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Behavioural ecology of the Namibian Violet Woodhoopoe *Phoeniculus damarensis*

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We studied the behavioural ecology of the Violet Woodhoopoe *Phoeniculus damarensis*, a rare species endemic to Namibia and southern Angola. Groups in Namibia consisted on average of 4.3 ± 1.6 individuals, with apparently only a single breeding pair. Non-breeding group members of both sexes brought food to the incubating female, to nestlings, and to fledglings. Groups defended relatively small (c. 12ha) core territories along river courses, where the only cavities suitable for roosting and breeding were situated, but they spent much of their days foraging in undefended home ranges of between 60 and 150ha in size. Violet Woodhoopoes were similar to Green (Red-billed) Woodhoopoes *P. purpureus* in most other respects, particularly as far as behavioural displays were concerned, but appeared to engage in terrestrial (as opposed to arboreal) foraging to a greater extent. The cooperatively breeding social system of this species and apparent hybridisation between *P. damarensis* and *P. purpureus* reduces its effective population size significantly, and Namibia may therefore contain only about 500 breeding units. This has serious implications for the conservation of the species, but nest boxes placed away from the ephemeral rivers inhabited by Green Woodhoopoes may be a fruitful starting point.

Introduction

The Violet Woodhoopoe *Phoeniculus damarensis* is the least numerous of the 10 recently-assessed Namibian endemic bird species (Jarvis and Robertson 1999). In fact, with an estimated 1 834 ± 394 individuals, its total population size is an order of magnitude lower than the others. Threats to Namibia's endemic bird species include the effects of environmental degradation, a rapidly expanding human population and, in the case of its cavity-breeding parrots, illegal trade (Simmons and Brown 2006). Since woodhoopoe dispersal is constrained by obligate cavity-roosting habits (du Plessis 1992), they are also threatened by the clearing of woodland for the commercial manufacture of charcoal (du Plessis 1995) and the damming of the larger ephemeral rivers in Namibia, which reduces flood events and kills many of the large trees downstream (Jacobson *et al*. 1995). As such, Violet Woodhoopoes are the only critically endangered endemic species in Namibia (Simmons and Brown 2006).

To prevent the extinction of such species, steps must be taken to stem or reverse population declines by enhancing recruitment or survival (Green 1994). The success of such efforts frequently depends on the extent to which a species' natural history, ecological requirements, and behaviour are understood (e.g. Ulfstrand 1996, Caro 1999). Unfortunately, very little is known about the behaviour and ecology of the Violet Woodhoopoe; although the nest has been described by Brown (1963) and cooperative breeding has been alluded to (Clinning in Ginn *et al*. 1993), neither has been documented in the primary literature. In stark contrast, the biology of the closely-related Green (also Red-billed) Woodhoopoe *P. purpureus* has been well studied in both Kenya (e.g. Ligon and Ligon 1978, 1990) and South Africa (e.g. du Plessis 1991, 1992, Radford 2003, 2004a, 2004b, 2005, Radford and du Plessis 2003, 2004). The lack of information concerning the Violet Woodhoopoe has serious implications relating to the way in which authorities approach the conservation of the species.

Furthermore, there is some debate over the taxonomy of the Violet Woodhoopoe. Within the genus *Phoeniculus*, there are currently five recognised species of woodhoopoe (del Hoyo *et al*. 2001). However, the Green Woodhoopoe's range, which extends throughout sub-Saharan Africa, comes into contact with that of the Violet Woodhoopoe in Namibia. As a consequence of this overlap, and the great variability in the plumages of individuals from each species, some authors believe that the Violet Woodhoopoe should be subsumed into the Green Woodhoopoe (Cooper *et al*. 2001, Cunningham and Cherry 2005), while others believe it should remain a recognisable taxonomic entity (Simmons *et al*. 2005). Behavioural comparisons may assist in determining whether the Violet Woodhoopoe and Green Woodhoopoe are separate species.

In this paper, we therefore provide an initial description of the behavioural ecology of the Violet Woodhoopoe. We compare aspects of its grouping, cooperative behaviour, territoriality and foraging biology with that of its better-known mesic congener, the Green Woodhoopoe. Finally, we discuss how this information may be important for the long-term conservation of this rare species.

Methods

Study areas

We studied Violet Woodhoopoes during two periods. In March and April 1990, 22 woodhoopoe groups in the Waterberg area (20°30'S, 17°15'E) of north-central Namibia and along the Omaruru River (21°30'S, 15°45'E) in west-central Namibia were watched for between four hours and two days each (total observation period = 98h). At both sites, groups frequented the tree belt, which comprised 4–12m tall *Combretum imberbe*, along dry river courses. They also spent a significant proportion of their days in the spindly *Acacia* scrub away from the river course. The most detailed observations (i.e. those exceeding four hours per group) involved the breeding behaviour of five groups: two incubating eggs, one with nestlings, and two feeding fledglings.

In 1995, a less intensive study was conducted along the Ombosiro River (21°10'S, 15°40'E) of central-west Namibia. Thirty nest boxes (dimensions: 50cm x 16.5cm x 16.5cm; hole diameter: 45mm) were wired to riverine trees frequented by woodhoopoes, at 2–7m above the ground. Nine were taken by hornbills, one by owls and one by starlings, but four others were used by woodhoopoes. Breeding was observed in these active boxes from incubation until either depredation or fledging.

Data collection

Each woodhoopoe group was carefully assessed for species composition, group size and sex ratio. Violet Woodhoopoes can be distinguished from Green Woodhoopoes by the colour of the mantle, which is dull to coppery in the former, but an iridescent green in the latter (du Plessis in Hockey *et al*. 2005). We assumed that Violet Woodhoopoes could be sexed in a similar fashion to Green Woodhoopoes. In the latter species, males and females older than four months can be distinguished in the field on the basis of sexual dimorphism in both bill length (Radford and du Plessis 2003) and vocalisations (Radford 2004a). Individuals younger than four months can be sexed because males possess a brown throat patch that is not apparent in females (Ligon and Ligon 1978).

Accessible natural nests and nest boxes were checked for the number of eggs and nestlings. Active nests were watched to determine which individuals incubated and which brought food to the breeding female and the nestlings. Groups with fledglings were observed to assess which group members fed these dependent individuals.

To gain an insight into territorial behaviour, we observed four non-breeding groups in the Waterberg area from dawn to dusk (approximately 06:30 until 19:00) for one day each. The four groups possessed adjacent territories and were chosen for day-long watches because their group compositions differed, facilitating group identification. We plotted group locations at 30min intervals on a hand-drawn map based on commercial 1:50 000 contour maps. One hundred percent minimum convex polygons were drawn around these points and used to calculate the area utilised by each group. We also noted any intergroup interactions that occurred. To further assess the response of territory-holding groups to intrusions, we occasionally simulated the intrusion of a rival group, using playbacks of rallying calls (see Radford 2003 for details).

During detailed observations, we kept within c. 100m of groups for most of the time and could infer from their movements and vocalisations what they were doing. We were thus able to distinguish between ground and arboreal foraging, and could estimate the amount of time spent foraging as opposed to other activities, such as preening, group movements and inter-territorial interactions. Behavioural displays and foraging techniques were noted whenever they were observed.

Results

Group size and sex ratio

All 22 groups in the Waterberg and Omaruru areas were comprised entirely of Violet Woodhoopoes. The mean (± SD) size of these 22 groups was 4.3 ± 1.6, of which 2.4 ± 1.0 were males and 1.9 ± 0.9 females (Table 1). Half of the groups contained fledglings, and a further six groups were either incubating eggs or tending nestlings. When considering only individuals older than four months, mean group size was 3.6 ± 0.8.

The groups studied in the Ombosiro River area were comprised mainly of Violet Woodhoopoes, but each group contained at least one Green Woodhoopoe, including (in one case) the breeding male. The mean (± SD) of these four groups was 9.2 ± 2.1.

Cooperation during the breeding cycle

In the Waterberg area we observed two groups (one containing three individuals and one of five) at the incubation stage. In both cases, the nest was in a natural tree cavity and contained four eggs, and the breeding female was responsible for incubation. In both groups, the male breeder and all non-breeding individuals presented food to the incubating female, who begged at the cavity entrance. During a four-hour nest watch on the group of three, the male provided the breeding female with eight food items, and the non-breeding female brought five. In the nest box study, one group was incubating five eggs, but the breeding attempt failed due to desertion, while another group laid four eggs, of which three successfully fledged. In both cases, all adult group members appeared to provision the incubating female.

We observed two groups in the Waterberg area in which adults were feeding nestlings, one with at least two nestlings (a male and a female) and one with three nestlings. One adult male and two non-breeding females (i.e. all group members other than the breeding female) brought 36 food items to the former nest during four hours of observations. The breeding female usually accepted food items from them and then relayed the food items on to the nestlings. The older non-breeding female tried to bypass the breeding female by taking food directly to the nestlings, but the breeding female intercepted such food on six of seven occasions. Neither the male nor the immature female attempted to feed the nestlings directly. At the successful nest box site, seven adults were present in the group and all appeared to be feeding the three nestlings.

Table 1: Mean group sizes (± SD) of Violet Woodhoopoes (VWH) recorded in different studies in Namibia, and of Green Woodhoopoes (GWH) elsewhere

Mean group size	n	Male/female	Locality	Reference
4.3 ± 1.6	22	1.26	VWH – Namibia	This study
4.3 ± 3.0	8	--	VWH – Namibia	Robertson *et al*. (1995)
4.2 ± 2.4	13	--	VWH – Namibia	Jarvis and Robertson (1997)
4.9 ± 2.1	189	0.67–1.05	GWH – Lake Naivasha, Kenya	Ligon and Ligon (1990)
4.0 ± 1.5	138	0.80–1.36	GWH – Kubusi Valley, South Africa	MAdP (unpublished data)
3.0 ± 1.1	470	0.71–1.08	GWH – Morgan's Bay, South Africa	Radford and du Plessis (2004)

In two groups consisting of four adults and one fledgling, all adult group members offered food to the fledglings at least once during our observations. The breeding female in each group occasionally begged for food as well.

Space use and territorial behaviour

Whilst foraging, Violet Woodhoopoe groups ranged widely across areas that varied in size from 60–150ha (n = 4). These 'home ranges' were centred on a core section of the river course, but also included the surrounding arid woodland, where the trees were markedly smaller than those in the river course. While in the arid woodland areas, the birds ignored other groups and did not respond to playback of calls of other groups. In contrast, groups vigorously defended the core section of their territory: on hearing another group or the simulated intrusion of another group, they produced raucous, vocal rallying displays in which all individuals cackled loudly while bowing up and down. These core areas had a mean size of 12.3 ± 3.0ha (n = 4), were linearly arranged along river courses, and coincided with the distribution of trees (typically *Acacia eriobola* and *Faidherbia albida*) that were big enough to contain woodpecker/barbet holes and natural cavities suitable for roosting. Occasionally, vocal rallies developed into a 'flag-waving display' (*sensu* Ligon and Ligon 1978), when group members waved a piece of bark, a leaf or another inanimate object in their bills and passed it between one another: this behaviour was seen on three out of the 22 occasions when groups displayed rallying behaviour in response to playbacks. A similar experiment with Green Woodhoopoes in the Eastern Cape, South Africa, resulted in flag-waving displays in 42.0% of instances (n = 176), significantly more than those performed by Violet Woodhoopoes ($\chi^2 = 4.10$; $P < 0.05$).

Foraging behaviour

Violet Woodhoopoes were often seen probing into cracks and crevices of tree trunks and branches in search of invertebrates. They also spent about 2% of their time foraging on the ground (n = 78 hours of group observations). This figure is an underestimate of foraging time *per se*, as time spent on the ground was always for food-finding, whereas much of the 'arboreal time' was spent on other activities, such as allopreening and rallying. Ground foraging was seen in seven of the 11 groups observed away from the nest, and was usually initiated by the descent of one bird. The successful acquisition of food precipitated the arrival of other group members. Individuals remained on the ground for periods of between 10sec and 14min (mean ± SD = 4.8 ± 3.5min). Occasionally, all group members would be on the ground simultaneously (participation rates averaged 90 ± 10% of group members). Short bouts of foraging were usually undertaken to pick up a specific food item, which would then be carried back onto a branch to be devoured. Longer foraging bouts occurred at more abundant food sources, such as termite emergences. In these cases, individuals remained on the ground and took up to 56 termites before ascending.

Discussion

Violet Woodhoopoe behaviour and ecology

The mean group size of 4.3 birds recorded during this study was similar to that of other Violet Woodhoopoe groups in Namibia, but slightly higher than Green Woodhoopoe groups at various sites in southern Africa (Table 1). There is a tendency for woodhoopoe groups in the more arid regions of Namibia and Kenya to be larger than groups in mesic areas of South Africa, but samples are small. Violet Woodhoopoe groups appeared to have a stronger bias in favour of males than is generally the case with Green Woodhoopoe groups.

It was evident from nest watches that Violet Woodhoopoes are cooperative breeders. Adults of both sexes brought food to the incubating female. This is also the case in the Green Woodhoopoe (Radford 2004b), but has been rarely reported in other cooperative breeders (see Zack 1986 for one other detailed example). All group members also brought food for nestlings, as in the Green Woodhoopoe (du Plessis 1991). Neither male nor immature female Violet Woodhoopoes attempted to feed young nestlings directly, instead provisioning the breeding female, who transferred prey items to the chicks. Similar behaviour at this stage of breeding has been observed among Green Woodhoopoes (Ligon and Ligon 1978). Non-breeding females occasionally attempted to bypass the breeding female by feeding nestlings directly when the latter was distracted. As nestlings grew older, non-breeding group members increasingly passed food directly to them. Thus, in these respects, Violet Woodhoopoes are identical to Green Woodhoopoes.

The intergroup displays of Violet Woodhoopoes appeared to be largely similar to those of Green Woodhoopoes (see Radford 2003), although the former produced fewer flag-waving displays. Whereas Green Woodhoopoe groups vigorously defend every part of the habitat that they use

Table 2: Comparative territory sizes (± SD) of Violet Woodhoopoes (VWH) in Namibia, and Green Woodhoopoes (GWH) elsewhere. Territories are considered to be defended; home ranges are used, but not defended

Mean size (ha)	n	Locality	Reference
12.3 ± 3.0* and	4	VWH – Namibia	This study
51.0 ± 28.1	33	GWH – Lake Naivasha, Kenya	MAdP (unpublished data)
35.1 ± 8.0	24	GWH – Kubusi Valley, South Africa	MAdP (unpublished data)
23.5 ± 4.2	62	GWH – Morgan's Bay, South Africa	Radford and du Plessis (2004)

* 60–150ha home range

(Radford and du Plessis 2004), Violet Woodhoopoes spent extensive periods of time away from their core river-course territories (i.e. in their undefended home ranges). Both Violet and Green Woodhoopoes are obligate cavity-roosting species and need to defend several potential roost sites (du Plessis 1992). The core areas that Violet Woodhoopoes vigorously defended contain the trees that hold these vital cavities, but the patches of riverine vegetation appear inadequate in providing sufficient food resources. Hence, birds are compelled to utilise the surrounding scattered *Acacia* woodlands. The sparse foraging returns from this habitat force them to range over extensive areas, which are difficult to defend against intrusions by neighbouring groups. In contrast, the areas defended by Green Woodhoopoes in South Africa, which are much larger than those defended by Violet Woodhoopoes (Table 2), appear to contain sufficient food for groups larger in size than those generally found (Radford and du Plessis 2004).

Violet Woodhoopoes procured food from trees in a similar manner to Green Woodhoopoes: bills were probed into cracks and crevices of tree trunks and branches in search of invertebrates (Radford and du Plessis 2003). However, there was a relatively high incidence of ground foraging. During more than 5 000 hours of observations of Green Woodhoopoes in South Africa, ground foraging has been seen less than 0.1% of the time (MAdP and ANR pers. obs.).

Implications for conservation

There are a number of close similarities in the behavioural ecology of Violet and Green Woodhoopoes, but also some differences. In particular, Violet Woodhoopoes do not defend their entire foraging area; they forage on the ground with much greater frequency than do Green Woodhoopoes, and group sizes tend to be larger among Violet Woodhoopoes than in southern African Green Woodhoopoes. These differences may arise from differences in habitat or aridity in the relevant study areas or they may represent key differences between distinct species. Although there is an ongoing debate concerning the taxonomy of the Violet Woodhoopoe (Cooper *et al*. 2001, Cunningham and Cherry 2005), the prevailing view is that it is a species in its own right (e.g. Hockey *et al*. 2005, Simmons *et al*. 2005). As such, it is important to consider how best to conserve this rare species.

Our confirmation that Violet Woodhoopoes are cooperative breeders needs to be taken into account when considering the overall viability of the species. A cooperative social system reduces the effective population size, as there will be a number of reproductively mature, non-breeding helpers who do not contribute directly to the reproductive output of the species. Thus, given the recent estimate of 2 250 individuals (Jarvis and Robertson 1999), there are only about 500 breeding units in Namibia. Further study is required to cast light on whether non-breeding helpers enhance the reproductive output of Violet Woodhoopoe groups. This has not been the case in any of the three Green Woodhoopoe populations that have been intensively studied (Ligon and Ligon 1982, du Plessis 1991).

A further concern relates to the admixture of the two species in Namibian rivers and their apparent interbreeding. Several study groups clearly contained both species, with at least one group including an adult male Green Woodhoopoe and a breeding female Violet Woodhoopoe. Moreover, genetic evidence from unpublished cytochrome b studies confirms that some birds are hybrids (M Cherry, University of Stellenbosch, pers. comm.). This is a great concern and suggests that population estimates of *P. damarensis* may be inflated. On the other hand, aridification under climate change may separate the two species' contact zones, reducing the incidence of hybridisation in future.

Our study suggests that urgent research is needed in three main areas. First, it is vital to define the conservation unit. Wider-scale molecular genetic research is required to establish the taxonomic status of *Phoeniculus damarensis* in relation to *P. purpureus* in general, and the East African *P. damarensis granti* in particular. Population monitoring is crucial to establish whether numbers are currently decreasing and whether the low densities observed are natural or the result of environmental perturbations. These population censuses must take into account the species' pattern of space use (i.e. counts should be made in core territory areas in the first and last hours of daylight, when woodhoopoes ensure that the boundaries are well advertised vocally and thus groups are easiest to detect). Second, more behavioural data are needed to verify that only a single pair within each group breeds, and to quantify the effects of non-breeding group members during both the breeding and non-breeding seasons. Third, a conservation management plan must be forthcoming. This should verify the threats — identified by Simmons and Brown (2006) — which face the species throughout its range, quantify the effects of the various forms of land tenure, and assess the birds' response to the placement of nest boxes in arid

woodland areas away from river courses. This policy proved successful in rendering habitable previously-unoccupied woodland for Green Woodhoopoes (du Plessis 1992). However, unless accompanied by an intensive education campaign, this form of intensive management is unlikely to succeed in areas outside Namibia's conservancies because subsistence farmers are likely to use any nest boxes for beehives. We recommend that the management plan suggested here be undertaken by Namibia's Ministry of Environment and Tourism, particularly given that the use of nest boxes has already been implemented by them as a research and conservation tool in the Daan Viljoen Game Reserve, near Windhoek.

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