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Testing the importance of individual nest-site selection for a social and group-living vulture

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Abstract

Nest-site selection by species is expected to be adaptive and lead to improved breeding productivity, but in some settings, there exist mismatches between preferred nesting habitat and breeding productivity. We tested the expectation that nest-site selection is adaptive in a sample of 63 nests of a long-lived social species that breeds and forages in groups: the critically endangered white-backed vulture (*Gyps africanus*). By studying breeding groups in the same area, we controlled for landscape-level effects on habitat selection and investigated how fine-scale nest-site characteristics affect breeding productivity. We developed models to assess how nine characteristics of nest sites selected by breeding vultures compared with 70 random trees and tested associations between these characteristics and breeding productivity. White-backed vultures selected nest sites in taller trees (>7 m), but neither tree height nor any other nest-site characteristics had a clear effect on breeding productivity. Vultures selected nest trees closer to each other than random trees, and the associations between nest density, nearest neighbour distance and breeding success were all positive. These positive associations and the absence of an observable effect between nest-site characteristics and breeding productivity suggest that for this semi-colonial breeder, the social imperative of proximity to conspecifics (i.e., nesting near other vultures and group foraging) may be more important than individual nest-site selection.

KEYWORDS
breeding, Kimberley, productivity, South Africa, white-backed vulture

Résumé

La sélection du site de nidification par les différentes espèces doit être adaptative et déboucher sur une augmentation du taux de reproduction. Des décalages entre l'habitat de nidification préféré et le taux de reproduction ont néanmoins été constatés dans certains contextes. Nous avons testé l'hypothèse selon laquelle la sélection du site de nidification est adaptative sur un échantillon de 63 nids d'une espèce sociale longévive, qui se reproduit et se nourrit en groupe : le vautour à dos blanc (*Gyps africanus*), qui est gravement menacé. En étudiant les groupes de reproduction au sein de la même zone, nous avons contrôlé les effets au niveau du paysage sur la sélection de l'habitat et étudié la façon dont les caractéristiques des sites de nidification affectent le taux de reproduction sur une échelle réduite. Nous avons conçu des modèles afin d'évaluer la correspondance entre neuf caractéristiques liées aux sites de nidification sélectionnés par des vautours reproducteurs et 70 arbres choisis de façon aléatoire. Nous avons ensuite étudié les liens entre ces caractéristiques et le taux de reproduction de cette espèce. Les vautours à dos blanc ont choisi des sites de nidification situés dans les arbres les plus hauts (hauteur > 7 m), mais ni la hauteur des arbres ni aucune autre caractéristique des sites de nidification n'avaient d'impact notable sur le taux de reproduction. Les vautours à dos blanc ont sélectionné des arbres proches les uns des autres plutôt que des arbres placés de façon aléatoire, et les liens entre la densité des nids, la distance à laquelle se trouvait l'individu le plus proche et le succès de la reproduction étaient tous positifs. Ces liens positifs et l'absence d'effet notable entre les caractéristiques du site de nidification et le taux de reproduction de ce reproducteur semi-colonial suggèrent que l'impératif social de proximité avec ses congénères (c.-à-d.nidification à proximité d'autres vautours et recherche de nourriture en groupe) est peut être plus important que la sélection individuelle du site de nidification.

1 | INTRODUCTION

Habitat degradation is a leading contributor to declining wildlife populations and extinction risk (IPBES, 2019). Through the reduction in available habitat and also its quality, habitat degradation causes range contractions and increases risks to vulnerable populations (Ripple et al., 2015; Wolf & Ripple, 2017). For birds, the risks to breeding populations from habitat loss have been recognised for many years (Dolman & Sutherland, 1995), and ongoing habitat degradation creates an urgency to identify areas under threat and protect important habitat for species or their populations that are at risk (Beresford et al., 2011; United Nations, 2018).

There is a variety of methods for identifying important nest-site habitat (Jones, 2001). One approach is to use occupancy modelling to determine the difference between nesting and non-nesting trees and/or sites (Mateo-Tomás & Olea, 2010), but this method may not always be informative because while occupancy data may indicate preferred nest-site habitats, they may not highlight nest sites that are associated with increased fitness (i.e. breeding productivity). Given that ecological theory predicts habitat and/or nest-site selection to be adaptive (Southwood, 1977), or at least selective (Fuller, 2012), there can be a preference to use breeding productivity data instead of occupancy data to detect important nesting habitat (Johnson, 2007; Jones, 2001). However, if nest-site characteristics are not driving breeding productivity, this method may also fail to identify important habitat features. This contrast is exacerbated by occasional correlations between nest-site characteristics and productivity (Freund et al., 2017) and also cases where there is a mismatch between breeding habitat preferences and productivity (Chalfoun & Schmidt, 2012).

The white-backed vulture *Gyps africanus* has experienced major population declines across most of its sub-Saharan range and is critically endangered with a high risk of extinction (BirdLife International, 2017). A high rate of mortality from birds eating carcasses contaminated with poison is the main driver of the continent-wide decline of white-backed vultures (Ogada et al., 2016), but there is also some evidence that white-backed vulture populations are declining in areas were poison-related deaths are rare, with disturbance and loss of nesting habitat as possible negative factors (Murn et al., 2017). Understanding and identifying the nesting habitats that are important for WbVs is therefore a key component of conservation management for the species.

The white-backed vulture is a long-lived, semi-colonial species that nests in groups that are spatially discrete across the landscape (Mundy et al., 1992; Murn et al., 2002), and while the distribution and size of these breeding groups is dynamic (Murn et al., 2017), the semi-colonial nature of breeding white-backed vultures remains. Previous research on breeding white-backed vultures shows that they tend to nest in the taller trees in areas where they are breeding (Herholdt & Anderson, 2006; Kendall et al., 2017; Monadjem, 2003), but there is limited information on how nest tree characteristics affect breeding productivity. Nest densities of white-backed vultures are higher in protected areas with riparian habitat and where elephants are absent (Monadjem & Garcelon, 2005), higher in dense woodlands than grasslands (Virani et al., 2010), and overall highest in warmer, low-lying areas with low relief (Bamford, Monadjem & Hardy, 2009). The group/social nesting behaviour of white-backed vultures is obvious, and nest density increases in preferred areas, which conflicts with results that suggest white-backed vultures nest success is negatively density-dependent (Bamford, Monadjem, Anderson et al., 2009). However, because white-backed vultures are widely distributed across large parts of sub-Saharan Africa (Mundy et al., 1992), the areas they inhabit vary and conclusions about nesting habitat preferences or nest success from one region may not be relevant in another region (Bamford, Monadjem, Anderson et al., 2009). As a result, it is important to identify nest-site characteristics in different parts of the range of the species, to (1) inform species distribution models that may otherwise lack local specificity (Bamford, Monadjem, Anderson et al., 2009) and (2) facilitate conservation management decisions that incorporate regional characteristics for the species.

Here, we test the expectation that nest-site selection by white-backed vultures within their semi-colonial groups is adaptive (i.e., leads to increased breeding productivity). Our aim is to identify fine-scale nest-site characteristics in two white-backed vulture breeding areas within the Northern Cape, South Africa, and then assess the importance of these features to white-backed vultures using a combination of occupancy and breeding productivity data. Although landscape-scale effects have been identified as important to white-backed vulture nesting habitat selection (Bamford, Monadjem & Hardy, 2009; Bamford, Monadjem, Anderson et al., 2009) and are likely to influence breeding productivity overall and in any given year, in our study, all the nest sites are in close proximity to each other and within the same landscape. This setting means that all nest sites are subject to the same landscape-scale and temporal effects, and thus accounted for, so we focus solely on the importance of fine-scale characteristics. Furthermore, while adult mortality (and by extension breeding success) will be driven by landscape-scale effects like eating poisoned carcasses (Murn & Botha, 2017), there is evidence to suggest breeding success is affected by local-scale characteristics like nest-predator presence (Johnson & Murn, 2019) and the height of trees (Monadjem, 2001), which we investigate here.

2 | STUDY AREA AND METHODS

Near the city of Kimberley in the Northern Cape Province of South Africa, Dronfield Nature Reserve (Dronfield, 28.64S, 24.90E) and Mokala National Park (Mokala, 29.17S, 24.32E) are the two largest of several local breeding colonies of white-backed vultures, with c.70 and c.50 breeding pairs, respectively (Murn et al., 2017). The Kimberley region is in a savanna biome, with a principal vegetation type of Kimberley Thornveld (Mucina & Rutherford, 2006). The main large-tree species white-backed vultures use for nesting are Camel Thorn *Vachellia (Acacia) erioloba* and Umbrella Thorn *Vachellia (Acacia) tortilis* (Murn & Anderson, 2008). Human-induced habitat modification is low across most of the study area (Murn & Anderson, 2008), and the habitat of white-backed vulture nesting areas is homogeneous (Murn et al., 2002).

2.1 | Data collection

In June 2015, we surveyed Dronfield and Mokala and identified 63 active white-backed vulture nests with an egg by checking the nest (31 at Dronfield, 32 at Mokala). In October 2015, we revisited the nests to assess breeding success by checking the nest to see whether a nestling was present. White-backed vultures typically lay one egg and incubate it for approximately 56 days to hatching, after which the chick remains in the nest for up to 4 months before fledging and becoming independent 5–6 months later (Mundy et al., 1992). Monitoring nests for up to 6 months is therefore necessary to estimate fledgling rate, and by only checking nests in October, we were unable to do this. However, we recorded nests where nestlings survived for 2–3 months as being successful, and used this as a proxy for breeding productivity (Hustler & Howells, 1990; Murn & Holloway, 2014). We assessed nestling success in 52 nests (27 at Dronfield, 25 at Mokala).

A random selection of non-nesting control trees (38 at Dronfield, 32 at Mokala) was located using a random coordinate generator (nearest tree to the coordinate) within the spatial limit of each colony. The tree had to be >2 m tall (shortest vulture nest tree in the study is 2.3 m) and with a clearly defined trunk (not a multi-stemmed large shrub). Nesting and non-nesting trees were in close proximity, so landscape features were the same for all trees and meant we could focus on fine-scale nest-site characteristics, rather than landscape-level features, which have already been studied in southern Africa (Bamford, Monadjem & Hardy, 2009; Bamford, Monadjem, Anderson et al., 2009; Monadjem & Garcelon, 2005). At each nesting and non-nesting tree, we measured 17 tree and habitat characteristics, which we later reduced to seven tree characteristics that we considered important for white-backed vultures (Table 1). To assess the proximity of nests to each other, we recorded the nearest neighbour distance (NND) plus the number of nests within 1 km of each nest tree (nest density). Pied crow density *Corvus albus*, as a measure of nest predation risk, was assessed by extracting the fine-scale (30 m raster) crow density data from the distance density function in Johnson and Murn (2022).

2.2 | Analysis

We modelled tree occupancy (nesting trees [$N = 63$] vs. non-nesting trees [$N = 70$]) against the seven tree characteristics and pied crow density, and hatching success (egg hatched and chick is alive [$N = 19$] vs. trees where chicks or eggs failed [$N = 33$]) against all nine nest-site characteristics (Table 1). We excluded nest density from the occupancy model because non-nesting trees were specifically selected within the boundaries of each white-backed vulture colony, and so these data were ill-equipped for exploring occupancy patterns. We modelled the occupancy and hatchling responses using mixed-effect models with a binary logistic error distribution and treated all nest-site characteristics (Table 1) as a continuous distribution except the 'Species' variable which is binary. We included location (Dronfield or Mokala) as a random intercept to reduce any site-specific effects. Differences between the mean nearest neighbour distances of nesting trees and non-nesting trees were assessed using F-tests and two-sample *t*-Tests. We accounted for spatial non-independence between trees by calculating distances between each tree to create a covariance matrix and then specified an exponential correlation function across this covariance matrix. All predictors were

TABLE 1 Tree and surrounding habitat characteristics measured at African white-backed vulture *Gyps africanus* colonies near Kimberley, South Africa.

Tree	Definition (units)
Tree height	Tree height (m). Measured using the distance from tree in conjunction with a clinometer
Canopy width	Width of canopy at widest point (m)
Height of lowest branch	Distance from ground to the point the lowest branch connects with the trunk (cm)
Canopy density	Percentage of sky visible when looking through the canopy using a 3 cm diameter tube: 1 (0%–25%), 2 (25%–50%), 3 (50%–75%) and 4 (75%–100%). Given the sample size, we treated this variable as continuous to reduce the number of mode parameters
Tree species	Species being measured: *Acacia erioloba* or *Acacia tortilis*
Number of trunks	Number of trunks contained within one canopy (*N*)
Shrub coverage	Percentage of ground under the canopy covered by shrub (%). In 10% intervals.
Pied crow density	Number of pied crow individuals km^{-2} at each tree site extracted from the 30 m resolution raster in Johnson & Murn (2022)
Nest density	Number of white-backed vulture nesting trees within a 1 km radius around each nesting tree
Nearest neighbour distance	The distance (m) to the nearest active nest tree with another white-backed vulture

z-transformed before modelling (i.e., scaled to a mean of zero and standard deviation of one). We evaluated multicollinearity assumptions; in both models, all covariates had a variance inflation factor below 2.5. We report the marginal effect of important predictors, holding all non-target continuous predictors at their mean, and categorical predictors at their reference level. We also report within sample goodness of fit using the receiver operating characteristic (ROC). All analyses were completed using R 4.0.3 (R Core Team, 2021), and models were developed in glmmTMB 1.0.2.1 (Brooks et al., 2017).

3 | RESULTS

The only covariate to have an effect in the occupancy modelling was tree height (Figures 1 and 2a); birds tended to nest in taller trees (>7 m). In addition to being taller, nesting trees had shorter nearest neighbour distances (NND) to other nesting trees compared with distances between random trees (NND nest trees = 360 m vs. non-nesting trees = 472 m, $t = -1.231$, df = 51, $p = 0.046$). However, tree height, alongside all covariates, had no observable effect on hatching success, which was 36.5% across both areas. There was a weak association between hatching success and canopy density (coef = −1.08, CI: −2.26, 0.086, $p = 0.067$; Figure 2b), whereby hatching success was lower in denser canopy trees. A weak association was also observed between hatching success and nest density (coef = 0.67, CI: −0.13, 1.46, $p = 0.099$; Figure 2c); hatching success was marginally higher in nests with a high density of neighbours, and this unremarkable difference ($t = -2.259$, df = 18, $p = 0.099$) was also reflected in the mean NND between successful nests (300 m) and failed nests (395 m). We found no effect of crow density on hatching success (coef = 0.05, CI: −0.97, 1.07, $p = 0.92$; Figure 2d). The hatching success rate was similar between Dronfield (40%, $N = 27$) and Mokala (32%, $N = 25$). Despite the relative scarcity of important terms in both the occupancy and hatchling model, fit was generally high with an ROC of 94.8% and 77.5% in each model, respectively.

4 | DISCUSSION

We did not find strong evidence that the nest-site characteristics selected by vultures in our study area influenced their breeding productivity, but proximity to other vulture nests appeared to be positively associated with nest success. Like previous studies (Bamford, Monadjem & Hardy, 2009; Monadjem, 2003), our results highlight that white-backed vultures select taller trees in the areas where they nest, but we also found that important variables in modelling vulture occupancy were different to those variables that were important in modelling breeding success. In other words, occupancy modelling was more effective than breeding success at identifying the nest-site characteristics selected by white-backed vultures. This contrasts with conclusions that using breeding productivity (i.e. fitness) data to assess habitat selection is preferable (Johnson, 2007; Jones, 2001) and suggests that productivity data will not always be effective when modelling favourable or preferred nest-site characteristics for white-backed vultures, or habitat traits more generally (Chalfoun & Schmidt, 2012). Instead, a combined approach using both occupancy and fitness data may provide the clearest conclusions.

4.1 | Breeding productivity

Although 36.5% of chicks across both areas of our study hatched and survived until October, all these nestlings still had several more weeks before fledging, so the actual fledging rate may have been lower. This rate is lower than the long-term average (59%) for Dronfield (Angus Anthony, personal communication) and lower than other reported fledging rates of 47% in the Kgalagadi Transfrontier Park (Herholdt & Anderson, 2006) and 59% in the Masai Mara (Virani et al., 2010). Our study during a single year did not aim to investigate or explain the temporal variation in breeding productivity for the Kimberley white-backed vultures, but we recognise that the

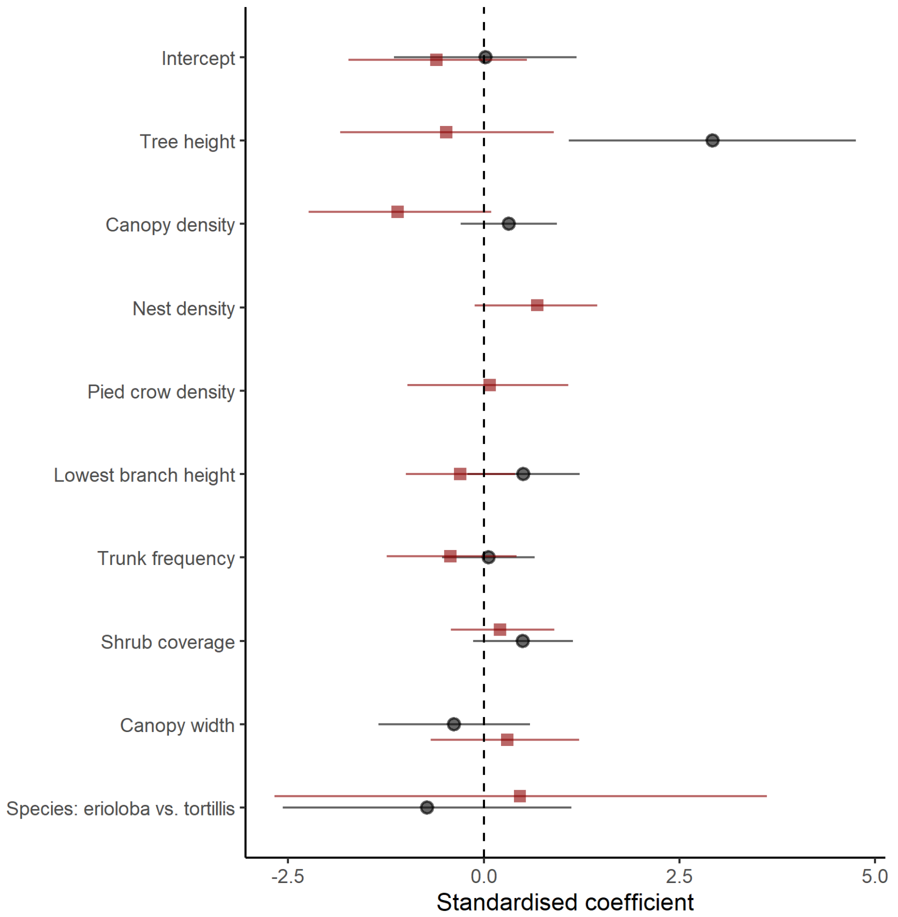

FIGURE 1 Forest-plot of occupancy (black-circle) and hatchling (red-square) standardised (z-transformed) coefficients and 95% confidence intervals for African white-backed vultures *Gyps africanus* near Kimberley, South Africa. Confidence intervals overlapping the dashed line at zero are not significant at the 95% confidence interval.

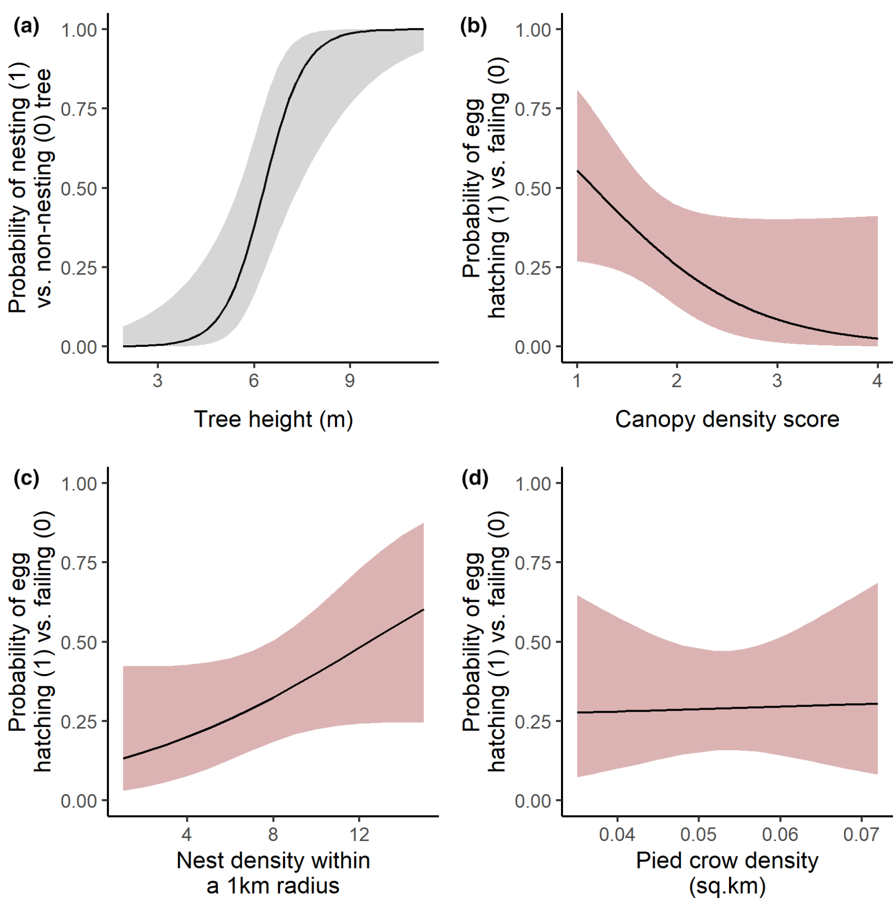

FIGURE 2 Marginal effect of tree height (a) on occupancy (nesting vs non-nesting); and canopy density (b), Nest density (c) and pied crow density (d) on hatchling success (chick survived vs. failed) of African white-backed vultures *Gyps africanus* near Kimberley, South Africa. Predictors were standardised (z-transformed) for modelling, but then converted back to their original units to improve interpretability. Model predictions and error ribbons/bars represent the 95% confidence intervals.

lower-than-average productivity during our study is probably due to landscape-level effects or factors such as increased rainfall.

One explanation for low breeding productivity at the landscape scale is lead toxicity, which can lead to breeding failure when blood-lead concentrations are elevated (Naidoo et al., 2017). Hunting is a common land use across the Kimberley area (Murn & Anderson, 2008), and this activity has been linked to increased blood-lead levels in vultures elsewhere (Garbett et al., 2018). Specifically, recent work has shown that nestlings at Dronfield do exhibit increased blood-lead levels (van den Heever et al., 2019), and this makes it essential to assess the extent to which lead toxicity may be the cause of low fledgling rates not only in Kimberley but elsewhere over the range of this critically endangered vulture.

Another explanation for the low fledgling rate in our study year is nest abandonment, disturbance or other environmental factors. Previous work in the Kimberley area has shown that pied crows can negatively affect nesting white-backed vultures (Johnson & Murn, 2019). We found no evidence of crow densities affecting breeding productivity, but the mechanism behind the impacts of pied crows on white-backed vultures remains unclear and our data on crow density lacked a temporal component (i.e., throughout the egg incubation period) to assess this further.

A general limitation of our study is that we do not analyse several years of data. The impact of a low breeding productivity year on our conclusions about breeding productivity and nest-site selection is unknown because we do not know whether it limits our ability to detect associations between these two characteristics. Despite this, we expect that the year of our study was a low year for breeding productivity in our study region, given that both colonies had lower-than-average breeding success.

4.2 | Nest-site selection

The only significant predictor of vulture occupancy was tree height, which suggests that white-backed vultures select mature and more stable trees that could be more difficult to reach, or resilient to disturbance, by ground-dwelling species. Within the Kimberley area, the only extant ground-dwelling predators of vulture eggs and/or chicks are Chacma Baboon *Papio ursinus* or Vervet Monkey *Chlorocebus pygerythrus*. However, we could not find any published records of these species predating vulture chicks in the area, and in one published account of a monkey chasing a vulture from a nest, the monkey seemed unable (or did not attempt) to predate the egg, because the egg hatched a few weeks later (Johnson & Murn, 2019). Furthermore, it seems unlikely that the trees around Kimberley, which rarely exceed 15 m in height, would pose a real obstacle to a persistent Chacma Baboon or Vervet Monkey. A possible explanation could be that white-backed vultures nest in taller trees to limit the impact of an historic threat—Elephants *Loxodonta africana*. Tall trees might be more resilient to disturbance by elephants. This explanation may reflect results from Eswatini where vulture nest densities are higher in areas without elephants (Monadjem & Garcelon, 2005). However, other studies have examined the impact of elephants on trees used by vultures for nesting and found that elephants caused minimal damage to both nesting and non-nesting trees (Vogel et al., 2014), so adaptive selection to avoid the impact of elephants as a possible explanation requires further investigation. Furthermore, elephants are extirpated from the Kimberley region and have been for over 100 years (Carruthers et al., 2008), thus making any selection pressure from their impacts historical. Another possible explanation is that white-backed vultures nest in tall trees above 7 m to reduce the risk of disturbance from Giraffe *Giraffa giraffa*, which rarely exceed 6 m, but we found no studies from elsewhere indicating that Giraffes disturb breeding white-backed vultures.

Apart from simply selecting a taller tree, perhaps the most important nest-site characteristic of all for a white-backed vulture is the presence of other breeding vultures nearby. White-backed vultures have been breeding in the Kimberley area for many decades (Forrester, 1967) and estimates suggest that there is sufficient food in the area for them (Murn & Anderson, 2008). With the advantages of social foraging (Cortes-Avizanda et al., 2014; Harel et al., 2017; Jackson et al., 2008) and the use of social cues for breeding site selection (Mateo-Tomás & Olea, 2011) and foraging (Kendall et al., 2012), it is possible that the social imperatives of group living have a stronger effect on vulture nest-site selection than the nest trees themselves. However, the social imperatives and potential benefits from group living may paradoxically exacerbate or reinforce sub-lethal effects (e.g., lead) that have negative effects on populations (Schmidt, 2016). Regionally specific risks to vultures such as the white-backed vulture, such as higher mortality from factors like poisoning (Monadjem et al., 2018), may also be increased by social grouping and feeding behaviours.

Finally, although we were not able to explore how the presence of other white-backed vultures influences nest-site selection, our results suggest that breeding productivity in white-backed vultures is positively density-dependent (cf. Bamford, Monadjem, Anderson et al., 2009) and support the idea that local-scale land management should aim to protect tall trees in and around existing white-backed vulture colonies. This highlights the potential benefit of studying nest-site and nesting habitat selection at the local scale, which can be incorporated into wider habitat preference assessments across landscape-level (Bamford, Monadjem, Anderson et al., 2009) or different spatial and temporal scales.

AUTHOR CONTRIBUTIONS

TFJ and CM conceived and designed the study. TFJ conducted fieldwork. TFJ and CM analysed the data and wrote the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available on request from the authors. The data that support the findings of this study are available from the corresponding author on request.

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