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Green woodhoopoe *Phoeniculus purpureus* territories remain stable despite group-size fluctuations

Andrew N. Radford and Morné A. du Plessis

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Cooperatively breeding groups may be constrained in size by the territory available to them, or territories may be expanded to accommodate extra group members. Here, we show that there was no relationship between the number of adult green woodhoopoes *Phoeniculus purpureus* in a group and the size of its territory. Furthermore, territories were remarkably stable between seasons, with no significant changes in area, despite fluctuating group sizes. These results suggest that food was not limiting at the group sizes found in this study: sufficient resources were available within existing territories for groups that were expanding in size. Following an increase in group membership, a larger proportion of the available area was utilised. Groups also used a larger area in the non-breeding season compared to when breeding: in the latter instance, foraging was concentrated in the vicinity of the nest.

A. N. Radford (correspondence), Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, U.K. E-mail: ar255@cam.ac.uk. M. A. du Plessis, Percy FitzPatrick Institute of African Ornithology, Department of Zoology, University of Cape Town, Rondebosch 7701, Cape Town, South Africa.

Many avian studies have shown that territory owners vary their territory size in relation to resource abundance. For example, nectar-feeding birds show daily changes in territory size depending on natural variation in their food supply (Gill and Wolf 1975, Gass 1979) or experimental manipulations (Eberhard and Ewald 1994). However, other species maintain a fixed territory size despite fluctuations in food supply. For example, pied wagtails *Motacilla alba* do not track daily changes in food availability by changing their winter territory size, perhaps because the constant setting of new boundaries would be too costly (Houston et al. 1985). Instead, owners vary the amount of time they spend on their territory (Davies and Houston 1983) and share it with a satellite when food is abundant (Davies and Houston 1981).

Group territoriality is more commonly associated with cooperatively breeding species, i.e. those in which offspring remain on their natal territory after independence and become helpers-at-the-nest of subsequent broods (e.g. Brown 1987, Stacey and Koenig 1990, Cockburn 1998). Recruitment of group members must place additional demands on the territory's food resources (Schoener 1968, Brown 1987, Koenig et al. 1992). Consequently, group size may be constrained as a result of increased food depletion when members are added (Brown 1969), or there may be an increase in territory size, to provide sufficient food resources for the expanding group (e.g. Curry and Grant 1990, Rabenold 1990, Jansen 1999). Alternatively, if territories are established for the defence of a resource other than food, for example shareable nesting or roosting sites (Davis 1982), there may be sufficient food to accommodate additional group members.

The green woodhoopoe *Phoeniculus purpureus* provides an ideal species in which to study the importance of group-size fluctuations on territory size, for two main reasons. First, groups of between two and 12 individuals defend well-defined, all-purpose territories throughout the year. All breeding and roosting, and the majority of their foraging for invertebrate prey, occur within the defended boundaries. Second, seasonal changes in group size are marked, as a consequence of: (a) large variation in breeding success, and (b) a relatively high annual mortality rate compared to other tropical and south temperate species (approximately 20%; du Plessis 1989a), including the possibility of all group members being depredated in the same roost hole (Ligon and Ligon 1990).

Woodhoopoes roost communally in cavities every night, even though they are unable to excavate these holes themselves and nocturnal predation in them appears common (Ligon and Ligon 1990, du Plessis 1992). This dependence appears critical for their survival by providing energetic benefits (Williams et al. 1991, du Plessis and Williams 1994). The establishment of several territories after the introduction of artificial roost sites, in an area which previously supported no woodhoopoes, indicated that roost cavities are probably the critical resource in determining the spacing of woodhoopoe groups (du Plessis 1992). If the defence of an area containing sufficient roost sites results in a surplus of food, we predict that territories should remain stable between seasons, even when groups increase in size.

In this paper we therefore ask three key questions. First, is green woodhoopoe territory size related to group size? Second, do fluctuations in group size result in changes in territory size? Third, do woodhoopoe groups use the same territory areas throughout the year?

Methods

Study area and population

The study was conducted in a 33 km^2 area near Morgan's Bay (32°43′S, 28°19′E), Eastern Cape Province, South Africa. Green woodhoopoes in this area inhabit riverine forest, which forms belts along river valleys (du Plessis 1989b). Valleys are separated by open grassland, which is not used by the birds. Territories are linearly arranged along the river courses.

Birds were caught in nets placed over roost holes before dawn, and marked with individual combinations of colour rings and an aluminium SAFRING ring with a unique number. Since green woodhoopoes become physiologically capable of reproducing after one year (unpubl. data), birds older than 12 months were classified as adults. Adults could be sexed on the basis of bill length (Radford and du Plessis 2003), or vocalisations (Ligon and Ligon 1990). From 1981 to 2002, between 10 and 31 groups were monitored each year, and the number of adults in each group was recorded before the start of the breeding season (when there was a single breeding attempt per group). Thus, presented group sizes do not include dependent young. We collected data on territory size and use from 23 groups during three field seasons (November to May in 1999/2000 and 2000/2001, and November to March in 2001/2002). A group was considered the same unit for analysis if its membership changed by less than 50% between consecutive seasons.

Territory use and analysis

Data on the position of groups were obtained between 05.00 and 11.00 and between 15.00 and 20.00, because this was when the birds were most active (pers. obs.). A territory was searched systematically until the birds were located, usually by sound (95% of cases). The group was then followed for as long as possible. Their position and activity were recorded on an orthophotographic map of the area (1:10,000), with fixes being marked every 10 minutes. This time interval was chosen because a group could reach any part of its territory within this period. In addition, the position of each territorial dispute was noted. Each group was followed for a cumulative minimum of 20 h ($\text{mean} \pm \text{se} = 31.4 \pm 5.2$ h) during each field season.

All probabilistic models of home range analysis assume independence of successive locations (i.e. an animal's current position is not influenced by its position during past observations). If the data are temporally autocorrelated, however, these models will tend to underestimate the true home range size, and the magnitude of the error is related to the degree of dependence between successive observations (Swihart and Slade 1985). We therefore calculated a valid 'time to independence' by using Schoener's index (Schoener 1981) and following the procedure of Swihart and Slade (1985). Fixes were highly autocorrelated: mean ± se for Schoener's index $= 0.42 \pm 0.09$ (range: 0.13–0.87; $N = 17$ groups for which there were more than 150 fixes in 1999/2000). The time interval necessary to achieve independence between successive observations was 157 ± 33 min (range: 88–316 min).

It was also necessary to determine the minimum number of fixes required to give an accurate representation of territory size (Harris et al. 1990). Graphs of incremental territory area against number of fixes were plotted for groups with more than 150 fixes in 1999/2000 ($N = 17$ groups). Since 82 ± 8 fixes were needed to reach an asymptote (resulting in $92.1 \pm 2.9\%$ of final territory size), insufficient independent data (i.e. fixes separated by 157 min) were available per group for territory size to reach an asymptote. Consequently, although kernel methods have been shown to provide more accurate estimates of territory size than minimum convex polygons (MCPs) (Seaman et al. 1999), these and other probabilistic techniques were not suitable for use here. Instead, the 'non-statistical' MCP technique was used, since this is not affected by the autocorrelation of fixes. Analyses were restricted to groups for which at least 82 fixes were available.

The ‘available’ territory was defined as the area bordered by points that were actively defended against neighbours, and included complete forest sections in which the group had been recorded. This area was calculated by plotting known points of territorial dispute and forest edges, and using MCP analysis in Ranges V (Kenward and Hodder 1996). The ‘used’ territory was defined as the actual area within the available territory that was utilised by the group for all daily activities. This area was calculated by plotting an MCP around the outermost marked positions of the group. One hundred percent MCPs are likely to over-estimate territory size by including outliers, hence incorporating large areas that are rarely used (Harris et al. 1990). We therefore followed other authors (e.g. Jansen 1999, Seddon et al. 2003) in using 95% MCPs instead. Sufficient fixes were available from some territories to allow a separate calculation of territory use in the breeding (defined as the period from two weeks before the first egg was laid until the young fledged) and non-breeding seasons.

Statistical analysis

To enable parametric testing, all proportions were arcsine square-root transformed prior to analysis. Weighted regressions were used when analysing the effects of group size because there were different numbers of groups of each size. Sequential Bonferroni corrections were applied in the case of multiple comparisons with the same data set (Rice 1989). Since territory size data were collected from the same groups for three years, the initial analyses were conducted for each year separately, as well as for the total sample. To avoid issues of pseudoreplication, all subsequent analyses were performed using each group only once: the first year for which the relevant data were available was used. Summary statistics are presented as mean ± se.

Results

Variation in group sizes

Groups included 2–9 adults (3.02 ± 0.05, N = 470 group-years). Mean adult group size varied between years (Kruskal-Wallis test: $H = 33.07$, $df = 20$, $P < 0.05$), and this variation was reflected in the proportion of territories occupied by simple pairs. Over all years, 57% of groups included more than two birds: this proportion varied annually (range: 33–77%), although the difference was not statistically significant ($\chi^2_{20} = 22.62$, $P = 0.3$). The proportion of birds living in groups larger than two totalled 72% in all years combined (N = 1,424 bird-years), but varied significantly between years (range: 48–87%; $\chi^2_{20} = 66.68$, $P < 0.001$). Group size varied more within groups than between groups across the 21 years (one-way ANOVA: between-group MS = 1.29; within-group MS = 2.67, $F_{30,438} = 2.08$, $P = 0.001$).

Variation in territory size between groups

Green woodhoopoes inhabited territories with a mean available area of 23.5 ± 1.7 ha (range: 12.4–35.2 ha; N = 62 group-years). The mean area used within these territories was 15.5 ± 1.1 ha (range: 9.5–22.2 ha), which represented 67.9 ± 1.5% (range: 44.0–92.1%) of the available area. In the non-breeding season, each bird foraged throughout this used area, usually in a close knit group (Radford and du Plessis 2003), and all birds participated in territorial displays at borders with neighbouring groups (Radford 2003). There was no significant relationship between adult group size, number of adult males or number of adult females and either the available area or the area used, in any of the three years or when combining data across years (Table 1; Fig. 1a,b). However, there was a significant positive relationship between group size and the percentage of the available area utilised by the group (Table 1; Fig. 1c).

Variation in territory size within groups

Between the 1999/2000 and 2000/2001 seasons, 11 groups became smaller (mean ± se change = 1.78 ± 0.26 individuals, 34.4 ± 3.8% of original group size), six remained the same size, and five increased in number (change = 1.2 ± 0.2 individuals, 36.7 ± 11.3%). One group disappeared completely and was thus discounted from the analysis. There was no significant change in the available territory size of groups between these two seasons (weighted regression: $F_{1,20} = 0.19$, $P > 0.6$; Fig. 2a). However, there was a significant change in both the absolute area used within a territory ($F_{1,20} = 8.34$, $P = 0.009$; Fig. 2b) and the percentage available area utilised ($F_{1,20} = 8.71$, $P = 0.008$; Fig. 2c).

Groups used a significantly smaller area during the breeding season than in the non-breeding season (breeding = 12.4 ± 0.6 ha, non-breeding = 14.6 ± 0.8 ha; paired t-test: $t = 3.59$, $df = 12$, $P = 0.004$). Birds tended to forage near nests when feeding incubating females and nestlings, although the area used always included the boundaries with neighbouring groups.

Discussion

We found no significant relationship between group size and territory size in our study population of the green woodhoopoe. Furthermore, defended territories remained relatively stable in size between seasons, even when group sizes fluctuated. Woodhoopoe survival is dependent on the presence of roost cavities, which

Table 1. Variation in green woodhoopoe territory size with the total number of adults, number of adult males and number of adult females in the group. Shown are F-values from weighted regressions: $^*P < 0.05$, $^{***}P < 0.001$. Sequential Bonferroni corrections were applied.

Year	Available area			Area used			% Used
	Adults	Males	Females	Adults	Males	Females	Adults
1999/2000 ($F_{1,21}$)	1.89	1.65	0.45	0.70	0.01	0.52	9.91***
2000/2001 ($F_{1,20}$)	0.16	0.01	0.05	0.26	0.10	1.25	2.80
2001/2002 ($F_{1,15}$)	0.91	0.55	0.23	0.29	0.10	0.55	7.25*
All years ($F_{1,60}$)	1.37	0.81	0.10	1.81	0.09	2.16	13.28***

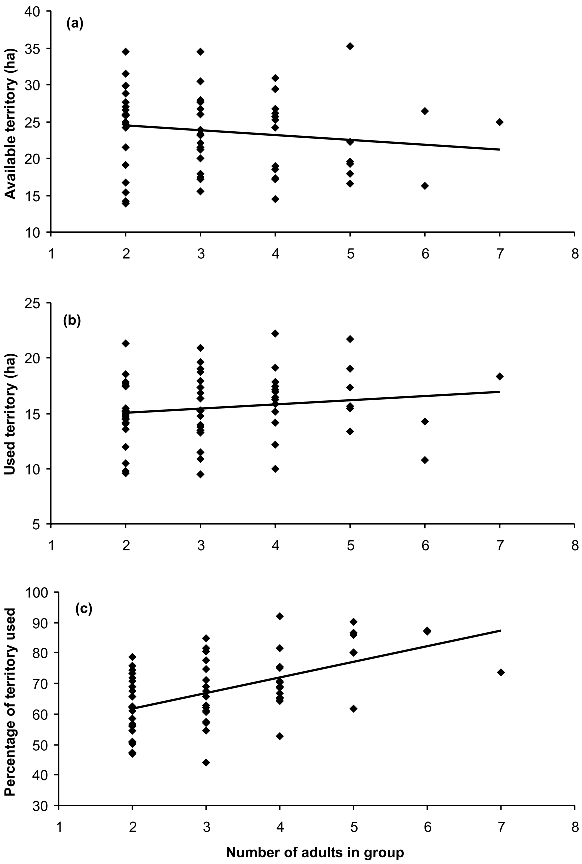

Fig. 1. Relationship between the number of adult green woodhoopoes in the group prior to the breeding season and: (a) the available territory ($y = -0.66x + 25.82$), (b) the used territory ($y = 0.37x + 14.34$), and (c) the percentage of the available area used ($y = 5.11x + 51.44$). Shown are least-squares regression lines. N = 62 group-years.

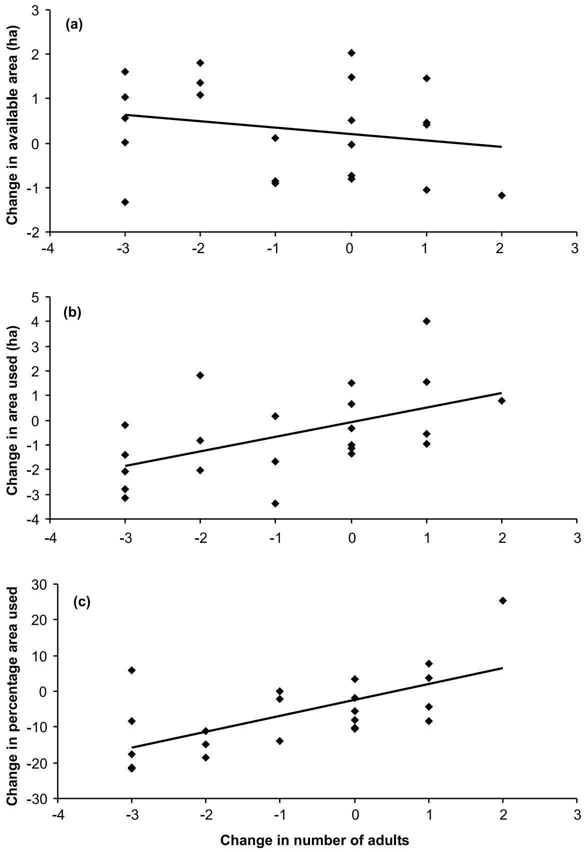

Fig. 2. Change in: (a) the available territory ($y = -0.15x - 0.20$), (b) the used territory ($y = 0.59x - 0.08$), and (c) the percentage of the available territory used ($y = 4.41x - 2.40$) by the same group of green woodhoopoes in consecutive seasons, following a change in the number of adults present prior to the start of the breeding season. Shown are least-squares regression lines. N = 20.

provide energetic benefits at night (Williams et al. 1991, du Plessis and Williams 1994). Group members normally occupy a single cavity, but large groups may require two or more holes (du Plessis 1993). Moreover, woodhoopoes may be supplanted from roost sites by other bird species (e.g. barbets or trogons) and holes may be lost if, for example, trees are damaged (Ligon and Ligon 1978). In these cases, they quickly seek a secondary tree hollow, being apparently unwilling to roost in open but protected sites used by other species (du Plessis 1989b). They therefore need to defend an area that includes several potential roost sites, to provide options for all group members and in case preferred cavities are unavailable.

One consequence of the need for multiple cavities may be that territories contain food resources capable of sustaining larger groups than those generally found in this study. This idea was supported because only 60.3 ±2.3% of the available area was used by groups consisting of a simple pair, whereas larger groups tended to utilise a greater proportion of the territory available to them. Moreover, when a particular group increased in size between seasons, it increased the percentage of the available territory that was utilised, perhaps because resources were depleted sooner and additional areas were required. However, since the largest groups in this study were using over 90% of their available area, it is possible that group sizes are eventually limited by territory size.

Alternatively, a large, stable territory may be adaptive in the long term, rather than the short term. Pied wagtails, for example, defended permanent areas of fixed ground along rivers in the winter, even when food was occasionally so low that the birds did not feed in them at all (Davies 1976). However, since they were permanently good for feeding, they were worth defending during short, unfavourable periods as an insurance for future use. Their choice of territory size maximised over-winter survival, rather than matching daily food abundance (Houston et al. 1985). Hence, if territory defence is not too costly in the green woodhoopoe, a group may benefit from defending an area which will support the greatest expected group size, rather than that prevailing at the time.

Previous investigations of territory-size fluctuations with changing group size have produced a variety of results. In hoatzins *Opisthocomus hoazin* (Strahl and Schmitz 1990), for example, there was no relationship between group size and territory size. However, a positive relationship between group size and territory size has been found in black tits *Parus niger* (Tarboton 1981), *Campylorhynchus* wrens (Rabenold 1990), Galápagos mockingbirds *Nesomimus parvulus* (Curry and Grant 1990) and chowchillas *Orthonyx spaldingii* (Jansen 1999), while there was a negative relationship in groove-billed anis *Crotophaga sulcirostris* (Vehrencamp 1978). Similar to our study, Galápagos hawk *Buteo galapagoensis* territory size did not increase with increasing group size (Faaborg and Bednarz 1990). Territory sizes in this species appeared to be fairly uniform, with boundaries often coinciding with natural features such as ridges.

Interestingly, previous research on green woodhoopoes demonstrated a significant positive relationship between group size and territory size (Ligon and Ligon 1990). In this Kenyan study, small groups struggled to retain territories, whereas they had no such difficulty in our study population. Moreover, Ligon and Ligon (1990) found that territories altered in size with changes in the size of the resident group and its neighbours. Although the habitat at the two study sites differs substantially (thickly forested riverine valleys in South Africa as opposed to open *Acacia xanthophloea* woodland in Kenya), the variation in territory occupation is most likely to be the result of differences in the spatial distribution of territories at the two sites. In Kenya, many territories are bordered on all sides by other groups, whereas Morgan Bay territories tend to have only one or two short, shared boundaries. The latter may be easier to defend, even by small groups. Furthermore, larger group sizes are found in Kenya (mean group size = 5.1; Ligon and Ligon 1990), compared to in our study population (mean = 3.0). Thus, changes in territory size might only become apparent in the South African population at particularly large group sizes, which were not reached during the period of our study. In the stripe-backed wren *Campylorhynchus nuchalis*, for example, traditional territory boundaries changed little except when neighbouring groups' relative sizes changed dramatically (Rabenold 1990).

To observe changes in territory size with changes in relative food abundance or group size, territorial boundaries must be flexible. Flexible boundaries may occur when territories are not contiguous (Hixon et al. 1983, Eberhard and Ewald 1994) or in territories defended by animals that are not highly territorial, such that individuals tolerate a high degree of territorial overlap (Sullivan et al. 1983, Sullivan 1990). At our study site, green woodhoopoe territories were contiguous along river systems, and territorial disputes were common and sometimes protracted (Radford 2004). In such species, where resources often appear to far exceed the amount required by the resident group, boundaries tend to be relatively inflexible (Verner 1977, Seastedt and MacLean 1979). Certainly, in this area of South Africa, green woodhoopoe territories seemed to be traditional and entrenched, even outliving the occupants: when group membership changed entirely, boundaries remained intact. Despite the maintenance of traditional boundaries, there were frequent occurrences of trespassing by neighbouring groups, either when the owners were on the other side of their territory or following a vocal rallying contest on the border (Radford 2004). While trespassing, groups examined roost cavities and other tree holes, so individual woodhoopoes can presumably learn the location and quality of cavities in surrounding territories. This information may be critical to a bird's decisions concerning dispersal when a breeding opportunity arises; the quality and number of available and potential roost sites may be the key factor in determining the overall lifespan and reproductive success of the birds occupying a particular territory (Ligon and Ligon 1990).

We found no significant relationship between territory size and the number of males or females in the group. By contrast, there was a positive relationship in subdesert mesites *Monias benschi* between territory size and the number of males, which was explained by males being more active than females in territory defence (Seddon et al. 2003). In the green woodhoopoe, however, both sexes are equally active in territorial defence, usually responding most vigorously to same-sex intruders (Radford 2003). As in white-winged choughs *Corcorax melanorhamphos* (Rowley 1978) and subdesert mesites (Seddon et al. 2003), the area of the territory used by the group declined in the breeding season, becoming concentrated around the nest site. This presumably reduced the time between feeds when provisioning either the incubating female or nestlings. Thus, in the population of green woodhoopoes studied here, the territory area that was utilised varied depending on the size of the group and the season, but changes in territory boundaries were rare.

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