





Habitat structure and diversity influence the nesting success of an endangered large cavity-nesting bird, the Southern Ground-hornbill



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Habitat features can have a profound effect on the nesting success of birds. Savannas are often managed with predators and large herbivores as priority species, with little thought to the many bird species that management decisions could affect. Using a data set spanning seven breeding seasons, we examined how nesting success of Southern Ground-hornbills (SGHs) *Bucorvus leadbeateri* in the Kruger National Park varied as a result of various environmental and habitat factors within a radius of 3 km surrounding the nest site. Identifying which factors affect nesting success will allow for targeted management efforts to ensure the long-term survival of SGHs both within and outside of protected areas. Habitat structure and diversity of the vegetation surrounding the nest were the most influential factors on SGH nesting success. SGHs require open grassy areas for foraging and areas with large trees for nesting. Savanna habitat drivers such as elephants and fire should be managed to ensure that sufficient large trees are able to establish in the landscape and to control for bush encroachment. This is especially important in areas earmarked for SGH reintroductions. Nest sites of SGHs should be monitored to mitigate any structural changes in the habitat surrounding the nests. Nests should be modified or artificial nest sites provided, where nests have been damaged or lost, to ensure the continued presence of these birds in African savannas.

Conservation implications: Habitat structure and diversity surrounding Southern Ground-hornbill nests has a significant impact on their nesting success. This highlights the importance of monitoring vegetation change in savanna habitats where they occur. Management of savanna areas should take factors that influence bush encroachment, such as fire and elephants, into account to ensure the long-term persistence of these birds.

Introduction

Determining nesting success is fundamental to understanding the breeding biology of birds (Dinsmore, White & Knopp 2002). There are many factors that affect nesting success, such as the availability of high-quality habitat and nesting sites (Loegering & Anthony 2006; Paredes & Zavalaga 2001; Vickery, Hunter & Wells 1992), food availability (Boulton, Richard & Armstrong 2008; Oro, Pradel & Lebreton 1999; Rastogi, Zanette & Clinchy 2006), predation pressure (Boulton et al. 2008; Oro et al. 1999; Rastogi et al. 2006; Robinson et al. 2000; Zarones et al. 2014), landscape effects (habitat loss and fragmentation) (Boulton et al. 2008; Reidy, Thompson & Peak 2009; Winter et al. 2006) and human disturbance (Blackmer, Ackerman & Nevitt 2004; Woolaver et al. 2014). Identifying the suite of habitat characteristics that influence particular species and populations is important for management decisions for the conservation of these species (Martin 2014).

The Southern Ground-hornbill (SGH) *Bucorvus leadbeateri* inhabits savannas throughout much of Africa and is currently listed as *vulnerable*, mainly as a result of habitat loss, land-use change and persecution (Birdlife International 2016). In South Africa, this species is considered *endangered* and has suffered significant declines throughout its range (A.C. Kemp & R. Webster unpubl. data; Taylor, Peacock & Wanless 2015), with around 50% of the national population residing within the Kruger National Park (Kemp 1995). SGHs are terrestrial, carnivorous and co-operative breeders. They generally occur in groups of between 2 and 11 birds (Kemp, Joubert & Kemp 1989), consisting of an alpha breeding pair and related subordinate helpers (Kemp 1995). They are secondary cavity nesters and occupy territories within the Kruger National Park ranging from approximately 3000 ha – 12 000 ha (L. Combrink unpubl. data). Nests are most often located in natural cavities in large trees, but are occasionally in cliffs or earth banks (Kemp 1988). The majority of known nests within the Kruger National Park are in trees, with only 1 of the 38 nests referred to in this study being a nest in a cliff face. Females lay two eggs, 3–7 days apart. Only the first-hatched chick is

provided for, while the second-hatched chick mostly perishes as a result of starvation (Kemp 1995).

The SGH species recovery plan (Jordan 2011) highlights the use of captive-reared birds and reintroductions as conservation interventions for this species. However, the exact habitat requirements for SGHs are considered a knowledge gap (Jordan 2011). Before reintroductions of SGHs can occur, it is essential to first understand the factors that affect SGH nest site selection and that influence their nesting success. Kemp and Kemp (1991) suggest that suitably sized nest cavities for SGH are limited within savannas. However, in their study from 1967 to 1995, Kemp and Begg (1996) did not find any of the nest site characteristics tested to have an influence on SGH nesting success. Recent changes in management strategies in the Kruger National Park, in particular those relating to fire and elephants (Van Wilgen et al. 2008; Young, Ferreira & Van Aarde 2009), could have significantly affected the survival and recruitment of large trees. This in turn could affect the availability of suitably sized cavities in the landscape.

Wilson and Hockey (2013) found that SGH groups nesting in natural cavities were more successful when there was 3 km of open woodland surrounding the nest. They also found that SGH groups using artificial nests were more successful than those occupying natural nests. Their study was conducted in a private nature reserve adjacent to the central Kruger National Park which is 180 000 ha in extent (around 9% the size of the Kruger National Park).

Using data from seven complete breeding seasons of nest monitoring (2008–2015), we investigated what factors affected the nesting success of SGH groups in the Kruger National Park. Specifically, we asked (1) whether the harvesting of the second-hatched chicks impacted on the survival to fledging age of first-hatched chicks and (2) what nest characteristics, habitat and environmental factors affected overall nesting success of SGHs. We also tested whether the habitat structure within 3 km surrounding the nest and aspects of the nest site itself affected SGH nesting success for all vegetation types with known SGH nests throughout the Kruger National Park. Using our results, we suggest possible management implications and interventions needed to ensure the long-term sustainability of the SGH throughout its range.

Methods

Study area

This study was conducted within the Kruger National Park, South Africa (22–26°S, 30–32°E), which comprises around 2 million ha with an average annual rainfall of 350 mm – 750 mm (Gertenbach 1980). The park is largely divided longitudinally with more granitic soils in the west and basaltic soils in the east (Venter 1990). The habitat consists mainly of savanna, with pockets of dense woody vegetation within broader grasslands (Gertenbach 1983).

Nest surveys

We monitored all known and accessible SGH nesting sites within Kruger National Park ($n = 38$) from the 2008/2009 breeding season until 2014/2015 (Figure 1). The breeding season for SGHs coincides with the wet season, from October to April each year. Initial nest checks were usually conducted in November, with active nests being revisited throughout the breeding season to determine the outcome of the nesting attempt. In some instances, the second-hatched chick was removed or harvested from the nest for the purposes of being included in the captive rearing and reintroduction programme (Jordan 2011). Characteristics and measurements of each nest site were also collected. The nest site characteristics that we measured were: diameter of the base of the cavity (length and breadth), depth of the cavity (nest lip to base), volume of the nest (length \times breadth \times height), height of the nest entrance from the ground and the diameter at breast height of the nest tree. We were only able to collect chick survival and nesting success data from one cliff nest, which is completely inaccessible for measurements to be taken. Only measurements from nest tree cavities were included in this analysis ($n = 37$).

Chick survival and nesting success

The nestling period in SGHs is around 86 days in length. Nestlings were fitted with alphanumeric metal rings and

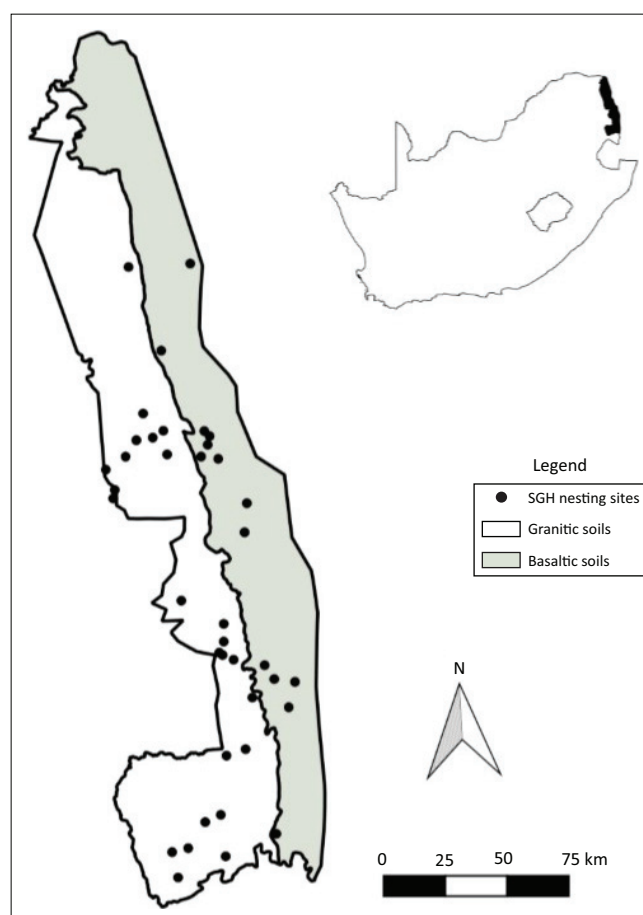


FIGURE 1: The locations of Southern Ground-hornbill nesting sites within the Kruger National Park, South Africa.

colour rings at 60–70 days for future individual identification. We considered the nestling to have fledged and the nest successful if the nestling reached ringing age. Reports of sightings of the fledged ringed chicks have confirmed that this is a reasonable assumption (L. Combrink unpubl. data). Chick survival was recorded as 0 if the nest failed and 1 if the nest was successful. Nests were also considered to have failed if the eggs were infertile or the eggs or chicks were predated.

As a result of the large distances and travel times between SGHs nests in the Kruger National Park, it was not possible to calculate daily nest survival rate. We calculated nesting success per group over the entire study period using the following formula: Nesting success is equal to the number of years where the chick survived divided by the number of years where the outcome was known. Years, where the outcome was not known, were excluded from the analyses. This yielded a proportion between 0 and 1. Models were weighted using the number of years of known outcome.

Nest habitat

GIS layers obtained from the South African National Parks (SANParks) were used to extract environmental variables related to each SGH nest. SGHs are thought to be central-place foragers, concentrating their breeding season activity around the nest site. We, therefore, included a circular buffer with a radius of 3 km around each nest for the purpose of extracting the related environmental variables and to test Wilson and Hockey's (2013) proposal about the area of open woodland surrounding each nest across the extent of the Kruger National Park.

Habitat was classified according to the 2013–2014 South African National Land Cover data set (GeoterraImage 2014). For each 3 km buffer zone, the proportions of the various land types were calculated. These data were then used to calculate the Shannon-Wiener Diversity Index (Shannon & Weaver 1949; Spellerberg & Fedor 2003) as a measure of vegetation diversity, using the R package *vegan* (Oksanen et al. 2016).

Insect species richness has been shown to be positively correlated with the Normalised Difference Vegetation Index (NDVI – measure of vegetation greenness) (Pettoirelli et al. 2011). In the Kruger National Park, the NDVI calculated for the growing or wet season is highly correlated with above-ground biomass and rainfall (Wessels et al. 2006). For the nesting success models, the mean seasonal NDVI and mean NDVI yield (seasonal biomass increase) values were averaged for the seasons where the outcome or fate of the nest attempt was known. Mean seasonal NDVI and mean NDVI yield layers were obtained from the MOD13Q1 product of version 6 of the MODIS 16 day Terra Vegetation Indices data set (Didan 2015) via the MODISTools package (Tuck & Philips 2015).

Soil type was classified as the proportion of granite, basalt, gabbro, eccla shale and rhyolite within the buffer zone and expressed as a percentage. The length (total number of kilometres) of all streams and rivers and the distance from

the nest to the nearest stream were calculated using Quantum GIS (QGIS). Similarly, length (total number of kilometres) of all tourist and management roads, and distance from the nest to the nearest road (tourist or management) were included.

Rainfall for the current breeding season (mm), the previous breeding season (mm) and the previous non-breeding season (mm) were determined using SANParks' rainfall data, collected at weather stations throughout the Kruger National Park. The rainfall data from the weather station closest to each nest site were used as a proxy for rainfall within the buffer zone for the particular time period. The mean annual rainfall (percentage of the buffer zone within the various rainfall categories – see Table 1) was calculated using the most current continuous vector layer of interpolated rainfall data provided by SANParks.

Data analyses

We conducted all statistical analyses using R (Version 3.2.2; R Core Team 2015). A generalised linear mixed model with a binomial distribution and logit link function was applied using the *lme4* package (Bates et al. 2015) for both chick survival and nesting success. In the chick survival model, chick survival was the response variable and treatment (whether the nest was harvested or not) included as a fixed effect. Group (defined using the nest name) and year were included as random effects, to account for any effects on chick survival related to the individual group or season, which were not explicitly measured or modelled here.

For the nesting success models, nesting success was the response variable with group included as a random effect. Some of the predictor variables were found to be highly correlated ($r \geq 0.7$) and these were examined separately against the response variables to determine which produced the model with the lowest Akaike information criteria (AIC) ranking. Only those variables were kept in the model. Where two correlated variables had the same effect in the model, the variable that was present for the larger number of samples was retained. Owing to rank deficiency, we could not include all predictor variables in one model for nesting success. For this reason, similar variables (water related, habitat related and nest related) were grouped together and these models were compared with the final selected models having the lowest AIC rankings.

For SGH chick survival, we had a TREATMENT model looking at the effect that removing the second-hatched chick from the nest had on the first-hatched chick. For nesting success, we had three models namely, a NEST model looking at nest dimensions, tree species, et cetera; a LAND model focusing on habitat related features; and a WATER model including streams, rainfall, et cetera. Further variables in the LAND and WATER models were excluded, owing to rank deficiency, as their contribution to the buffer zone areas were negligible or only present for a small number of nests. For the NEST models, nest cavity width, breadth, depth and height of cavity entrance were all highly correlated with nest volume

TABLE 1: Fixed effects included in the Southern Ground-hornbill nesting success LAND and WATER generalised linear mixed models.

Land model	Description	Type	Mean	s.d.	Minimum	Maximum
Latitude	-	Continuous	-	-	-	-
Longitude	-	Continuous	-	-	-	-
Land cover	Thicket and dense bush (t)	Percentage	17.05	11.78	2.14	49.13
	Grassland (g)	Percentage	25.08	21.24	1.75	75.34
	Low shrubland (s)	Percentage	0.96	2.73	0.00	17.01
	Bare ground (b)	Percentage	0.38	0.93	0.00	3.59
Soils	Granite (g)	Percentage	61.73	46.53	0.00	100.00
	Ecca Shale (e)	Percentage	7.64	22.04	0.00	99.74
	Gabbro (b)	Percentage	4.47	16.86	0.00	100.00
Roads (km)	Length of Tourist Roads (t)	Continuous	9.01	6.34	0.00	21.33
	Length of Management Roads (m)	Continuous	4.60	4.30	0.00	19.05
	Distance from nest to nearest road (d)	Continuous	0.16	0.15	0.00	0.61
Mean seasonal NDVI†	-	Continuous	0.51	0.07	0.33	0.63
Mean NDVI Yield (biomass)†	-	Continuous	0.23	0.06	0.10	0.35
Diversity index	-	Continuous				
Water model						
Mean annual rainfall	450 mm – 500 mm	Percentage	19.90	27.31	0.00	90.08
	500 mm – 550 mm	Percentage	31.00	32.50	0.00	100.00
	550 mm – 600 mm	Percentage	23.30	30.56	0.00	93.34
	600 mm – 650 mm	Percentage	14.81	27.32	0.00	99.02
	650 mm – 700 mm	Percentage	2.80	9.47	0.00	47.00
	700 mm – 750 mm	Percentage	1.26	7.67	0.00	47.93
Streams (km)	Length of streams and rivers	Continuous	7.21	2.93	1.74	15.22
	Distance from nest to nearest stream or river	Continuous	0.16	0.22	0.00	0.95

s.d., standard deviation.

†, Denotes values obtained only for years where the fate of the nesting attempt was known.

($r \geq 0.7$). As a result, only nest volume and diameter at breast height were included in the NEST models as fixed effects.

All models with significant variables were checked for over dispersion and Drop1 (Bates et al. 2015) was then used to determine the model with the best fit and lowest AIC value. If significant results were produced, the p -values for the final models were then adjusted using false discovery rate (FDR) to account for multiple comparisons on a small data set (Pike 2011) using the base package in R (R Core Team 2015). Table 1 details the fixed effects that were included in the respective LAND and WATER models for nesting success.

Results

Chick survival

We monitored 100 SGH nesting attempts in the Kruger National Park during the study, for which the outcome of the nesting attempt was known. Of these 100 nesting attempts, 76 were successful and 24 failed. Second-hatched chicks were harvested from 32 of these nesting attempts (L. Combrink unpub. data).

We tested the effect of the removal of the second-hatched chick on the survival to fledging age of the first-hatched chick (TREATMENT model), but found no significant impact of the nest treatment (Estimate = 0.8538, standard error = 0.7704, $z = 1.108$, $p = 0.2677$). Although not significant, the log odds of the first-hatched chick surviving to fledging age when harvesting is conducted, were 92% and when the nests were only monitored, the log odds of the first-hatched chick surviving to fledging age were 83%. This indicated

that removing the second-hatched chick had no significant effect on the survival to fledging age of the first-hatched chick, although there does seem to be some benefit to the first-hatched chick when the second-hatched chick is removed.

Nesting success

Of the 37 SGH tree nests in our study, cavities had a mean length of $48.7 \text{ cm} \pm 2.0 \text{ cm}$ (30 cm – 71 cm), a mean breadth of $43.1 \text{ cm} \pm 2.6 \text{ cm}$ (25 cm – 102 cm) and a mean depth of $49.3 \text{ cm} \pm 4.2 \text{ cm}$ (11 cm – 160 cm). All nests were situated in trees with a mean diameter at breast height of $129.6 \text{ cm} \pm 17.0 \text{ cm}$ (64 cm – 544 cm) and cavities were located at a mean height of $5.6 \text{ m} \pm 0.4 \text{ m}$ (3 m – 12 m) from the ground. We modelled group nesting success as a factor of the various nest site parameters, but did not find that any played a significant role (nest volume [$p = 0.948$], DBH [$p = 0.179$]).

Nesting success was calculated for 38 SGH nests (37 tree nests and 1 cliff nest) across the Kruger National Park. The best of the LAND models relating habitat features to nesting success (Tables 2 and 3) included all four of the major habitat classes (thicket and dense bush, grassland, low shrubland and bare ground), latitude, longitude, percentage of gabbro soils, distance from the nest to the nearest road and habitat diversity. Although longitude and the low shrubland habitat type did not have significant effects on nesting success, removing them from the model increased the AIC, possibly owing to them being almost significant after adjusting the p -values. For the WATER model, none of the variables included showed any significant effect on overall nesting success (Table 4).

Latitude had a significant effect on SGHs' nesting success, with nests in the north being less successful than those in the south. An increase in amount of thicket and dense bush, grassland or bare ground surrounding the nest caused nesting success to decrease. Similarly, the greater the percentage of gabbro soils within the buffer zone around each nest, the lower the overall group nesting success. Nests with a higher diversity of habitats within the buffer zone had a higher nesting success than those with more homogenous surrounding habitat. The proximity of nests to roads improved overall nesting success, with more successful nests being situated closer to road networks (Table 3).

Ethical considerations

This work was part of a registered research project with SANParks (POTTL988) and was approved by the relevant animal ethics committee.

TABLE 2: Output of generalised linear mixed model selection comparing nesting success of Southern Ground-hornbills.

LAND models	K	AIC	ΔAIC	Deviance
Lat + Long + LANDCOVER + SOILb + Diversity + ROADd	9	144.6	0.0	122.6
Lat + Long + LANDCOVER + Diversity + ROADd	8	146.1	1.5	126.1
Lat + LANDCOVER + SOILb + Diversity + ROADd	8	146.5	1.9	126.5
Lat + Long + LANDCOVER + SOILb + Diversity	8	147.9	3.3	127.9
Lat + Long + LANDCOVERtgs + SOILb + Diversity + ROADd	8	148.7	4.1	128.7
Lat + Long + LANDCOVER + SOIL + ROAD + Diversity + NDVI + Yield	15	154.6	10.0	120.6

All models included group as a random effect. The top five models are included with the last model (with 15 variables) being the complete model. Where not all variables are included in a group, these are specified for example LANDCOVERtgs is for thicket and dense bush, grassland and low shrubland. LANDCOVER with no specifications will include all four variables (see Table 1).

TABLE 3: Parameter estimates, standard errors, z values, p -values and adjusted p -values (using False Discovery Rate) for variables in the best LAND model for Southern Ground-hornbill nesting success (with the lowest Akaike information criteria).

Variables	Estimate	s.e.	z value	p	Adjusted p (FDR)	Significance
Intercept	1.883	0.459	4.100	0.000	0.000	***
Latitude	-2.091	0.722	-2.897	0.004	0.007	**
Longitude	-0.977	0.528	-1.852	0.064	0.064	.
Thicket and dense bush	-2.624	0.653	-4.021	0.000	0.000	***
Grassland	-1.562	0.549	-2.846	0.004	0.007	**
Low shrubland	-2.097	1.071	-1.957	0.050	0.056	.
Bare ground	-1.319	0.462	-2.852	0.004	0.007	**
Gabbro soils	-0.913	0.436	-2.092	0.036	0.046	*
Diversity index	2.663	0.744	3.581	0.000	0.001	**
Distance from nest to nearest road	-0.785	0.352	-2.232	0.026	0.037	*

*, 0.05; **, 0.01; ***, 0.001; ., 0.1.

s.e., standard error; FDR, false discovery rate.

TABLE 4: Parameter estimates, standard errors, z values, p -values and adjusted p -values (using False Discovery Rate) for variables in the best WATER model for Southern Ground-hornbill nesting success (with the lowest Akaike information criteria).

Variables	Estimate	s.e.	z value	p
Intercept	9.6075	19.5144	0.492	0.622
Ann. Rainfall 450 mm – 500 mm	2.1657	1.5901	1.362	0.173
Ann. Rainfall 500 mm – 550 mm	1.8684	1.5082	1.239	0.215
Ann. Rainfall 550 mm – 600 mm	2.0458	1.5244	1.342	0.180
Ann. Rainfall 600 mm – 650 mm	1.8749	1.4241	1.316	0.188
Ann. Rainfall 650 mm – 700 mm	26.4019	66.9240	0.394	0.693
Length of all rivers and streams in buffer zone	0.7975	0.8247	0.967	0.334
Distance from nest to the nearest stream	-0.1025	0.8021	-0.128	0.898

s.e., standard error.

Discussion

In this study, we analysed data spanning seven breeding seasons to determine what factors contribute to SGH nesting success in the Kruger National Park. In particular, we investigated whether harvesting of second-hatched redundant chicks impacts on the survival to fledging of first-hatched chicks. Our results showed that this practice had no detrimental effects and could even benefit the first-hatched chick in some ways (although this potential benefit was not significant). This was an important finding for the conservation of SGH, as harvesting of second-hatched chicks is crucial to the established captive-rearing programme and the subsequent formulation of groups for future reintroductions.

We found that the habitat features in the area immediately surrounding SGH nest sites will greatly impact their nesting success. Shifts in habitat structure can often result in changes in species assemblages which may in turn impact the reproductive output of the associated bird species through loss of potential nesting habitat (Martin 2014), changes in prey base (Burke & Nol 1998), changes in foraging ability (Butler & Gillings 2004) and increased predation risk (Badyaev 1995; Haensly, Crawford & Meyers 1987; Yurizharikov & Cooke 2007). For territorial species, which are already restricted to finding nest sites and sufficient prey within their territory, these impacts can be exacerbated, as changes in prey availability or accessibility or the availability of suitable nesting sites within their territory will lead to a reduction in productivity.

SGHs require a territory with delicate balance between more open grassy areas for foraging and woodland areas for

nesting. The dominance or increase in density of any one of the vegetation types (thicket and dense bush, grassland, low shrubland and bare ground) around the nest site will negatively affect SGH nesting success. Dense grass was associated with both vegetation types found on gabbro soils (Venter 1986), another factor found to negatively influence nesting success. The diversity index results supported these findings in that SGH groups with a greater diversity of vegetation types surrounding the nest had a significantly greater nesting success than those with more homogenous vegetation around the nest site.

One interesting result was the increase in nesting success with an increase in the proximity of a nest site to the road. This was the only feature of the actual nest, in terms of characteristics, that showed any influence on SGH nesting success. This result may again reinforce the positive influence of a diversity of habitats, as road verges are often more vegetated as a result of increased precipitation runoff (Smit & Asner 2012), which could make these good foraging areas. Some SGH groups in the Kruger National Park beg from vehicles, mostly during the winter months (Combrink pers. obs.). In winter, when the abundance of available prey is at its lowest, SGHs are known to concentrate their foraging in areas around sources where prey abundance is higher (Kemp et al. 1989). Thus, a steady food source associated with roads in the winter months could increase the health and fitness of the alpha pair and thereby increase their nesting success.

SGHs spend around 70% of the day walking (Kemp 1995), and have been known to cover distances of around 7 km in a day (Wilson & Hockey 2013). Knight (1990) showed that SGHs favour areas where the grass is less than 50 cm in height. A change in habitat structure, such as an increase in grassland, and thicket or dense bush would likely impact SGH foraging efficiency. Not only would prey detection and acquisition be more difficult, but also the denser habitat structure could increase the risk of ambush by predators (Butler & Gillings 2004; Wilson & Hockey 2013).

Over the past century, there has been an increase in woody plants in grasslands and savannas (Buitenwerf et al. 2012; O'Connor, Puttick & Hoffman 2014; Wigley et al. 2010). This woody or bush encroachment can significantly alter the biodiversity in the area (Buitenwerf et al. 2012) and have large consequences for conservation and protected areas (Wigley et al. 2010). Bush encroachment is often considered the result of changes in disturbance regimes (Buitenwerf et al. 2012; Parr et al. 2014; Wigley et al. 2010). Disturbance, such as fire and herbivory (with African Elephants *Loxodonta africana* in particular), is known to engineer savanna vegetation (O'Connor et al. 2014; Sankaran, Ratnam & Hanan 2008). With the increasing elephant densities in the Kruger National Park (Young et al. 2009) and the occurrence of frequent fires, many trees will have difficulty establishing (Helm et al. 2011). Without recruitment, the loss of woody species and canopy trees can significantly alter the habitat

composition with a potential change in habitat structure through bush encroachment (Baxter & Getz 2005; Smallie & O'Connor 2000) from more open savannas to dense woodland (Hibbard et al. 2001; Parr et al. 2014).

In addition, the loss of tall canopy trees in the landscape will reduce the number of potential nesting trees for SGH and many other large tree nesting raptors, such as White-backed Vultures *Gyps africanus* (Murn et al. 2013) and Martial Eagles *Polemaetus bellicosus* (Van Eeden et al. 2017). Nest sites for SGHs are thought to be limited in the Kruger National Park (Kemp et al. 1989) owing to a scarcity of suitably sized cavities. The loss of a SGH nest site within a territory could be detrimental to the group's productivity. Following nest loss or collapse, some groups in the Kruger National Park have failed to breed for the remainder of our study period – in one case, for a total of four seasons.

Wilson and Hockey (2013) found SGH nesting success for natural nests to be significantly correlated with the amount of open woodland within 3 km of the nest site. In our models, open woodland and grassland habitat types were negatively correlated. The grassland habitat type was retained in our final LAND model, as of the two habitat types, it produced the model with the lowest AIC value. We found that an increase in the grassland habitat type had a negative effect on nesting success. Therefore, we can deduce that an increase in open woodland around the nest will be beneficial to SGH. This means that the amount of open woodland surrounding the nest site is an important factor to consider when deciding on the placement of nest boxes or when creating nest sites for SGHs, regardless of the vegetation type in which the nest is located.

Authorities responsible for vegetation management should take into account the possible influence that management decisions and actions can have on habitat composition and structure and the influence this has on overall biodiversity (Skowno & Bond 2003). The influence of climate change on bush encroachment into grasslands (Wigley et al. 2010) and the subsequent changes to the structure of savanna vegetation (Buitenwerf et al. 2012; Parr et al. 2014) cannot be actively controlled. However, management authorities can control and even mitigate other drivers, such as the influence of frequent fires and elephants. In the Kruger National Park, where the elephant population is seemingly on the increase (Young et al. 2009), the potential impact of high densities of elephants on the vegetation structure and subsequent impacts on overall species diversity should not be ignored. Elephant impacts on large trees in African savannas should therefore be monitored and managed where necessary to allow for the establishment of sufficient large trees. Similarly, in areas where SGH nests are located, and in particular, those known to be successful, fires should be managed so as not to damage the large nest trees and alter the habitat structure towards a more homogenous surrounding habitat.

Conclusion

Our data support the harvesting of second-hatched chicks as a viable conservation initiative, as set out in the SGH species recovery plan (Jordan 2011). Removal of second-hatched chicks from SGH nests was found to have no significant effect on the survival to fledging of the first-hatched chick. We therefore recommend that harvesting of second-hatched chicks from wild SGH nests continues to support the captive rearing and reintroduction programme (Jordan 2011).

Our results showed that habitat structure and diversity are critical when deciding on a suitable reintroduction site for SGHs. It is also imperative that nest site placement maximise the amount of open woodland and a diversity of habitats surrounding the nest. Annual monitoring of SGH nest sites will allow for the early detection and possible mitigation of bush encroachment or changes in habitat structure surrounding nest sites. In addition, monitoring would detect when natural nest sites collapse or are no longer suitable. Maintenance of these natural nest sites and the erection of artificial nest boxes, in cases where natural nests collapse, should be considered as a conservation intervention. SGHs readily take to nest boxes and groups nesting in artificial nests have been shown to have a significantly higher breeding success when compared with groups using natural nest sites (Wilson & Hockey 2013).

SGHs, as with many other large bird species, are considered to be safe within protected areas, with most of the threats to the birds affecting those populations occurring in unprotected areas. We have shown that even within protected areas, without sufficient management interventions to control the drivers of bush encroachment and nest site losses, the nesting success and population status of SGHs, and potentially all large tree canopy nesting birds, will decline.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

L.C. and C.T.D. conceptualised the article. L.C., H.J.C. and A.J.B. conducted the field work. L.C. and H.J.C. analysed the data. L.C. wrote the article. All authors provided editorial input for the article.

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