January to May 2001 and January to March 2002. During this period, all group members foraged together, because either breeding had failed or young had fledged. Individuals were monitored continuously from when they were first seen until they vanished from sight. To increase sample independence, each individual was observed only once per day, although sequences shorter than 10 s were discarded and the bird was watched again. On any given day, data were collected from all group members. Observations were made during clear weather between 0500 and 1000 h and between 1500 and 1900 h, as this was when birds were most active (personal observation). The following were recorded into a dictaphone and later transcribed: (a) individual; (b) substrate condition (alive or dead, smooth or flaky); (c) foraging height (2 m intervals); (d) substrate diameter (estimated relative to the width of the woodhoopoe's back); and (e) foraging technique. Foraging techniques recognized were: (i) end probing (probing the broken end of a branch); (ii) hole probing (probing existing cracks and narrow crevices); (iii) scaling (removal of loose bark); (iv) pecking; and (v) surface gleaning (picking prey off the surface). Each successful attempt was noted, and the success rate for each individual using each technique was calculated. Where possible, the identity and size of the prey item were noted. In addition, all agonistic interactions and the identity of any bird foraging within 1 m of the focal individual were recorded. The proportion of time devoted to foraging, as compared to allopreening, vocal rallying and movement, was estimated for each individual. On occasion, group members moved a considerable distance (> 200 m) to forage alone. Foraging data were collected from subordinates separated from the group in this fashion. Due to the strict queuing system operating in this species, breeders tend to be those individuals of each sex that have been in the group the longest (unpublished data). When this information was unknown, breeding status was established by watching copulation attempts (preliminary paternity analysis has confirmed that only

the dominant pair breed; unpublished data). Breeders were referred to as 'dominants', while 'subordinate' encompassed all adult helpers.

#### DATA ANALYSIS

To normalize the data, all morphometric variables were log<sub>e</sub> transformed and all proportions were arcsine square-root transformed prior to statistical analysis. Summary statistics are presented as means  $\pm$  SE. Stepwise discriminant function analysis (DFA) was used to provide a set of weightings that indicated the degree of accuracy with which sex could be assigned from knowledge of certain morphometric measurements.

To investigate variations in prey delivered to the nest, only individuals which brought at least 10 items were included in the analysis. Foraging behaviour was analysed using individuals for which at least eight foraging sequences were recorded. The proportion of observations per variable (e.g. pecking) within each category (e.g. technique) was calculated for each individual. For substrate diameter and foraging height, the average per individual was calculated. Because the proportions of all variables in a given category sum to one, they are not independent (Aebischer, Robertson & Kenward 1993). To circumvent this unit-sum constraint, those variables of each category having the lowest values in most individuals were excluded from the analysis (see e.g. Pasinelli 2000).

Variables describing different aspects of foraging behaviour are likely to be correlated (e.g. foraging height and substrate diameter). Therefore, a principal components analysis (PCA) was first conducted. Components with eigenvalues > 1.0 were then used as independent variables in a DFA, to test whether the sexes differed significantly in foraging behaviour. A similar analysis was carried out for each sex separately, to predict the dominance status of each adult based on its foraging behaviour.

Foraging niche breadth was calculated for each individual with a standardized version of Levins' index (Hurlbert 1978):

$$B_A = \frac{(1/\sum p_j^2) - 1}{n - 1}$$

where  $B_A$  = Levins' standardized niche breadth,  $p_j$  = proportion of times resource state  $j$  was used ( $\sum p_j = 1.0$ ),  $n$  = number of possible resource states. The degree of niche overlap was determined using Schoener's index (Schoener 1968):

$$O = 1 - 1/2 \sum |p_{x,i} - p_{y,i}|$$

where  $O$  = Schoener's index which varies from 0 (no overlap) to 1 (complete overlap), and  $p_{x,i}$  and  $p_{y,i}$  are the frequencies for classes  $x$  and  $y$ , respectively, for the  $i$ th category.

Agonistic interactions during foraging were analysed using ANOVA, to test for differences in the rate of

displacement between the sexes and between dominance classes. This rate was corrected for the relevant number of individuals within the group and thus the likelihood of encountering such an individual. To investigate the impact of male proximity on female foraging behaviour, paired *t*-tests with Bonferroni corrections (Rice 1989) were used to compare the technique and the diameter of the substrate used by the same 17 females when foraging separately or within 1 m of a male. Changes in the foraging behaviour of subordinates when feeding away from the group were similarly examined. However, since there were insufficient data for all individuals under both conditions (i.e. within a group and while foraging alone), unpaired *t*-tests with Bonferroni corrections (Rice 1989) were used.

## Results

### MORPHOMETRICS

Data from 550 individuals (277 males and 273 females) were analysed, although not all measurements were

available for every individual. Bill length varied significantly with age (ANOVA:  $F_{1,404} = 127.04$ ,  $P < 0.001$ ), because bills of both males and females continued to grow for several months after fledging (Fig. 1). Juvenile males overlapped with females in bill length; both were shorter than those of adult males (sex  $\times$  age interaction:  $F_{1,404} = 19.29$ ,  $P < 0.001$ ; Fig. 1). Adult males were significantly heavier and had significantly longer wings, tarsi, tails and bills than adult females (Table 2). There was no overlap between the bill lengths of adult males and females. DFA indicated that bill length alone resulted in 99.5% of all adults being assigned to the correct sex (Wilk's  $\lambda = 0.116$ ,  $F_{1,194} = 1418.2$ ,  $P < 0.001$ ; 99.0% of males and 100% of females). Controlling for body mass, males had significantly longer bills than females (ANCOVA:  $F_{1,191} = 598.88$ ,  $P < 0.001$ ).

### PREY DELIVERED TO THE NEST

Twenty-eight nests, each from a different group, were watched for a total of 232 h ( $8.29 \pm 0.77$  h). Sufficient data were available from 58 adults. A single prey item

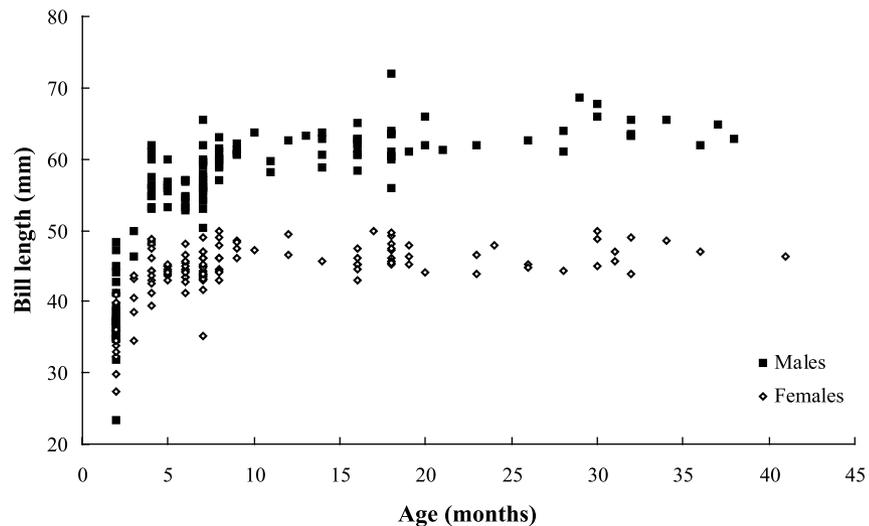
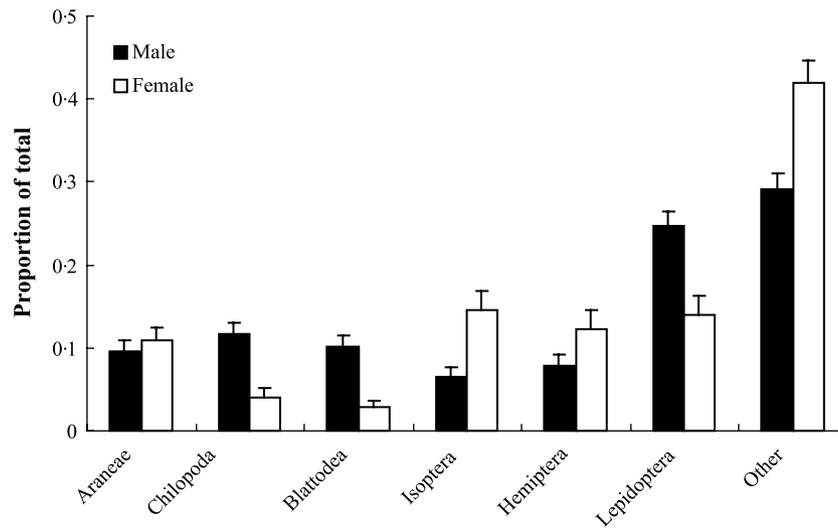


Fig. 1. Distribution of bill length with age in wild-caught green woodhoopoes. Each data point represents a different individual.  $n = 125$  males, 127 females.

Table 2. Univariate comparisons of measurements from wild-caught, adult green woodhoopoes. The percentage difference is expressed as the difference in mean values between the sexes in relation to that for females. \*\*\* $P < 0.001$

Measure	Sex	<i>n</i>	Mean	Sd	Range	<i>t</i> (d.f.)	% difference
Bill length (mm)	M	98	62.6	3.3	51.4–72.0	43.28*** (193)	35.5
	F	98	46.2	2.0	41.0–50.6		
Tail length (mm)	M	80	174.7	8.8	140–192	5.95*** (160)	5.4
	F	82	165.7	9.7	125–179		
Tarsus length (mm)	M	93	24.5	1.8	16.0–26.7	6.66*** (187)	7.5
	F	97	22.8	1.4	17.0–26.8		
Wing length (mm)	M	99	140.4	3.4	130–148	46.40*** (197)	6.0
	F	101	132.4	3.5	124–140		
Mass (g)	M	99	83.0	4.5	70.0–96.6	18.25*** (195)	17.1
	F	99	70.9	4.7	57.4–88.5		
Cube root mass	M	99	4.4	0.1	4.1–4.6	18.25*** (195)	7.3
	F	99	4.1	0.1	3.9–4.5		



**Fig. 2.** Distribution of the seven main prey types brought to the nest by adult green woodhoopoes. Shown are means + SE.  $n = 34$  males, 24 females.

was delivered on each of the 1792 recorded visits to the nest. Nine categories of prey were identified: spiders (Araneae), centipedes (Chilopoda), cockroaches (Blattodea), mantids (Mantidae), termites (Isoptera), bugs (Hemiptera), caterpillars (Lepidoptera), fruit and ‘other invertebrates’, which encompassed prey types not readily identifiable in the other groups. A MANOVA, using the seven most common prey types (which made up 94.2% of the selection), showed no significant effect of dominance class on the proportion of prey types brought to the nest ( $F_{7,47} = 0.61$ ,  $P = 0.748$ ). However, both year ( $F_{14,47} = 2.37$ ,  $P = 0.007$ ) and sex ( $F_{7,47} = 9.06$ ,  $P < 0.001$ ) had a significant influence on prey delivered. Separate ANOVA revealed that males delivered significantly more caterpillars ( $F_{1,53} = 15.98$ ,  $P < 0.001$ ; Fig. 2), centipedes ( $F_{1,53} = 26.00$ ,  $P < 0.001$ ) and cockroaches ( $F_{1,53} = 21.86$ ,  $P < 0.001$ ) and significantly fewer termites ( $F_{1,53} = 10.93$ ,  $P = 0.004$ ) and ‘other invertebrates’ ( $F_{1,53} = 14.21$ ,  $P < 0.001$ ) than females. The proportion of ‘other invertebrates’ ( $F_{2,53} = 3.97$ ,  $P = 0.032$ ) and spiders ( $F_{2,53} = 3.79$ ,  $P = 0.041$ ) varied significantly between years.

Males delivered significantly heavier prey than females (males =  $0.47 \pm 0.03$  g, females =  $0.27 \pm 0.05$  g;  $t = 3.51$ , d.f. = 56,  $P < 0.001$ ). There was no significant difference in the biomass of prey delivered by dominant and subordinate males ( $t = 0.56$ , d.f. = 32,  $P = 0.580$ ) or females ( $t = 0.40$ , d.f. = 22,  $P = 0.690$ ). Caterpillars, centipedes and cockroaches were significantly heavier than other prey items delivered (ANOVA:  $F_{6,1631} = 106.26$ ,  $P < 0.001$ ).

#### FORAGING BEHAVIOUR OF ADULTS

Sufficient data were available from 55 adults, with a total observation time of 11 h 05 min. In all, there were 1174 sequences of observations (mean time per sequence  $34 \pm 8$  s, range: 11–94 s). PCA reduced the eight variables

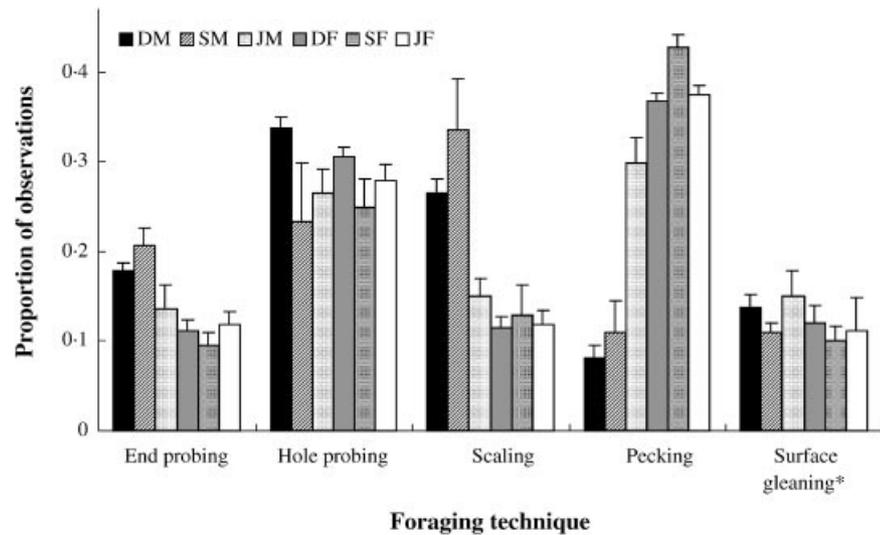
describing foraging behaviour to three components, accounting for 73.4% of the total variation (Table 3). Variables with loadings  $\geq |0.45|$  were used for interpretation (Aspey & Blankenship 1977). Component 1 characterized foraging behaviour and substrate diameter: end probing and scaling were combined with substrate diameter, and the component was positively correlated with the proportion of pecking. Component 2 reflected the proportion of hole probing. Component 3 contrasted type of substrate with average foraging height.

DFA indicated successful discrimination of adult male and female foraging behaviour based on component 1 (Wilk’s  $\lambda = 0.22$ ,  $F_{1,53} = 184.06$ ,  $P < 0.001$ ): males foraged on thicker substrates (male =  $7.25 \pm 0.19$  cm, female =  $5.96 \pm 0.16$  cm) and spent more time scaling and end probing, and less time pecking, than females (Fig. 3). The model correctly classified 100% of adult males and females.

DFA also indicated successful discrimination of both dominant and subordinate males (Wilk’s  $\lambda = 0.66$ ,

**Table 3.** Components extracted by principal components analysis (eigenvalue > 1.0) of foraging variables for 55 adult green woodhoopoes. Numbers in bold are loadings  $\geq |0.45|$  used for interpretation of the components

Variables	Component		
	1	2	3
Living substrate (%)	-0.022	-0.362	<b>-0.530</b>
Smooth surface (%)	0.154	0.418	<b>-0.614</b>
Foraging height (m)	0.031	0.397	<b>0.482</b>
Substrate diameter (cm)	<b>-0.457</b>	0.000	-0.051
End probing (%)	<b>-0.457</b>	0.136	-0.277
Hole probing (%)	0.055	<b>0.656</b>	-0.105
Scaling (%)	<b>-0.521</b>	-0.150	0.143
Pecking (%)	<b>0.531</b>	-0.256	-0.004
Eigenvalue	2.909	1.692	1.267
Explained variance (%)	36.4	21.2	15.8



**Fig. 3.** Foraging techniques used by green woodhoopoes. DM = dominant adult male ( $n = 22$ ), SM = subordinate adult male ( $n = 6$ ), JM = juvenile male less than 4 months after fledging ( $n = 7$ ), DF = dominant adult female ( $n = 21$ ), SF = subordinate adult female ( $n = 6$ ), JF = juvenile female less than 4 months after fledging ( $n = 8$ ). Shown are means + SE. \*Variable excluded from analysis (unit-sum constraint, see Methods).

$F_{1,26} = 13.42$ ,  $P = 0.001$ ) and females (Wilk's  $\lambda = 0.76$ ,  $F_{1,26} = 8.02$ ,  $P = 0.009$ ) based on component 2: for both sexes, dominants hole probed more often than subordinates (Fig. 3). The models correctly classified 78.6% of males and 81.5% of females.

There was no significant difference in the type of prey caught by males and females using the same foraging technique (end probing:  $\chi^2_6 = 1.39$ ,  $P = 0.967$ ; hole probing:  $\chi^2_6 = 8.38$ ,  $P = 0.212$ ; scaling:  $\chi^2_6 = 6.57$ ,  $P = 0.363$ ; pecking:  $\chi^2_6 = 2.10$ ,  $P = 0.910$ ; surface gleaning:  $\chi^2_6 = 5.06$ ,  $P = 0.536$ ). When combining prey caught by both sexes, there was a significant difference in the types caught using different techniques ( $\chi^2_{24} = 42.68$ ,  $P = 0.011$ ). By combining the proportion of time spent using a technique with the likelihood of capturing a particular prey type using that technique, values for overall prey-type acquisition were calculated for each sex. There was no significant difference between these values and the proportion of each prey type delivered to the nest (paired  $t$ -test:  $t = 0.17$ , d.f. = 14,  $P = 0.866$ ). Neither was there any significant difference in the biomass of prey caught for themselves by dominant and subordinate males ( $t = 0.16$ , d.f. = 26,  $P = 0.830$ ) or females ( $t = 0.29$ , d.f. = 25,  $P = 0.680$ ).

Comparing individuals from the same group, there was no significant difference between the sexes in the proportion of time spent foraging (paired  $t$ -test:  $t = 0.39$ , d.f. = 19,  $P = 0.702$ ). However, there was a non-significant tendency for subordinates to forage for longer than dominants ( $t = 1.96$ , d.f. = 13,  $P = 0.074$ ).

#### FORAGING BEHAVIOUR OF JUVENILES

The following analysis compared the foraging techniques of adults (combining dominants and subordinates of the same sex) with those of juveniles less than 4 months

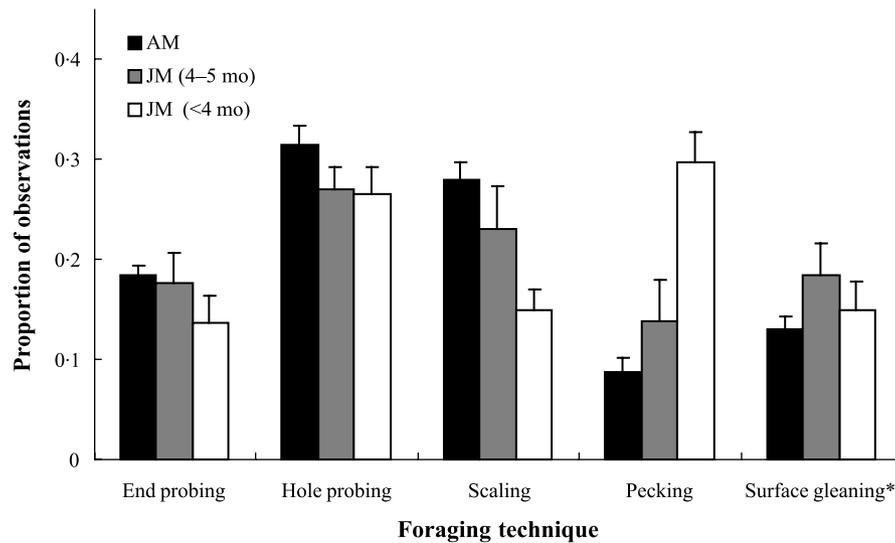
old. Sufficient data, collected over the same time period as those for adults, were available from 15 of these growing juveniles. A MANOVA revealed that the key result was the interaction term between sex and age ( $F_{4,63} = 17.69$ ,  $P < 0.001$ ). Both male and female juveniles foraged in a similar fashion to adult females: there was a significant difference in the proportion of end probing, scaling and pecking used by adult and juvenile males (Fig. 3).

Figure 4 shows the switch in foraging behaviour of juvenile males when aged 4–12 months but, due to time constraints, insufficient data were collected to test this statistically. Full-grown juvenile males scaled for a greater proportion of time than growing juveniles, with a concurrent decrease in pecking. Thus, they foraged in a fashion more similar to adult males than adult females.

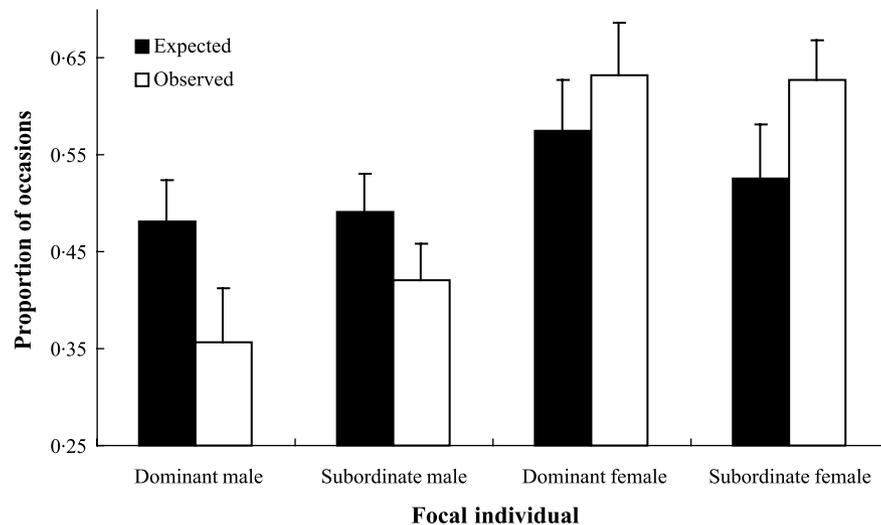
#### PROXIMITY OF OTHERS

Within a foraging group, males were significantly more likely than females to forage separately, rather than within 1 m of another individual (ANOVA:  $F_{1,41} = 11.55$ ,  $P = 0.002$ ), as were subordinates compared to dominants ( $F_{1,41} = 5.47$ ,  $P = 0.025$ ). When foraging within 1 m of another individual, that individual was significantly more likely to be of the opposite sex than expected from the group composition ( $\chi^2_1 = 27.41$ ,  $P < 0.001$ ; Fig. 5). This was also true when considering dominants ( $\chi^2_1 = 13.14$ ,  $P < 0.001$ ) and subordinates ( $\chi^2_1 = 14.26$ ,  $P < 0.001$ ) separately.

Dominants were significantly more likely than subordinates to displace another individual ( $t = 5.56$ , d.f. = 40,  $P < 0.001$ ). Intrasexual displacement was significantly more likely to occur than intersexual displacement (paired  $t$ -test:  $t = 6.76$ , d.f. = 42,  $P < 0.001$ ; Fig. 6).



**Fig. 4.** Differences in foraging technique used by green woodhoopoe males of different ages. AM = adult male ( $n = 28$ ), JM = juvenile male ( $n = 7$ ). Shown are means + SE. \*Variable excluded from analysis (unit-sum constraint, see Methods).



**Fig. 5.** Expected and observed proportion of occasions that the nearest foraging individual (within 1 m) was a male. Shown are means + SE.  $n = 18$  males, 24 females.

#### PLASTICITY IN BEHAVIOUR

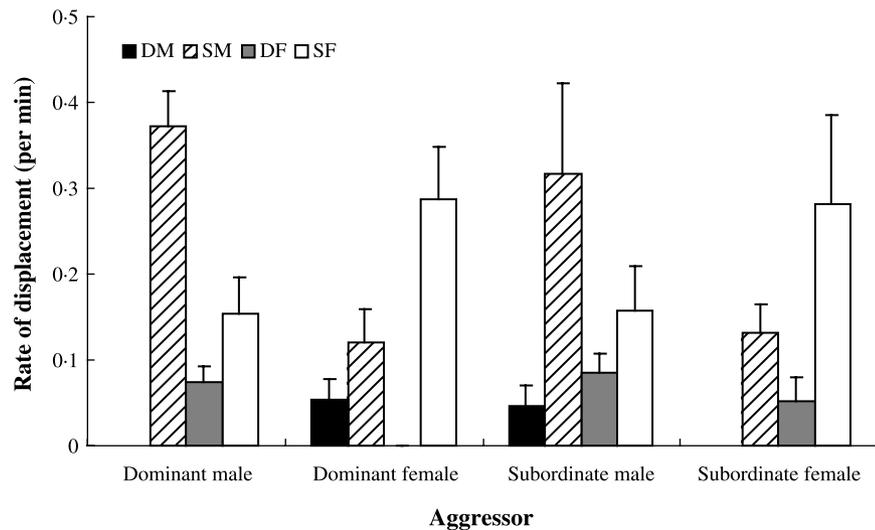
Within a foraging group, adult females did not alter their technique (paired  $t$ -test: end probing:  $t = 1.59$ , d.f. = 16,  $P = 0.131$ ; scaling:  $t = 1.40$ , d.f. = 16,  $P = 0.179$ ; pecking:  $t = 0.61$ , d.f. = 16,  $P = 0.548$ ) nor use a substrate with a different average diameter ( $t = 0.71$ , d.f. = 16,  $P = 0.487$ ) when foraging separately compared to in close proximity to a male.

Subordinate females changed their foraging behaviour when they temporarily left the group. They increased their hole probing significantly ( $t = 3.55$ , d.f. = 11,  $P = 0.005$ ; Fig. 7) and decreased their pecking ( $t = 5.31$ , d.f. = 11,  $P < 0.001$ ), although there was no significant change in the proportion of end probing ( $t = 0.11$ , d.f. = 11,  $P = 0.920$ ) or scaling ( $t = 0.72$ , d.f. = 11,  $P = 0.490$ ), nor in the average diameter of

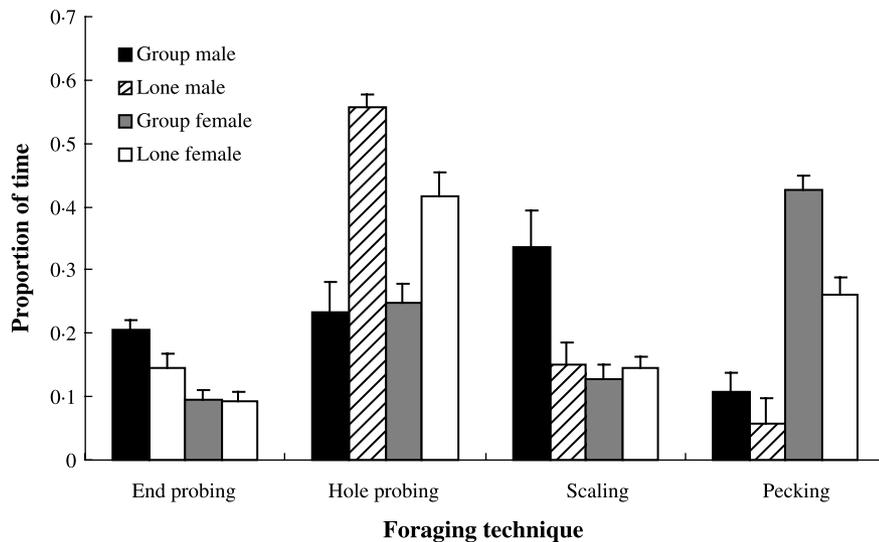
substrate used ( $t = 0.61$ , d.f. = 11,  $P = 0.550$ ). Subordinate males increased their hole probing significantly ( $t = 5.08$ , d.f. = 9,  $P < 0.001$ ; Fig. 7) and decreased their end probing ( $t = 2.61$ , d.f. = 9,  $P = 0.028$ ) and scaling ( $t = 3.11$ , d.f. = 9,  $P = 0.013$ ) when foraging away from the group. No other significant differences were apparent (pecking:  $t = 1.68$ , d.f. = 9,  $P = 0.130$ ; diameter:  $t = 1.98$ , d.f. = 9,  $P = 0.079$ ). The foraging success rates of subordinate individuals significantly increased when they foraged away from the group (group =  $0.14 \pm 0.01$ , alone =  $0.17 \pm 0.01$ ;  $t = 4.06$ , d.f. = 22,  $P < 0.001$ ).

#### FORAGING NICHE

Adult males had a broader foraging niche than adult females with respect to height in tree, substrate



**Fig. 6.** Displacement of different classes of individual during foraging. Rates are given as the number of displacements per minute by the focal individual during watches on that individual, corrected for the number of that sex and dominance class in the group. DM = dominant male, SM = subordinate male, DF = dominant female, SF = subordinate female. Shown are means + SE.



**Fig. 7.** Differences in foraging behaviour exhibited by subordinate adult green woodhoopoes foraging away from the group (lone) compared to with dominant group members of the same sex (group). Some individuals provided data for both categories. Shown are means + SE.  $n = 10$  males, 8 females.

diameter and foraging technique, but the difference was significant only for technique (Table 4). Subordinate birds had a broader foraging niche than dominants with respect to height in tree, substrate diameter and foraging technique, although the difference was significant only for height. Niche overlap was high for all variables.

#### SUCCESS RATES

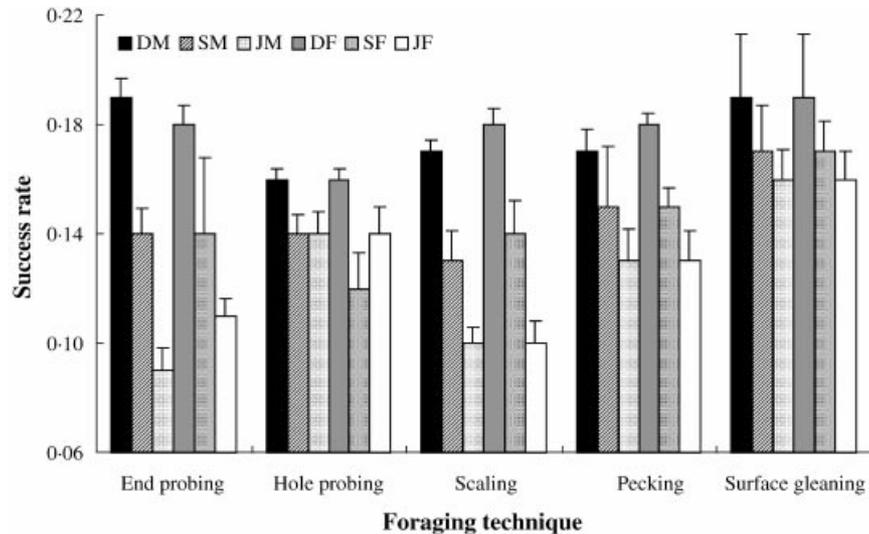
Adult males and females did not differ significantly in their success rates for any of the five foraging techniques (MANOVA, controlling for group size:  $F_{5,48} = 1.18$ ,  $P = 0.334$ ; Fig. 8). Dominant males were significantly

more successful than subordinate males when end probing, hole probing and scaling (all  $F_{1,26} > 12.50$ ,  $P < 0.001$ ; Fig. 8). Dominant females were significantly more successful than subordinate females with all foraging techniques except surface gleaning (all  $F_{1,25} > 10.10$ ,  $P < 0.001$ ; Fig. 8). There was no increase in success rate by either adult males (MANOVA:  $F_{5,22} = 0.78$ ,  $P = 0.693$ ) or females ( $F_{5,21} = 0.55$ ,  $P = 0.843$ ) foraging within 1 m of a member of the opposite sex compared to separately.

Both growing juvenile males and females were less successful than subordinate adults when foraging using any of the techniques (MANOVA:  $F_{5,17} = 3.03$ ,  $P = 0.039$ ), although the difference was significant only for end probing and scaling (Fig. 8).

**Table 4.** Foraging niche dimensions of 55 adult green woodhoopoes. Niche breadth calculated for each individual separately by standardized Levins' index (Hurlbert 1978) and niche overlap with the index of Schoener (1968); 0 = smallest and 1 = largest breadth/overlap. Shown are medians or means for the relevant class. *U* and *t*-values are from Mann–Whitney *U*-tests and unpaired *t*-tests, respectively. †Not significant, \**P* < 0.05, \*\**P* < 0.01

Foraging category	Niche breadth			Niche overlap M/F	Niche breadth			Niche overlap D/S
	Male	Female	<i>U/t</i>		Dominant	Subordinate	<i>U/t</i>	
Alive/dead	0.95	0.95	<i>U</i> = 806†	1.00	0.96	0.94	<i>U</i> = 1280†	0.93
Smooth/flaky	0.96	0.96	<i>U</i> = 745†	0.98	0.97	0.96	<i>U</i> = 1262†	0.95
Height in tree	0.59	0.58	<i>t</i> = 0.33†	0.97	0.60	0.51	<i>t</i> = 2.60*	0.93
Substrate diam.	0.66	0.59	<i>t</i> = 1.84†	0.91	0.63	0.62	<i>t</i> = 0.30†	0.85
Technique	0.75	0.67	<i>t</i> = 3.04**	0.71	0.71	0.69	<i>t</i> = 0.70†	0.91



**Fig. 8.** Success rates of green woodhoopoes foraging using different techniques. DM = dominant adult male (*n* = 22), SM = subordinate adult male (*n* = 6), JM = juvenile male less than 4 months after fledging (*n* = 7), DF = dominant adult female (*n* = 21), SF = subordinate adult female (*n* = 6), JF = juvenile female less than 4 months after fledging (*n* = 8). Shown are means + SE.

## Discussion

### SEXUAL DIFFERENCES

Foraging differences between the sexes should be strongest when males and females forage in a common area (Hogstad 1976, 1978). Groups of green woodhoopoes often forage as a close-knit unit, creating potential within-group conflict over food resources. However, males and females brought different prey items to the nest and preferred different foraging techniques: males spent more time end probing and scaling, while females spent more time pecking. Moreover, females foraged on smaller-diameter substrates.

### SPECIALIZATION HYPOTHESIS?

In most species studied, sex differences in foraging are the result of behavioural plasticity, with the larger sex preventing the smaller from feeding in preferred areas (e.g. Desrochers 1989; Aho *et al.* 1997; but see also, e.g.

Aulén & Lundberg 1991). In the green woodhoopoe, however, differences in phenotype, specifically bill length, were likely to be important. This specialization hypothesis was supported by several lines of evidence. First, individuals were more likely to forage with a member of the opposite sex than predicted by group composition. This did not simply reflect mate-guarding, because data were collected after breeding was completed and subordinates also foraged more often with an individual of the opposite sex. Second, there was more intrasexual than intersexual displacement activity, despite individuals of the opposite sex foraging in close proximity. In fact, aggression between the sexes during foraging was relatively rare. The increased intrasexual aggression could reflect competition for breeding vacancies or helpers jostling for long-term positions. However, much less displacement behaviour was seen in non-foraging situations, such as preening and vocal rallying (personal observation), suggesting the aggression was related to foraging. Third, there was no significant alteration in the behaviour of females

foraging separately compared to in close proximity to a potentially dominating male. Fourth, males had broader foraging niches than females, contrary to what would be predicted if larger males were forcing smaller females into less preferred feeding sites (Morse 1980). In reality, morphological differences may lead to either a broader or a narrower niche, since the number of available foraging sites may increase or decrease depending on the specialization.

The only prediction of the specialization hypothesis that was not met concerned foraging success rates. However, the lack of a significant difference in male and female success rate when using the same technique, despite certain preferences, may be because individuals chose to use a less preferred technique only when the rewards were unusually high. The low success rate of juveniles was not because they were excluded from all but the worst sites, since they often foraged in close proximity to the dominant pair (personal observation). Thus, although young animals are generally poor competitors, which adversely affects their feeding opportunities (e.g. van Horne 1982; Goss-Custard & Durell 1983), interference competition does not seem to play an important age-related role in the green woodhoopoe. Exploitative competition may have resulted in the lower juvenile success rate if dominant adults removed many prey items before juveniles foraged in the same area. Alternatively, the lower success rate, particularly when scaling and end probing, could have resulted from inexperience. Juveniles may need time to learn and perfect particular foraging techniques: foraging skills of white-winged choughs, *Corcorax melanorhamphos*, for example, improve for at least 4 years (Heinsohn, Cockburn & Cunningham 1988).

#### LINKING BILL LENGTH TO FEEDING METHOD

Variations in the use of foraging techniques by males and females can be related to bill size and shape. The longer, more decurved male bill may be a more efficient tool for probing (see, e.g. Durell, Goss-Custard & Caldow 1993; Ferns & Siman 1994). The shorter, straighter bill of the female green woodhoopoe may function better as a pecking device. Foraging behaviour of juveniles also indicated the importance of bill length. During the first three months after fledging, the bill lengths of juvenile females and males were similar to those of adult females, and they foraged in a similar way to adult females. At 4–5 months after fledging, male bill length exceeded female bill length and the data indicated that this may also be the time when juvenile males switched to a more adult-like foraging strategy.

The extreme sexual dimorphism in green woodhoopoe bill length may have evolved as a result of the ecological separation still seen today (e.g. Selander 1966). Alternatively, it may be a consequence of sexual selection or reproductive role division (Hedrick & Temeles 1989; Shine 1989), and is now maintained by niche

partitioning. It seems likely that neither sexual selection nor reproductive role division were responsible in this case (Radford 2002), so niche partitioning is likely to have been important throughout.

#### LINKING DIET TO FEEDING METHOD

The difference in prey types brought to the nest by woodhoopoe males and females might result either from active prey choice (see e.g. Naef-Daenzer, Naef-Daenzer & Nager 2000) or because different prey are encountered by foraging on different substrate diameters or using different techniques. Because there was no significant difference in the prey types captured by males and females using the same technique, but there was in the prey types caught when using different techniques, the latter is more likely. For example, caterpillars tend to forage at night and conceal themselves during the day, thus avoiding most avian predators. Male woodhoopoes can reach into crevices and the ends of branches to collect them more easily than females. Furthermore, the proportion of each prey type brought to the nest could be predicted quantitatively from the average proportion of time spent using each technique and the likelihood of capturing each prey type with that technique. The intersexual difference in prey types brought to the nest explains the difference in mean prey biomass delivered by the sexes, since caterpillars, centipedes and cockroaches were, on average, significantly heavier than other prey and were delivered most frequently by males.

#### SOCIAL DOMINANCE

In cooperatively breeding species that forage in groups, there is also potential for foraging conflict between individuals of the same sex. In the green woodhoopoe, this conflict is unlikely to be resolved through morphological specialization, since there is no difference in bill length between dominants and subordinates of the same sex (Radford 2002). Instead, several lines of evidence suggest the importance of interference competition. Interference competition has been demonstrated in a number of studies, but these have all involved temporary foraging flocks of unrelated individuals (Ligon 1968; Hogstad 1976, 1978; Peters & Grubb 1983; Aho *et al.* 1997; Pasinelli 2000; Cresswell, Smith & Ruxton 2001). Our study is the first to show that it is also important among related, same-sex members of breeding groups that spend most of their time together.

#### INTERFERENCE COMPETITION?

Within a green woodhoopoe foraging group, intra-sexual aggression, particularly among males, was more prevalent than intersexual displacement activity. This could be simply because individuals of the same sex foraged on similar substrate diameters and so

encountered one another more often. However, birds were significantly more likely to be found foraging within 1 m of an individual of the opposite sex. As a consequence of aggressive displacement, dominants probably monopolized preferred parts of the feeding habitat, resulting in a narrower fundamental niche breadth than that of subordinates. The difference in profitability of feeding areas is assumed because subordinates were significantly less successful than dominants when foraging in a group. Alternatively, this difference in success rates might result from differing levels of experience, as dominants are significantly older than subordinates (Radford 2002) and foraging expertise may continue to improve over a period of years (Heinsohn *et al.* 1988). However, the success rate of subordinates improved when they foraged away from the group (see below), suggesting that it is not lack of experience that limited their success rate in a group. Compared to dominants, subordinates exhibit greater levels of interspecific perch displacement behaviour, particularly of species smaller than woodhoopoes (du Plessis 1989), perhaps implying that they have to compete with other species for access to remaining resources.

#### COMPENSATION BY SUBORDINATES

Given their reduced success rate when foraging in a group, subordinates could theoretically compensate by spending a greater proportion of time foraging, catching larger prey items or foraging alone in preferred areas. Although there was a tendency for subordinates to forage for longer than dominants, the relationship was not significant. Furthermore, there was no difference in the mean biomass of prey items caught by dominants and subordinates foraging for themselves. Subordinates did, however, move away from the remainder of the group on some occasions and, when they did, they increased their proportion of hole probing and benefited from an increased success rate.

Given that dominance hierarchies render conditions uncertain for subordinates (Morse 1974), and that subordinates gained some benefit from foraging alone, why do all members of a green woodhoopoe group normally forage together? Foraging in a group could confer antipredator benefits from increased vigilance (Bednekoff & Lima 1998) or diluted risk of attack (Hamilton 1971; Foster & Treherne 1981). Nocturnal predation by arboreal mammals and driver ants (Tribe Dorylini), which may take all individuals roosting together in a cavity, may be a significant cause of woodhoopoe mortality (Ligon & Ligon 1990), but diurnal predation by *Accipiter* species is also important (du Plessis 1989; Williams, du Plessis & Siegfried 1991). Alternatively, if prey resources are renewed at a certain rate after depletion, groups might follow set routes around their territory to optimize foraging efficiency (e.g. Davies & Houston 1981). This strategy would be successful only if all members of the group return at the same time. Grouping may also facilitate territory

defence (Packer, Scheel & Pusey 1990). Vocal rallying contests determine the outcome of disputes between woodhoopoe groups on territory boundaries and larger groups usually win extended conflicts (Radford 2002). Thus, arriving as a united group may help prevent encroachment.

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