

Observations of nesting strategies of three African hornbill species

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Abstract

Rainfall is known to be a determining factor for the onset of avian breeding in semi-arid regions due to its positive effect on food availability. The effect of rainfall as a cue for timing of breeding as well as the nesting success (clutch size, hatching rate and number of successful fledglings) was investigated among three sympatric hornbill species: African Grey Hornbill (AGH) *Lophoceros nasutus*, Southern Red-billed Hornbill (SRH) *Tockus rufirostris*, and Southern Yellow-billed Hornbill (SYH) *T. leucomelas* breeding in nest boxes in a private nature reserve in a semi-arid region of South Africa. The first ecologically relevant rainfall (>10 mm) preceded the initiation of breeding in all three species. The AGH and SYH were the first species to start breeding, followed by the SRH. We monitored 28 nesting attempts by hornbills during the breeding season of 2019/2020. All three species showed hatching rates higher than 70% with the SYH having the highest (85%). All nesting attempts of the AGH ($n = 6$) and SYH ($n = 7$) were successful resulting in at least one successfully fledged chick, while seven of the 15 nesting attempts by SRH failed. Rainfall and subsequent food availability were proximate factors associated with the onset of breeding and nesting success of all three hornbill species. The effects of changes in temporal and spatial patterns of rainfall linked to climate change on breeding initiation and nesting success of birds should be closely

monitored to identify potential negative effects on population persistence.

Keywords: hornbill breeding, nesting success, hatching rate, nest boxes, climate change

Introduction

Found in Africa and southeast Asia, hornbills are well known and studied for their unique breeding strategy (Kemp, 1995; Datta and Rawat, 2004). All hornbills (Family Bucerotidae) are hollow-dependent and make use of natural cavities as nesting sites (Kemp, 1995). However, with the exception of ground-hornbills (*Bucorvus* spp.), their nesting strategy is unique in the sense that the female seals herself inside the nesting cavity, only leaving a narrow vertical slit through which the male can feed her and the chicks (Kemp, 1995).

Hornbills are secondary tree cavity users, and the availability of nesting cavities is crucial for breeding and ultimately nesting success (Datta and Rawat, 2004; Poonswad et al., 2013). Considering the alarming rate of deforestation in parts of the hornbills' distribution range (Amrutarane and Datta, 2015; Cooper et al., 2017; Wickramasinghe et al., 2018), tree cavity scar-

city accompanied with habitat loss have been recognised as major causes in the decline of various African hornbills (Trail, 2007) such as the Yellow-casqued *Ceratogymna elata* and Brown-cheeked *Bycanistes cylindricus* Hornbills in Ghana (Holbech *et al.*, 2018). Apart from plantation expansion and the development and urbanisation of natural habitats, the high demand for fuelwood in South Africa contributes to habitat loss as millions of tonnes of fuelwood is removed annually from natural areas (Shackleton and Shackleton, 2004; Munyati and Kabanda, 2009; Wessels *et al.*, 2013). With cavity availability reduced, inter-and intraspecific competition for nesting cavities could affect species interactions, population structures as well as life-history strategies (Williams and Shackleton, 2002; Cornelius *et al.*, 2008).

Although finding a suitable nesting site is crucial (Latif *et al.*, 2012), the timing of avian breeding is considered one of the determining factors of nesting success (Barrientos *et al.*, 2007) and it is commonly triggered by the lengthening of daylight (Barrientos *et al.*, 2007). However, in semi-arid regions, rainfall is more likely to be the determining factor to trigger breeding due to its positive effect on primary productivity and food availability (Kemp, 1974; Poulin *et al.*, 1992; Boyer *et al.*, 2003; Illera and Diaz, 2006). In recent years however, the start of the wet season has become more unpredictable, rainfall is more erratic and extreme events such as droughts and extreme precipitation are more common (Easterling *et al.*, 2000; Jennings and Magrath, 2009). The reproductive effort and output of several avian species have been associated with changes in seasonal rainfall (Bolger *et al.* 2005, Mares *et al.* 2017). Climatic changes could possibly affect the nesting success of hornbills, since their breeding is triggered by rainfall and a mismatch between food availability and chick rearing could ultimately affect the

nesting success (Van de Ven, 2017). The objective of this study was to compare the nesting strategies of three sympatric hornbill species by (1) examining the effect of rainfall as a cue for breeding initiation and (2) recording the nesting success in terms of clutch size, hatching rate and number of fledglings. We predicted that the first ecological relevant rain (>10 mm) of the wet season would trigger the onset of breeding in the three hornbill species as observed by an increase in nest box occupancy. Belonging to the same family and having similar breeding strategies, we expected similarities in clutch size, hatching rate and number of fledglings between the three hornbill species.

Methods

Study area

This study took place at the Mogalakwena River Reserve (MRR), a 1500 ha private nature reserve located in the Limpopo Province of South Africa at an altitude of 700 m above sea level (22°44'S, 28°47'E). The region is semi-arid with a mean annual precipitation of 370 mm (range: 180–730 mm) throughout the austral summer season (October to April, data obtained from Mogalakwena Research Centre between 2013–2019). During the summer months of the study period (October to April) the MRR had a mean daily minimum temperature of 21 °C (range: 12–33 °C) and a mean daily maximum temperature of 34 °C (range: 23–44 °C) (data obtained from Mogalakwena Research Centre between 1 October 2019 to 30 April 2020). In 2015, 81 vertical, plywood (1.5 cm) nest boxes (48 x 25 x 25 cm) with a circular entrance of 6 cm wide were installed at various heights (range: 1.5–4 m) throughout the reserve to serve as artificial tree cavities as part of a study investigating inter-specific competition for tree cavities (Engelbrecht *et al.*, 2017). The study site is inhabited by three cav-



Fig. 1. Three African Grey Hornbill nestlings removed from the nest box in order to fit them with unique metal rings (SAFRING) and to collect morphometric data.

ity nesting hornbill species: African Grey Hornbill (AGH) *Lophoceros nasutus*, Southern Yellow-billed Hornbill (SYH) *Tockus leucomelas* and Southern Red-billed Hornbill (SRH) *T. rufirostris* which readily make use of the nest boxes for breeding.

Data collection

After the first significant downpour of the summer season, all nest boxes were inspected once a week to detect the presence of sealed entrances. At every sealed nest box, the hornbill species and the number of eggs and hatchlings were recorded weekly until the last chick of every occupied nest box fledged. Morphometrical measurements were taken when either the female or chicks were fitted with a unique SAFRING metal ring (Fig. 1). These measurements included body mass to the nearest gram taken with a weighing scale, tarsus length and width, head and culmen length to the nearest millimetre taken with a calliper and wing and tail length to the nearest millimetre using a ruler. A nesting attempt was defined as a female present in a nest box with a sealed entrance for a minimum of 24 hours and considered successful if at least one nestling fledged successfully. The hatching rate was defined as the probability of an egg producing a live hatchling and was calculated by dividing the number of hatchlings by the

number of eggs laid (Mayfield, 1975). A substantial downpour was defined as rainfall exceeding 10 mm within 24 hours (Finnie, 2012).

Results

Of the 81 nest boxes, 28 nest boxes were occupied by hornbills during the 2019/2020 breeding season which spanned the period from November 2019 to May 2020 (Table 1). The total rainfall in the 2019/2020 summer season was 294 mm and the first substantial rain (15 mm) was recorded on 8 November 2019 (Fig. 2). Nesting attempts of both the AGH and SYH were first recorded on 5 December 2019, after the area had received a total of 86 mm of rain since the beginning of the rainy season. The first nesting attempt by a SRH female was observed two weeks later on 19 December 2019 after the area received a total of 134 mm rain since the beginning of the rainy season. There was a sharp increase in nesting attempts by SRH after a rain shower (34 mm) on 9 January 2020 (Fig. 2).

Twenty-one of the 28 hornbill pairs breeding in the nest boxes in the 2019/20 breeding season managed to fledge at least one chick. All the nesting attempts of AGH and SYH were successful (Table 1). The SRH initiated 15 nesting attempts of which five were abandoned before egg-laying. By the end of March 2020, the chicks of two SRH nests were predated on, presumably by a monitor lizard (*Varanus* spp.) resulting in eight successful nesting attempts (Table 1).

The mean clutch sizes were similar across the three species with the AGH having the largest mean clutch size of the three species (Table 1). The hatching rate of all three species were similar with the SYB having the highest hatching rate of 0.85 (85%) (Table 1). The AGH breeding pairs successfully fledged a total of 10 chicks (Fig. 4), while the SYH and SRH breeding pairs successfully fledged

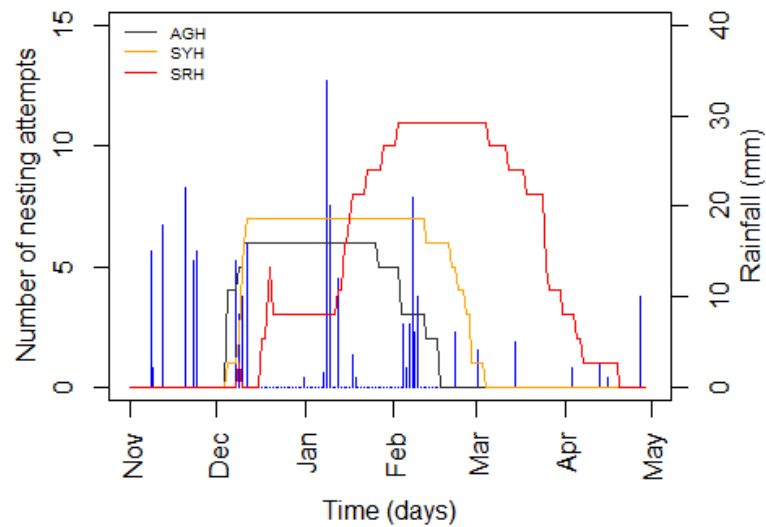


Fig. 2. The number of nesting attempts per species (left y-axis) and rainfall (mm; right y-axis) between 1 November 2019 and 1 May 2020 at the Mogalakwena River Reserve. The grey (AGH: African Grey Hornbill), yellow (SYH: Southern Yellow-billed Hornbill) and red (SRH: Southern Red-billed Hornbill) lines represent the daily total number of nesting attempts per hornbill species and the blue lines indicate daily rainfall events.

a total of 11 and 20 chicks, respectively (Table 1). This is expressed as fledged young per pair (overall).

Discussion

The three sympatric hornbill species found on the MRR all started breeding approximately a month after the area received more than 10 mm of rain in a single shower. All nesting attempts by AGH and SYH were successful whereas seven of the 15 nesting attempts by SRH failed. Various factors such as rainfall, food availability, breeding density, hormones as well as photoperiod have all been identified as proximate factors influencing the onset of avian breeding and there is great variation between species, geographic regions and breeding seasons (Dunn and Winkler, 2010). In semi-arid regions the climatic parameter, rainfall, is considered an important trigger for the start of avian breed-

ing, mainly due to an increase in prey availability (Illera and Diaz, 2006; Barrientos *et al.*, 2007). Ideally, breeding individuals should gain sufficient pre-breeding body condition (Kemp, 1974; Van de Ven, 2017) and the peak in food availability should coincide with energetic de-



Fig. 3. A Southern Red-billed Hornbill, with two eggs visible, nesting in one of the nest boxes at Mogalakwena River Reserve. Note the absence of the tail feathers due to moult.



Fig. 4. Accessing the contents of nest box #81. This was one of the first boxes to be occupied and the African Grey Hornbill breeding pair successfully fledged two chicks.

mands of the growing chicks in the nest (Dunn and Winkler, 2010). In the current study, the AGH, followed by the SYH, were the first species to attempt breeding in early December, possibly taking advantage of the peak in food availability after the rain in November. Although a few SRH females initiated breeding mid-December

and early January, the majority waited until early February. Although food availability was not determined in the current study, all three hornbill species entered the nest boxes after the MRR received a substantial downpour (>10 mm within 24 hours). This could indicate that rainfall is used as a predictor for food availability for the coming breeding period (Illera and Diaz, 2006). Therefore, rainfall could be considered as a factor influencing the onset of breeding in the three sympatric hornbill species. However, it is important to note that rainfall is not the only climatic variable to affect food availability in semi-arid regions. Temperature affects invertebrate activity and the germination of plants (Barrientos *et al.*, 2006), which in turn affects herbivorous invertebrates (Sanz *et al.*, 2003) and thus food availability. Even though rainfall preceded the onset of breeding in the three sympatric hornbill species in the current study, further studies combining multiple breeding seasons and including the effects of rainfall, temperature and food availability are needed to test alternative hypotheses.

The difference in feeding behaviours of the three hornbill species could possibly explain the delayed breeding of SRH in contrast to

Table 1. Summary of nesting success by three hornbill species (AGH: African Grey Hornbill, SYH: Southern Yellow-billed Hornbill and SRH: Southern Red-billed Hornbill), including the ranges for the mean clutch size, hatching rate and mean number of fledglings per nest at the Mogalakwena River Reserve in the 2019/2020 summer breeding season.

Species	AGH	SYH	SRH
Nesting attempts	6	7	15
Successful nests	6	7	8
Mean clutch size	4.0 (3-5)	3.7 (3-4)	3.6 (3-5)
Hatching rate	0.75 (0.25-1)	0.85 (0.5-1)	0.78 (0.33-1)
Mean no. fledglings/nesting attempt	1.7 (1-3)	1.6 (1-2)	1.3 (0-3)
Total number of fledglings	10	11	20

the AGH and SYH. The AGH is principally an arboreal feeder and SRH essentially obtain all their food on the ground, whereas SYH are the least specialized and feed opportunistically using hawking, gleaning and digging methods (Kemp, 1995). Kemp (1974) noticed that a flush of new leaves before the onset of the wet season allowed arboreal feeding hornbills to exploit arboreal invertebrates feeding on the fresh leaves, hence offering a potential explanation for the earlier occupation of nest boxes by AGH and SYH. Kemp (1974) also observed that the sprouting of new grass after the first rain coincided with SRH breeding initiation, possibly due to the increased availability of invertebrates to be gleaned off vegetation at or near ground level (Kemp, 1995). Thus, the difference in foraging strategy may allow the AGH and SYH to attain pre-breeding body conditions before SRH do and therefore start breeding earlier in the season.

Interspecific competition is another factor that could possibly explain the delayed breeding of the SRH. Being the smallest in wing length and body mass of the three sympatric species (Kemp, 1995), the SRH could possibly be less dominant and therefore be forced to wait for cavities to become available. Further studies focusing on interspecific competition for nesting cavities between the three sympatric species, as well as other cavity dependent species, is needed to confirm this. Following a few rain showers in November and early December, several SRH pairs attempted breeding. However, this was followed by a very hot and dry December and early January, when there were no follow-up rains, which resulted in the abandonment of these nesting attempts by SRH. The number of nesting attempts by SRH increased following a big rain shower in early January (34 mm).

The SRH had the highest number of nesting

attempts in nest boxes, followed by the SYH and the AGH. It is important to keep in mind that the number of nesting attempts monitored in this study are only those of nest boxes and not natural tree cavities. It could be that the AGH and the SYH prefer nesting in natural tree cavities rather than nest boxes. Since the SRH started to breed later compared to the other two species, suitable natural tree cavities may have already been occupied and SRH resorted to using nest boxes for breeding. However, this would need to be investigated further since there are many factors at play when choosing a suitable nesting site (Latif *et al.*, 2012) and the total number of breeding pairs per species at MRR is unknown.

All nesting attempts of both the AGH and SYH were successful compared to the SRH which only had eight successful nesting attempts from fifteen initial nesting attempts. A possible explanation for the five SRH females abandoning the nest boxes, might be that hornbills are long-lived species and adhere to the life-history theory which states that adults will choose their own survival over that of their offspring (Mills *et al.*, 2005). Since the MRR experienced a hot and dry December 2019 and January 2020, climatic conditions may have become unsuitable in the nest cavity or male provisioning may have been insufficient, forcing the females to abandon their nests to ensure their own survival. Another two failed nesting attempts of the SRH were the result of predation.

The clutch sizes of the three study species were very similar and ranged between three to five eggs compared to a study on the same three species in South Africa in which clutch sizes ranged from two to five eggs (Kemp, 1976). Although all three species had hatching rates higher than 70% (AGH: 0.75; SYH: 0.85; SRH: 0.78), the hatching rate of the SYH was the high-

est at 85%. Kemp (1976) found higher hatching rates for AGH and SRH (AGH: 0.84; SRH: 0.81), with a lower hatching rate for the SYH (0.73) compared to the current study. Observed hatching rates may have differed due to different methods used to observe nest contents. In his study, Kemp (1976) recorded nest contents from natural nesting sites in tree cavities by inserting a little mirror through the nest opening, whereas the current study assessed nest contents by opening up the nest boxes. Kemp's study (1976) was conducted in the Kruger National Park, South Africa, which has a different habitat and climate than the MRR, which could also contribute to the different results. The study by Kemp (1976) was also conducted over four consecutive breeding seasons, in comparison to the current study which only takes into account one breeding season. Hatching rate can however be influenced by different factors including poor to no development of the embryo due to temperature extremes and inadequate gas exchange (Lourens et al., 2006; Mortola 2009; Du and Shine, 2015), maternal hormones provided to the embryo (Schwabl et al., 2007), genetic makeup of the breeding pair as well as the embryo itself (Cordero et al., 2004; Hasson and Stone, 2009). Cannibalism of eggs has also been observed in some hornbill species, such as the SYH, which is considered a result of insufficient food provisioning by the male (Finnie, 2012; Van de Ven, 2017). Hatching rates vary naturally between species as well as between individuals within the same species (Stewart and Westneat, 2012). Further studies investigating differences in hatching rate should include environmental and ecological variables as well as genetic and behavioural data of the breeding pair across various breeding seasons (Stewart and Westneat, 2012).

The mean number of fledglings per nesting attempt was similar across the species (AGH: 1.7; SYH: 1.6; SRH: 1.3) and corresponded with the

SYH and SRH mean fledgling numbers of the study conducted by Kemp (1976) (AGH: 2.4; SYH: 1.4; SRH: 1.5). The AGH showed a much lower mean number of fledglings in the current study (1.7) compared to the estimate of 2.4 obtained by Kemp (1976). Conditions, such as rain and food availability, might have been better in the breeding season for the AGH in the study conducted by Kemp (1976), which possibly resulted in a higher mean number of fledglings compared to the other two species. Brood reduction in hornbills is a common phenomenon observed when conditions become suboptimal (Finnie, 2012). Females have been observed to selectively feed only the oldest chick when male provisioning is insufficient to ensure the survival of at least one chick (Davis et al., 1999; Chan et al., 2007). Infanticide cannibalism has also been recorded in some hornbill species (Chan et al., 2007; Ng et al., 2011) including the SYH (Finnie, 2012; Engelbrecht, 2013). The lower mean number of fledglings of the SYH and SRH in the study of Kemp (1976) might have been a result of unfavourable conditions and insufficient male provisioning, forcing the females to cannibalise. It is important to note that the method used to inspect nest contents in this study differed from those by Kemp (1976), which may result in different findings. Further studies including multiple seasons are recommended to conclude if any of the three study species has a more successful breeding strategy than the others and what factors influence the nesting success of AGH, SYH and SRH.

Although the results of this study comprise one season only, they support the importance of rain and subsequent food availability on the initiation of breeding by the three sympatric hornbill species (Kemp, 1974; Dunn, 2004; Dunn and Winkler, 2010). It is suggested that in years with low rainfall, food availability will be lower, and this may have repercussions for the start of

the breeding season, clutch sizes, the physical condition of the breeding pairs and nestlings, as well as the number of fledglings (Van de Ven, 2017; Van de Ven *et al.*, 2020). We predict that nesting success could possibly also be affected if the wet season becomes shorter, if the start of the wet season becomes more unpredictable, and if the annual rainfall becomes more erratic, which are all phenomena associated with climate change (Simmons *et al.*, 2004; Jennings and Magrath, 2009; Dunn and Winkler, 2010; Skagen and Adams, 2012). It is therefore important that regular monitoring of the nesting strategies of the three sympatric hornbill species as well as other cavity nesting birds be conducted to identify the impact of climate change on the breeding success of these species.

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