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Breeding biology of the White-headed Vulture *Trigonoceps occipitalis* in Kruger National Park, South Africa

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Information on the breeding biology of the White-headed Vulture *Trigonoceps occipitalis* is limited and published data are few. Within the Kruger National Park in north-east South Africa there is a regionally important population of about 60 White-headed Vulture pairs, of which 22 pairs were monitored for five years between 2008 and 2012 to determine key aspects of their breeding biology. Across 73 pair/years the mean productivity of 55 breeding attempts was 0.69 chicks per pair. Median egg-laying date across all of the Kruger National Park was 27 June, but northern nests were approximately 30 d later than southern nests. Mean (±SD) nearest-neighbour distance was 9 976 ± 7 965 m and inter-nest distances ranged from 1 400 m to more than 20 km, but this did not differ significantly between habitat types. Breeding productivity did not differ significantly between habitat types. The results presented here are the first for this species in Kruger National Park and provide details against which future comparisons can be made.

Keywords: breeding biology, Kruger National Park, *Trigonoceps occipitalis*, White-headed Vulture

Introduction

The White-headed Vulture *Trigonoceps occipitalis* is a large and conspicuous raptor that has a broad but patchy distribution south of the Sahara (Mundy et al. 1992). It occurs mainly in protected areas such as national parks and game reserves and is encountered much less frequently outside these areas (Herremans and Herremans-Tonnoeyr 2000; Thiollay 2007; Virani et al. 2011).

Ecological knowledge of the White-headed Vulture is generally low (Virani and Watson 1998; Monadjem 2004) and in particular its breeding biology is not well-known. Nests of White-headed Vultures have been monitored in Tanzania (Pennycuick 1976), South Africa (Hitchins 1980) and also in Zimbabwe (Mundy 1982), and a long series of aerial surveys over multiple years using fixed-wing aircraft in Hwange National Park in Zimbabwe provides the most detailed information on breeding productivity and inter-nest distances to date (Hustler and Howells 1988).

There are no recent studies that provide breeding information on White-headed Vultures. This is possibly because the species occurs at low densities, even in large protected areas (Murn et al. 2013), and obtaining data from a sufficient number of nests can be logistically challenging.

In this study we describe key features of the breeding biology of White-headed Vultures in Kruger National Park, the largest (c. 20 000 km^2) protected area in South Africa. Apart from reporting productivity data for breeding White-headed Vultures, we also describe egg-laying dates, nest tree species, and some aspects of breeding and courtship behaviour.

Methods

Study area

The study was conducted between 2008 and 2012 in Kruger National Park (KNP), in the Lowveld of north-east South Africa (Figure 1). White-headed Vultures were monitored in two areas of the park: a southern area and a northern area, each approximately 3 000 km^2 and separated by about 150 km (Figure 1). The southern study area is located between the Crocodile River in the south and the area north of Skukuza rest camp (approximately 24°47′ S, 31°52′ E). The area is of low to moderate relief and comprises mainly mixed bushwillow *Combretum* bush savanna with knob thorn *Senegalia nigrescens* (*Acacia nigrescens*) and marula *Sclerocarya birrea* tree savanna (Gertenbach 1983). The northern study area is roughly centred on Shingwedzi rest camp and extends from approximately 23°53′ to 22°79′ S. The landscape is generally flat with areas of low relief and vegetation consists mainly of mopane *Colophospermum mopane* shrubveld interspersed with more complex vegetation communities in the riparian zones along the four main rivers (Shingwedzi, Mphongolo, Phugwane and Bububu).

Data collection

Breeding areas of White-headed Vultures were located using a combination of prospective surveys by vehicle and on foot, aerial surveys and information from park field rangers. Information on breeding attempts and breeding success was obtained mainly by visiting nests from the ground. In 2010 and 2011 aerial surveys were completed specifically to count and monitor vultures (Murn et al. 2013), but the bulk of observations were made from the ground. The helicopter proved extremely useful in saving time when seeking new locations of pairs that moved between years. Wherever possible, the nest trees of failed breeding attempts were climbed to seek evidence for the failure and also to look for prey remains and/or regurgitated pellets.

Calculating egg-laying dates to a high degree of accuracy was not possible because nests were not climbed (or disturbed at all) during the early part of the breeding season, given that White-headed Vultures are prone to deserting nests if disturbed at this time (Mundy et al. 1992). Nesting phenology was calculated most often by counting backwards from observed chick sizes and comparing these against age categories (Mundy 1982; Hustler and Howells 1988). We developed a series of chick age categories (Table 1), which were similar to the categories used previously (Hustler and Howells 1988). The incubation period was assumed to be 55 d and occasionally it was possible to estimate the egg-lay date from when adults were observed to start incubation.

Breeding productivity was assessed only for the years in which a nesting attempt was made. Breeding productivity was calculated across all these nests in all years and also separately for nests where there were two or more years of data. We wanted to compare our observations directly with the only long-term breeding data for the species (Hustler and Howells 1988), and so breeding attempts were treated as successful if the chick reached an age of about 60 d – the age at which the adults begin to leave the chick alone in the nest for more than a few minutes at a time.

The number of non-breeding attempts was calculated by identifying (usually known) breeding areas in which an adult pair was seen together but no nest found. For example, if a pair of birds bred in 2011 but not 2010 and they were not seen in 2010, the breeding productivity was determined from 2011 onwards. If the same pair had been observed several times in 2010, but no nest was found in that year, a non-breeding attempt was recorded.

Inter-nest distances between active White-headed Vulture nests were calculated using a GPS and GIS software.

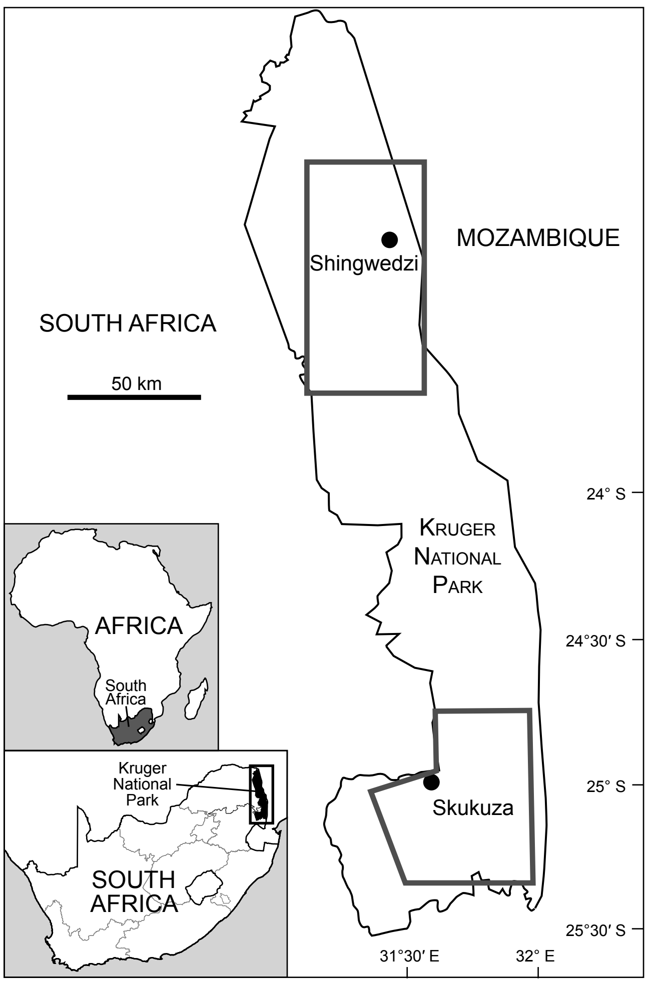

Figure 1: Location of Kruger National Park in South Africa and the northern and southern areas used in the study

Data analysis

Data were log-transformed where necessary to stabilise variance and checked with Anderson–Darling tests, after which *t*-tests or one-way analysis of variance (ANOVA) were used for comparisons across two or more variables, respectively. Data that did not conform to parametric assumptions after transformation were subject to Mann–Whitney or Kruskal–Wallis tests. Homogeneity of variance in sample ranks was checked with Levene's test. All values are presented as means ± standard deviation.

Results

Nest trees

A total of 22 White-headed Vulture pairs was monitored in Kruger between 2008 and 2012, from which we obtained information on 38 nest locations. Preferred trees (82% of nests) were thorny *Senegalia* species (Table 2) and all nests were located on the top of the canopy. Mean nest tree height was 14.1 ± 1.7 m, which was taller than the mean height (12.4 ± 2.8 m) of 30 trees selected completely at random within the boundaries of the study area ($T_{49} = 2.95$, $P = 0.005$). Compared to the random trees, nests were located in generally flat, low relief areas ($T_{49} = 3.17$, $P = 0.001$) and away from drainage lines.

Breeding productivity

The 38 nest locations represented 73 pair/years. Of these, the outcome was determined for 55 breeding attempts.

Table 1: Age classes and descriptions used to categorise White-headed Vulture chicks in the nest (after Hustler and Howells 1988)

Chick age	Description
Up to 14 d old	Newly hatched
15 to 30 d	Obviously larger than newly hatched, still covered in down
30 to 40 d	Mainly covered in down with wing and tail quills emerging
About 60 d	Well-feathered but still some down present.
About 90 d	Fully feathered, standing on the nest edge. Head beginning to turn brown along occipital ridge

Mean productivity over all years, across the nests where a breeding attempt was made, was 0.69 chicks per pair per year (Table 3).

Mean distance to the nearest White-headed Vulture neighbour was 9 976 ± 7 965 m over all nests across the years 2009 to 2012. Due to some habitat types generally being avoided by nesting White-headed Vultures (CM unpublished data), calculating mean nest spacing in relation to habitat was possible for five habitat types (Table 4). Nests in the northern study area had a higher mean inter-nest distance (17 029 ± 10 044 m), but this did not differ significantly from the mean inter-nest distance (9 606 ± 6 990 m) in the southern study area (ANOVA, $F_{4,33} = 1.73$, $P = 0.17$). Productivity was not significantly different between the habitat types in Kruger (Kruskal–Wallis, $H = 1.45$, df = 4, $P = 0.836$; Table 4).

Nest use and lay dates

Most nests (82%) had two or more years of data (mean = 2.5 years), but it was possible to collect data from only three nests that were in use across four years and only one nest was used in each of the five years of the study. Across all nests where an approximate date could be determined ($n = 27$), the average egg-laying date was 1 July (±5 d). The earliest known date was 8 June and the latest was 10 August. There was a significant difference in egg-laying dates between the study areas (Mann–Whitney *U*-test, $U = 2$, $P < 0.01$) with the median date in the southern area (27 June, $n = 23$) being approximately one month earlier than the median date in the northern area (23 July, $n = 4$). There was a small amount of overlap between the egg-laying date ranges for the southern and northern areas. The latest date in the south and the earliest date in the north were approximately the same (20 July, ±5 d).

Nest site fidelity was generally high and nine pairs moved nest during the study period. The average distance moved was 753 ± 597 m, which was much less than the mean nearest White-headed Vulture neighbour distance ($T_{11} = 7.85$, $P < 0.001$). There were no alternate nests in other habitat or landscape types; pairs built their new nests in the same habitat type. Where a clear reason could be determined, pairs changed location due to the nest being usurped by White-backed Vultures *Gyps africanus* ($n = 6$) or the nest falling out of the tree ($n = 5$). Pairs often moved nest location after a failed breeding attempt, but it is unknown if this was the reason for moving.

Table 2: Tree species used by nesting White-headed Vultures in Kruger National Park, South Africa

Tree species	No.
Knob thorn *Senegalia nigrescens* (*Acacia nigrescens*)	22
Black monkey thorn *Senegalia burkei* (*Acacia burkei*)	5
Leadwood *Combretum imberbe*	5
Delagoa thorn *Senegalia welwitschii* (*Acacia welwitschii*)	4
Baobab *Adansonia digitata*	1
Apple-leaf *Philenoptera violacea*	1
Total	38

Copulation and breeding behaviour

Copulation was observed five times and it was only ever seen to occur on the nest. It is a subtle and inconspicuous process that lasts between 15 and 20 s. Prior to actual copulation the birds stand in the nest together, usually with the female standing perpendicular to and in front of the male. So-called ‘head-turning’ behaviour, a behavioural characteristic of Aegypiine vultures, was not observed in relation to copulation. The sound made by the birds during copulation is unusual and is best described as a very deep squeak, but longer than a grunt. After copulation, one or

Table 3: Breeding and productivity data for White-headed Vultures monitored in Kruger National Park, South Africa

Breeding/productivity	2008	2009	2010	2011	2012	Total
Known pairs	4	15	22	22	10	73
Nesting attempts	4	14	16	16	5	55
Chicks reared	3	9	10	12	4	38
Productivity	0.75	0.64	0.63	0.75	0.80	0.69

Table 4: Nearest-neighbour distances and mean breeding productivity of White-headed Vulture nests in different habitat types in Kruger National Park, South Africa. Landscape/habitat types after Gertenbach (1983)

Landscape/habitat type	Nests	Mean distance to nearest White-headed Vulture neighbour (m; ± SD)	Mean breeding productivity (2008–2012)
Sabie/Crocodile River thorn thickets (granitic lowlands with *Acacia* tree savanna)	13	8 123 ± 5 497	0.55
Delagoa thorn thickets (Karoo sediment plains with Delagoa thorn tree savanna)	4	5 600 ± 3 467	0.66
Thorn veld (basalt or gabbro plains with marula tree or knobthorn bush/shrub)	8	9 388 ± 9 803	0.67
Knobthorn/marula savanna (basalt or gabbro plains)	6	9 467 ± 6 278	0.66
Mopane shrubveld (flat basaltic plains with open mopane shrub savanna)	7	17 029 ± 10 044	0.73

both birds may leave the nest, but both birds remaining in the nest was not recorded.

Several other noteworthy behaviours were observed either at the nest or nearby in association with the nest. None of these was observed many times, but it is considered warranted to include the behaviours here on the basis of them being unrecorded previously and also that they are interesting.

On one occasion, approximately two weeks before egg-laying, a male left the nest after copulation and performed what appeared to be a courtship behaviour flight. Whilst the female remained in the nest, the male took off and reached a flying height of approximately 100–150 m, whereupon he began a series of big, fast, swooping dives with folded wings each followed by an upflight into a type of stall. This was repeated four times only, but would have been visible to the female standing in the nest. The male then flew to a much greater height and drifted out of sight whilst the female remained in the nest. This behaviour is well-known as pre-laying and courtship behaviour in eagles from the genus *Aquila* (Steyn 1973; Gargett 1990), but has not been recorded previously for White-headed Vultures. Indeed, courtship flights of any type for the species have not been recorded previously (Mundy et al. 1992).

Several instances of what we termed 'eagle feeding' were observed separately at three nests. Vultures invariably feed their chicks by regurgitation (Houston 1976; Steyn 1982; Mundy et al. 1992), sometimes beak to beak and at other times into the nest cup for the chick to eat. Eagles do not regurgitate but bring food to the nest from which the adults tear small pieces to feed the chick(s) (Collopy 1984; Meyburg 1987). During the (directly) observed feeding events, adult White-headed Vultures were clearly seen to pull food morsels from a larger piece of food in the nest and feed 15–20 of these to the chick over about the same number of minutes. In each case the chick was approximately 30 d old and the response of the chick to the offer of each food morsel was subdued – not at all like the frantic begging, wing-flapping and head-bobbing usually associated with young vultures seeking food.

A final noteworthy observation was that of a pair copulating in front of a mid-aged (approximately 60 d old) chick in the nest. A possible explanation for this is that the birds were reinforcing the pair-bond between adults, although this is likely to be an anthropomorphic perspective.

Discussion

The apparent courtship flight, chick feeding behaviour and unusual copulation are three aspects of White-headed Vulture behaviour that need to be better understood. The birds are very subtle and inconspicuous in their behaviour at the nest, and rarely does any specific behaviour last more than a minute. Rather than being particularly rare, it is more likely that lack of information about these behavioural features is a function of the limited observations made of the species. In previous studies of White-headed Vulture breeding biology (Pennycuick 1976; Hustler and Howells 1988), nests were not placed under observation for any length of time. Mundy (1982) recorded breeding behaviour of White-headed Vultures over approximately 120 h but did not observe courtship flights and noted that nestlings are fed by regurgitation. Since these studies, the breeding biology of White-headed Vultures has not been investigated any further and a general lack of knowledge about the species has been noted for some time (Benson 1997; Monadjem 2004). Based on what is known, incubation and rearing duties are performed by both the male and female (Mundy et al. 1992), and the relative contribution of each sex during the breeding season is approximately equal (CM unpublished data).

Prior to this study, the two most detailed studies of White-headed Vulture breeding biology were by Mundy (1982) primarily at Gonarezhou National Park in south-east Zimbabwe, and by Hustler and Howells (1988) in Hwange National Park in north-west Zimbabwe, referred to respectively here as Gonarezhou and Hwange. Compared with these studies, the breeding parameters for White-headed Vultures described here for KNP are within a similar range. The average egg-laying date estimated for KNP (1 July) was close to that estimated for Gonarezhou (28 June), and is virtually in the middle of the stated egg-laying season for the species of late May to late July in southern Africa (Mundy et al. 1992). The egg-laying season in KNP appears slightly later than Hwange, where 30% of eggs were laid in May and nearly 70% of eggs were laid before the end of June; there were no recorded egg-lay dates in May in this study. Whilst the egg-laying dates between the northern and southern study areas were approximately a month apart, they did overlap slightly. We conclude that the difference between the two sites is more likely to be a reflection of the broad egg-laying season for White-headed Vultures than a result of latitudinal variation; the egg-laying dates for the southern study area were very similar to Gonarezhou (both late June), whilst the northern study is located almost halfway between the two but with a later egg-laying date.

Unlike the Hwange study, which showed higher productivity for White-headed Vulture nests on basaltic soils compared to granite soils, there was no clear evidence to indicate that productivity varied between broad habitat types in KNP (Table 4). It is possible that differences in productivity do exist between habitats in KNP and these may become apparent with a larger sample of nests over a longer period of observation. Different habitat types were not investigated specifically in Gonarezhou, and that study entailed a degree of disturbance such that productivity was likely to be less than expected. It has been suggested (Mundy et al. 1992: 182) that a 'truer' indication of productivity incorporates all known pairs in an area, including those that do not attempt to breed. The authors go on to suggest that White-headed Vultures have a high success when they attempt to breed (as high as 75%), but conclude that failures occur through birds not breeding. By applying these criteria, the productivity for White-headed Vultures in Hwange (46 pair/years) is reduced from 0.65 down to 0.42 and productivity in Gonarezhou (17 pair/years) reduces from 0.57 to 0.47. Similarly, if one re-examines the data from Kruger presented here (calculated only from 2009 to 2011 – 59 pair/years), productivity reduced from 0.69 to 0.49. These are still relatively high rates of productivity for a large vulture. For example, Lappet-faced Vultures *Torgos tracheliotos*, although there are no data for KNP specifically, are reported to have a breeding productivity of approximately 0.4 (Hustler and Howells 1990; Mundy et al. 1992).

However, it is difficult to see the rationale of a reduced productivity measure, given that it is not entirely accurate to describe a pair of birds not breeding as 'failing to breed'; they simply may have not bred for reasons such as lower body condition or behavioural factors. For example, during the study described here, much information was recorded about the post-fledging dependence period in juvenile White-headed Vultures, and whilst it is peripheral to the aims of this study, it is clear that juveniles persist in associating with their parents for much longer than was previously thought (CM unpublished data). It is possible that subsequent breeding attempts are delayed whilst parental care of the previous chick continues. Juvenile White-headed Vultures in KNP regularly visit the nests of adult White-headed Vultures (very likely the nest of their parents) for as much as two years after fledging, and long periods of post-fledging dependence have also been noted in Hwange and elsewhere (Pennycuick 1976; Mundy et al. 1992). The effects of juvenile dependence on adult breeding productivity thus require further investigation, particularly if the opportunities for juveniles to disperse are generally limited to the boundaries of a national park or other protected area. This highlights the need for marked and individually identifiable birds because, although adults can be recognised from their plumage (Murn 2012), juveniles cannot be reliably identified, and these young and inexperienced birds may be visiting multiple White-headed Vulture nests rather than just their natal site.

Nearest-neighbour distances (NND) of White-headed Vultures in southern KNP were comparable to those in the higher nest density area of Hwange (i.e. on basaltic soils), whilst in northern KNP inter-nest distances were comparable to Hwange nests in the transitional zone between basaltic soils and Kalahari sands (referred to in that study as the ecotone). Inter-nest distances on the Kalahari sands in Hwange were larger than anywhere in KNP, whilst in Gonarezhou nests were approximately 8–9 km apart, which is similar to KNP.

The shortest reported mean NND for White-headed Vultures is 4 300 m in Swaziland (Monadjem and Garcelon 2005), whilst at another site in Mozambique (CM unpublished data) a shorter mean NND distance of 3 960 m has been recorded. Both of these are less than half the 9 976 m mean NND recorded in KNP. However, the shortest recorded distance between two active (and successful) White-headed Vulture nests was 1 400 m in southern KNP, which is less than the previously reported minimum of 1 600 m (Monadjem and Garcelon 2005). In combination with the shorter mean NNDs from other sites, this suggests that the species can potentially breed at higher densities than is currently the case in KNP. While higher nest densities have been found on soils with higher primary productivity such as basalts (Hustler and Howells 1988), this is not the case in KNP (Table 4) and high breeding densities are rarely reported for White-headed Vultures – the overall density of breeding birds is consistently low across a range of protected areas (Murn et al. 2013 and references therein). This highlights that the factors affecting nesting densities of White-headed Vultures remain poorly understood. A short minimum NND distance combined with both consistent productivity and mean NND across habitat types seemingly discounts the importance of habitat-based density dependent factors as drivers of White-headed Vulture breeding distribution in KNP. By comparison, in KNP, Lappet-faced Vultures breed at higher densities with a shorter mean NND (4 520 $\pm$ 2 200 m, n = 25; CM unpublished data), but only in habitats that are preferred for nesting. Other influences such as interspecific relationships or abiotic factors such as fire regime have yet to be investigated for either species.

Whilst White-headed Vultures in KNP tend to nest in the same area for a number of years and do not move far when changing nest locations, this is insufficient evidence to support the conclusion of territoriality that has been suggested previously (Hitchins 1980; Mundy 1982; Hustler and Howells 1988; Mundy et al. 1992). The breeding distribution in KNP for White-headed Vultures is either spread or very spread and with a variation in NND that is either random or highly variable (Murn et al. 2013). Data from the higher nest-density areas in Hwange (mean NND 10.96 km, range 2.35 km to 24.8 km, n = 20) seem to suggest that a similar breeding distribution exists there. Like any vulture, White-headed Vultures are capable of travelling large distances quickly and this means that conclusions regarding territoriality need to be based on movement data rather than nesting distribution. Currently, there are no published data on the detailed movements of adult White-headed Vultures.

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