An Assessment of Tree Availability as a Possible Cause of Population Declines in Scavenging Raptors

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Short title: Nest site availability for vultures in Kenya

Abstract

Lack of suitable nesting trees is an increasingly common issue for avian conservation given rampant habitat and tree destruction around the world. In the African savannah, habitat loss and particularly tree damage caused by elephants have been suggested as possible factors in the decline of large bird species. Given the recent declines of vultures and other scavenging raptors, it is critical to understand if nest availability is a limiting factor for these threatened populations. Loss of woodland, partially due to elephant populations, has been reported for the Mara-Serengeti ecosystem. Data on characteristics of trees used for nesting were collected for White-backed, Lappet-faced, White-headed vulture, and Tawny eagle nests in Masai Mara National Reserve, Kenya. Nest tree characteristics were compared with the distribution of a random subsample of trees to assess nest preferences and determine suitability of available trees. Breeding pair density was estimated as well as availability of preferred nesting trees to determine if tree availability is a limiting factor for tree-nesting vultures. Tree availability was found to greatly exceed nesting needs for African vultures. We thus conclude that on a landscape scale, tree availability is not a limiting factor for any of the species considered here (White-backed, Lappet-faced, White-headed vultures, and Tawny eagles).

Keywords: raptors, nest availability, limiting factor, population, habitat loss

Introduction

Success of conservation efforts may be enhanced by focusing on the factors that limit population growth of threatened species. For many birds, breeding success can be mediated by external factors, such as food availability, disease, or rainfall, but also by characteristics of the nest itself, which may impact suitability or susceptibility to disturbance (Arroyo and Razin 2006, Monadjem and Bamford 2009). The availability of suitable nesting sites thus has potential to be a limiting factor for population growth (Newton 2010, 1994). Rapid declines in African raptors, particularly avian scavengers, have been documented locally, such as in the Masai Mara National Reserve, Kenya (hereafter referred to as the Mara) and more broadly throughout Africa (Thiollay 2006a, b, 2007, Virani et al. 2011, Ogada et al. 2016). The decline of African vultures has been of particular concern, given the recent Asian vulture crisis, which saw precipitous declines of three vulture species in less than a decade (Green et al. 2006). Although the causal factor in the Asian vulture crisis has been well established as a single factor, diclofenac exposure (Pain et al. 2003), the reason for the decline in African populations is more complicated. Direct and indirect poisoning, direct persecution, collision with and electrocution by powerlines are among the long list of threats thought to be negatively impacting African vultures (Ogada et al. 2016). However, tree availability has not been tested as a limiting factor for African vulture populations in the Masai Mara or elsewhere, and could be related to the declines.

Woodland areas have declined across much of the African savannah over the last thirty years, potentially due to increases in elephant density (Laws 1970, Caughley 1976, Kuiper and Parker 2014). Similar woodland declines have been noted across the Mara-Serengeti ecosystem (Glover 1968, Lamprey et al. 1967, Dublin, Sinclair, and McGlade 1990, Walpole, Nabaala, and Matankory 2004). With ongoing destruction of big trees in protected areas with large elephant populations (Jacobs and Biggs 2002, Edkins et al. 2008, Vanak et al. 2012), there is a concern that suitable nesting sites for raptors may disappear from such areas (Monadjem and Garcelon 2005, Hustler and Howells 1986, Virani et al. 2010).

In addition, little is known about tree nesting preferences of many tree-nesting African vultures, particularly Lappet-faced (*Torgos tracheliotos*) and White-headed vultures (*Trigonoceps occipitalis*), and there have been few studies of tree nesting behavior in East Africa (Virani et al. 2010, Houston 1976). In addition, the majority of studies describe nest characteristics or breeding success, but few have considered nesting preference in relation to tree availability (Bamford, Monadjem, and Hardy 2009, Monadjem 2003). White-backed vultures (*Gyps africanus*) are known to frequently use tall trees near rivers, particularly in the Mara, and Tawny eagles have also been shown to have a preference for nesting near rivers (Bamford, Monadjem, and Hardy 2009, Virani et al. 2010, Houston 1976, Bamford et al. 2009, Monadjem and Garcelon 2005, Herholdt and Anderson 2006). The particular tree species selected by nesting White-backed vultures vary greatly from site to site. For example, some populations are known to prefer thorny trees such as various species of *Acacia* (Mundy et al. 1992), whilst in Swaziland, White-backed vultures actively avoid *Acacia* trees (Monadjem 2003). Other studies in the Mara found *Ficus* and *Balanites* species to be most commonly selected (Virani et al. 2010). For White-headed vultures, studies of nests of 22 breeding pairs in Kruger National Park in South Africa, reported the most common nesting tree to be *Senegalia nigrescens*, and the average nest tree height to be 14 m, which was taller on average than 30 randomly selected trees (Murn and Holloway 2014). An understanding of the fine-scale nesting preferences, particularly the characteristics of the nest tree and its immediate surroundings, can be useful for predicting the distribution of suitable nesting sites; hence there is value in further exploration of these characteristics (Bamford et al. 2009, Bamford, Monadjem, and Hardy 2009).

Thus, the primary objective of this study was to determine if tree availability was a limiting factor for avian scavengers, namely vulture and Tawny eagle populations. In order to determine this, we first describe the nest tree preferences for all tree-nesting avian scavengers found in Masai Mara National Reserve, Kenya, and compare these withthe characteristics of a random sample of trees. We predicted that White-backed vultures and White-headed vultures would prefer tall trees while Lappet-faced vultures would prefer short trees (Mundy et al. 1992, Murn and Holloway 2014, Bamford et al. 2009). We expected that White-backed vultures would prefer to nest near rivers, where the density of desired trees is higher (Virani et al. 2010, Houston 1976). Tawny eagles are known to prefer flat-topped trees in riverine areas (Hustler and Howells 1989). We thus predicted that Tawny eagles would prefer to nest near rivers. We then used nesting preferences established by our study to estimate the availability of trees suitable for nesting for each species. By comparing suitable tree density with density of breeding pairs, we were able to address the question of whether or not tree availability is a limiting factor, which would restrict breeding opportunities and could thus affect population growth, for several critically endangered vulture species, as well as Tawny eagles, in the Mara.

Material and methods

Study area

The Mara-Serengeti ecosystem is one of the most important areas for avian scavengers in Africa (Kendall 2013), due in part to the open savannah habitat and high densities of ungulates, including the migratory herds of Blue Wildebeest (*Connochaetes taurinus*), Burchell’s Zebra (*Equus burchelli*), and Thomson’s Gazelle (*Gazella thomsonii*). Masai Mara National Reserve, Kenya, covers approximately 1,523 km^2 and is primarily composed of savannah habitat with patches of woodland. Rainfall in Masai Mara National Reserve is bimodal with long rains falling from March to June and short rains from November to December (Ogutu et al. 2008). Tree-nesting vultures are known to start breeding in the Mara-Serengeti ecosystem from mid-April to May and for chicks to fledge from August to October, which maximizes the overlap between fledging and the high mortality period of the migratory ungulate herds (Houston 1976, Virani et al. 2010). Tawny eagles are known to lay eggs from May to June (Herholdt, Kemp, and Du Plessis 1996, Hustler and Howells 1986). Pastoral community areas surrounding the Mara have undergone considerable habitat degradation, but are still used by avian scavengers (Ogutu et al. 2009, Kendall 2013).

Nests

Active avian scavenger nests were recorded during fieldwork conducted from May to July 2009, February to May and July to September 2010, and March to May and July to October 2011 in Masai Mara National Reserve, Kenya. We searched for nests of all tree-nesting avian scavenger species commonly found in the area including Bateleur (*Terathopius ecaudatus*), Tawny Eagle (*Aquila rapax*), White-backed vulture, Lappet-faced vulture, White-headed vulture, and Hooded vulture (*Necrosyrtes monachus*). Nests were searched for opportunistically by vehicle throughout the reserve, though the Mara Conservancy Trust area to the west of the Mara River was surveyed less frequently, as were communal lands to the north and east of the reserve, Koiyaki and Siana respectively. Data were only collected from active nests, defined as nests where a bird was sitting on or building the nest when sighted. Where possible, nests that had been empty upon first sighting were re-visited during the breeding season to determine whether they were used in a given season or not. Following Berkleman (1997), nest site characteristics were recorded including tree species, height of nesting tree, and diameter at breast height of nesting tree (DBH). In addition habitat characteristics such as distance to nearest tree, and distance to nearest river were estimated using ArcGIS. The tree genus *Acacia* has recently been splitted into *Vachellia* and *Senegalia*. To avoid confusion and to allow our results to be compared with previous studies, we retain all these species within *Acacia*. However, we refer to them by their correct current names in the list of tree species utilized for nesting (Table 4, 5, Supplementary material Appendix 1).

Random trees

The same information (mentioned in the previous section above) was recorded for an evenly distributed sample of 200 trees along road-based transects that had been set up for the purpose of surveying raptors in the study area. Every kilometer along the transect, trees were sampled by choosing a random direction and sampling the closest tree. If no tree was within 500 m of the road in the direction chosen, then tree sampling was omitted for that particular point and we continued on to the next kilometer.

Calculation of tree density, breeding pair density, and the proportion of suitable nesting trees

Data from Crowther et al. (2015) were used to extract estimates of tree counts for the study site including within Masai Mara National Reserve and in the two surrounding conservancies of Koiyaki and Siana. These data are based on a global model of tree density and include only trees larger than 10 cm in DBH.

Using transect data for the reserve, the avian scavenger population was estimated for the study site (Virani et al. 2011). We assumed that during transects birds could be seen for 500 m on either side and thus treated transect estimates of birds/100 km as density estimates of birds/100 km^2. We then calculated population numbers for each study species within the Masai

Mara National Reserve (1,523 km^2). Assuming that 50% of birds are adults, that 75% of these adults would breed in a given year, and that 50% of these are breeding pairs (i.e. two birds sharing a single nest), we calculated the number of breeding pairs that would require a nest site annually within Masai Mara National Reserve (Murn et al. 2016).

We then calculated the proportion of trees available for nesting. Suitable nesting trees were defined as tree species that a given vulture or eagle species had been observed nesting in as part of this study. Furthermore, we specified that the height of these tree species, should be within one standard deviation of the mean height of known nesting trees used by each of the scavenging species. Because taller trees were found to be preferred and trees with larger diameter at breast height (DBH) were preferred by White-backed vultures, all trees with height or DBH larger than average minus one standard deviation of nesting trees were included (i.e. tree heights of 7.9 m or taller and DBH of 34 cm or larger) for this species. We then determined the total trees suitable for nesting within the reserve by multiplying the tree count by the proportion of trees likely to be suitable for a given species. From this, we determined a total count of suitable nesting trees in the Masai Mara National Reserve for each vulture or eagle species.

Data analysis

A student t-test was used to test whether the characteristics of nesting trees (listed above) was different from the randomly sampled trees. For nesting preference analysis, we developed generalised linear mixed models to examine the effect of the following covariates: DBH of nesting tree (DBH), height of nesting tree (tree height), distance of nesting tree to the nearest tree (nearest tree) and distance of nesting tree to nearest river (nearest river), on the response variable: presence or absence of a nest in the tree. We included land use (protected area, conservancy or settlement) and year as random effects to account for dependence of nests situated in the same land use or sampled in multiple years. Models were ranked using the corrected Akaike's information criterion (AICc) (Burnham and Anderson 2002). The model with the lowest AICc was deemed the best model; where delta AICc (the difference in AICc between models) for any two (or more) models was ≤ 2.0, they were both deemed to be equally good. Analyses were conducted in R statistical software ver. 3.2.4. (R Core Team), using the lme4 package (Bates et al. 2014).

For nearest neighbor analysis, only nests within a given year were considered and for White-backed vultures, only nests from 2011 (when largest nest survey efforts were made) were considered. Following Monadjem (2003), the proportions of each tree species used by White-backed, Lappet-faced, White-headed vultures and Tawny eagles and expected usage given availability (calculated from random sample) was calculated. Note that tree species used for just a single nest by any of the four scavenging species were lumped as “other”. Trees were lumped by genus where multiple species occurred (e.g. *Acacia* and *Ficus*).

Results

Scavenger nests in Masai Mara National Reserve

Across the three years of our study, 113 White-backed vulture, 51 Lappet-faced vulture, 15 White-headed vulture, and 21 Tawny eagle distinct nests were located. Only one Bateleur nest was located during this study and no Hooded vulture nests were found, despite the regular presence of these at carcasses.

Nesting preferences and aggregations

Though survey effort was less outside of protected areas, the majority of the nests were located in the Masai Mara National Reserve, suggesting that all species prefer nesting in areas with less human habitation and higher wildlife density. Results from t-tests comparing tree and spatial characteristics for nests and random trees are presented in Table 1. White-backed vultures selected for taller trees with larger DBH. Lappet-faced vultures preferred shorter trees than expected, but there was no difference in DBH between nesting and random trees. Tawny eagles and White-headed vultures showed no preference in relation to tree or spatial characteristics. Both White-backed and Lappet-faced vulture nests were closer to the river than random and distance to nearest tree did not appear to be important for nest selection for any species considered.

Table 1*: Comparison of tree characteristics for random trees and trees in which four species of avian scavengers nested in the Masai Mara, Kenya. The values are presented as means ± SE with the t-test test statistic and P-values provided in parentheses. Bold values are significant at P < 0.055 level*

Tree characteristics	*Random tree (n=200)*	*White-backed Vulture Nest trees (n = 113)*	*Lappet-faced Vulture Nest trees (n = 51)*	*White-headed Vulture Nest trees (n = 15)*	*Tawny Eagle Nest trees (n = 21)*
Tree height (m)	9.6 ± 4.0	**11.6 ± 3.7 (t=4.539, P<0.001)**	**7.5 ± 2.4 (t=4.723, P<0.001)**	9.1 ± 2.5 (t=0.717, P=0.482)	10.5 ± 2.0 (t=1.754, P=0.087)
Tree DBH (cm)	59.8 ± 35.7	**67.6 ± 33.6 (t=1.937, P=0.054)**	56.7 ± 30.2 (t=0.622, P=0.536)	55.2 ± 34.1 (t=0.494, P=0.628)	59.6 ± 39.9 (t=0.020, P=0.985)
Nearest tree (m)	79.7 ± 247.1	64.8 ± 139.3 (t=0.683, P=0.495)	217.6 ± 743.3 (t=1.306, P=0.197)	133.9 ± 272.5 (t=0.747, P=0.466)	84.0 ± 196.5 (t=0.092, P=0.927)
Nearest river (m)	4713.9 ± 4828.5	**2751.4 ± 4177.6 (t=3.769, P<0.001)**	3751.4 ± 6326.1 (t=1.0139, P=0.314)	**2660.4 ± 3119.5 (t=2.347, P=0.030)**	3727.3 ± 3441.0 (t=1.196, P=0.241)

White-backed and Lappet-faced vultures nested close to conspecifics, possibly due to congregation of nests in the Mara or near rivers, whereas White-headed vulture and Tawny eagle nests tended to be farther apart (Table 2).

Table 2*: Distance to nearest conspecific neighbor nest for four raptor species nesting in the Masai Mara National Reserve, Kenya. The values are means ± SE*

Species	Distance to nearest neighbor (m)
White-backed vulture	1454.9 ± 1749.5 (n=48)
Lappet-faced vulture	2208.4 ± 1717.5 (n=43)
White-headed vulture	5397.2 ± 5322.1 (n=13)
Tawny eagle	5439.7 ± 3857.1 (n=19)

Results for GLMM analysis are shown in Table 3. For the African white-backed vulture, the best model included just ‘tree height’ and had a model weight of 0.451. The next best model had delta of almost 2.0 and included ‘tree height’ and ‘nearest river’. The remaining models, which included the ‘full’ model (including all the covariates) and the ‘null’ model (including no covariates), had delta AICc ≥ 2.0 with declining AICc weights (results not shown), and were therefore discounted as best candidate models.

Table 3*. The candidate models used to investigate the effects of various nesting tree characteristics including DBH, height, distance to nearest tree and distance to nearest river on the response variable which was the presence or absence of a nest of one of four avian scavenger species. Each species is shown separately. For all models, landuse and year were incorporated as random effects. The number of estimated parameters is indicated by 'n'. The models are arranged from best (top of table) to worst (bottom) based on the corrected Akaike's Information Criteria (AICc). Only competing models (Delta AICc < 2.0) are shown. Also included is the difference in AICc from the best model (Delta AICc), and the weight of each model (AICc Weights)*

Model	**n**	**AICc**	**Delta AICc**	**AICc Weights**
White-backed vulture				
Height	4	202.3	0	0.451
Height + Nearest River	4	204.3	1.97	0.169
Lappet-faced vulture				
Height	4	137.2	0	0.403
Height + DBH	5	138.7	1.49	0.191
Height + Nearest River	5	139.0	1.80	0.164
White-headed vulture				
Null	3	50.0	0	0.157
Nearest Tree	4	50.0	0	0.157
Height + Nearest Tree	5	50.6	0.54	0.120
Nearest River	4	50.7	0.69	0.111
DBH	4	51.0	1.02	0.095
Height + Nearest River	5	51.2	1.17	0.088
Height	4	51.2	1.20	0.086
Tawny eagle				
DBH	4	56.1	0	0.262
Null	3	56.9	0.77	0.178
Height	4	57.9	1.83	0.105
Height + DBH	5	57.9	1.83	0.105

For the lappet-faced vulture, the best model included just tree height and had a model weight of 0.403. The next two models had delta AICc ≤ 2.0 and were hence competing models, and both of them included the covariate 'tree height' with either 'DBH' or 'nearest river'. The remaining models, which included the ‘full’ model (including all the covariates) and the ‘null’ model (including no covariates), had delta AICc ≥ 2.0 with declining AICc weights (results not shown), and were therefore discounted as best candidate models.

For the white-headed vulture, the best models were the ‘null’ model and the model that included only the ‘nearest tree’; both of these two models had weights of 0.157 each. There were five competing models which included various combinations of all the measured covariates. For the tawny eagle, the best model included just ‘DBH’ and had a model weight of 0.262. Competing models included the ‘null’ model, ‘tree height’ and ‘tree height’ plus ‘DBH’.

Tree species utilized for nesting

The numbers of nests situated in different species of trees by the various scavenging raptors and their proportional use is shown in Tables 4 and 5, respectively. The majority of white-backed vulture nests were located in just five species of trees (Table 4), of which *Boscia angustifolia*, *Ficus* spp. and *Albizia gummifera* were utilized more frequently than expected, whereas *Acacia* spp. in proportion to that expected (Table 5). In contrast, lappet-faced vultures used *Balanites aegyptiaca* and *Gardenia ternifolia* more than expected and *Acacia (Vachellia* and *Senegalia)* spp. less so. White-headed vultures used *Boscia angustifolia* and *Olea europea* more than expected, whereas tawny eagles used *Boscia angustifolia* and *Euclea divinorum* more than expected. Details on all tree species seen are provided in Supplementary material Appendix 1–2.

Table 4*: The number of times of particular tree species was used as a nesting site by four raptor species in the Masai Mara National Reserve, Kenya. Also shown is the number of times each tree species appears in the random sample of trees. All species of* Vachellia *and* Senegalia *are lumped under "*Acacia *spp."*

Tree species	Number of trees with AWB nests	Number of trees with LFV nests	Number of trees with WHV nests	Number of trees with TE nests	Number of trees in random sample
Boscia angustifolia	32	10	4	5	32
Ficus sp.	26	1	0	0	8
Acacia sp.	20	1	3	2	33
Olea europea	12	4	5	1	18
Albizia gummifera	10	0	0	1	6
Diospyros abyssinica	3	0	0	0	13
Warburgia ugandensis	3	0	0	0	1
Balanites aegyptiaca	2	15	2	1	38
Gardenia ternifolia	0	16	1	1	7
Maytenus senegalensis	0	2	0	0	0
Euphorbia candelabrum	0	0	0	6	12
Euclea divinorum	0	0	0	4	7
Other	4	0	0	0	23
Unidentified	1	1	0	0	2
Total	**113**	**50**	**15**	**21**	**200**

Table 5: *The proportion that a tree species was used for nesting in (i.e. the number of times a tree species was used to nest in by one of the four avian scavengers/total nests located for each species of avian scavenger) and the proportion that a tree species was expected to be used (i.e. the number of times that a tree species appears in the random sample/total number of trees in the random sample) in the Masai Mara National Reserve, Kenya*

Tree species	Proportion used (AWB)	Proportion used (LFV)	Proportion used (WHV)	Proportion used (TE)	Proportion expected
Boscia angustifolia	0.283	0.200	0.267	0.238	0.160
Ficus sp.	0.230	0.020	0.000	0.000	0.040
Acacia sp.	0.177	0.020	0.200	0.095	0.165
Olea europea	0.106	0.080	0.333	0.048	0.090
Albizia gummifera	0.088	0.000	0.000	0.048	0.030
Diospyros abyssinica	0.027	0.000	0.000	0.000	0.065
Warburgia ugandensis	0.027	0.000	0.000	0.000	0.005
Balanites aegyptiaca	0.018	0.300	0.133	0.048	0.190
Gardenia ternifolia	0.000	0.320	0.067	0.048	0.035
Maytenus senegalensis	0.000	0.040	0.000	0.000	0.000
Euphorbia candelabrum	0.000	0.000	0.000	0.286	0.060
Euclea divinorum	0.000	0.000	0.000	0.190	0.035
Other	0.044	0.020	0.000	0.000	0.125

Estimating tree density and number of breeding birds

Based on Crowther et al. (2015), there are an estimated 13 million trees in the Masai Mara National Reserve. We determined the proportion of trees likely to be suitable for nesting for each bird species based on preferred tree species and height, and DBH for white-backed vultures for which this was an important characteristic, and also calculated the potential number of breeding pairs (Table 6). The proportion of suitable nesting trees ranged from 20% for tawny eagles to 49% for white-backed vultures. As a result, there are likely to be anywhere from 2 to 6 million suitable nesting trees for these raptors. In contrast, estimates for breeding pairs ranged from nine for white-headed vultures to 74 for white-backed vultures. 74 breeding pairs for white-backed vultures is clearly an underestimate as we found 113 nests during our survey. If we assume that birds ranging across Mara-Serengeti might nest exclusively in Masai Mara National Reserve, which would likely be an overestimate, it would increase the potential number of white-backed vulture breeding pairs needing a nest to roughly 1219. We thus found that the number of available nesting trees in Masai Mara was three orders of magnitude greater than the number of potential breeding pairs even across the entire Mara-Serengeti ecosystem.

Table 6: *Estimates of proportion and number of suitable nesting trees, the total populations of avian scavengers, and the total number of breeding pairs by avian scavenger species in Masai Mara National Reserve, Kenya*

Species	Proportion of trees suitable	Estimate of suitable trees in Masai Mara National Reserve	Estimate of total population	Estimate of total breeding pairs
White-backed Vulture	0.49 (96/198)	6,420,302	397	97
Lappet-faced Vulture	0.24 (48/198)	3,144,638	183	47
White-headed Vulture	0.32 (64/198)	4,192,850	46	9
Tawny Eagle	0.20 (39/198)	2,620,531	113	40

Discussion

Given the ongoing vulture declines, it is essential to determine the relative importance of factors that affect vulture population persistence and growth (Virani et al. 2011, Ogada et al. 2016). Tree availability for tree-nesting vultures and raptors has been suggested as a potential limiting factor (Newton 2010), but our results strongly suggest this is not the case for avian scavengers in the Masai Mara National Reserve, Kenya. There are approximately 15,000 times more trees than there are likely to be breeding pairs, even for the most populous species considered here, the White-backed vulture. Even if we assume a total breeding population of 4,000 (10x our estimate for White-backed vultures and four times greater than higher estimates from Virani et al. (2010)), the vultures would only need about 2.6 suitable nesting trees per square kilometer. Since nearly 50% of trees are suitable for nesting for this species, this would require only 5.2 trees per square kilometer (or 7,919 trees in the entire Masai Mara National Reserve). So while tree counts derived from Crowther's estimates are likely overestimates

(estimates over 13 million trees in the Masai Mara National Reserve), these numbers would have to be off by more than four orders of magnitude (or 1,640 times) for nesting availability to be a limiting factor for breeding birds, which is highly improbable. We can thus conclude that tree availability is not a limiting factor for any of the species considered here (White-backed, Lappet-faced, White-headed vultures, and Tawny eagles).

If territoriality is an important factor, this could also impact nesting densities. Nesting density varies considerably by vulture species and sites studied, and can even vary significantly within a site (Monadjem and Garcelon 2005, Murn and Holloway 2014, Murn, Anderson, and Anthony 2002, Mundy et al. 1992, Hustler and Howells 1988, Virani et al. 2010, Bamford, Monadjem, and Hardy 2009, Murn et al. 2013). In this study as elsewhere, distance between conspecific nests, was lowest for White-backed vultures as might be expected for a semi-colonially nesting species. For White-backed vultures, distances between conspecific ness were considerably lower than previously found in the Mara, probably due to larger and more representative sampling (Virani et al. 2010). Distance between conspecific nests was comparable to other sites for White-headed, Lappet-faced vultures, and Tawny eagles (Mundy et al. 1992, Monadjem and Garcelon 2005, Virani et al. 2010, Hustler and Howells 1988, Murn and Holloway 2014, Hustler and Howells 1986, Hustler and Howells 1989). This variability in nearest neighbor distance for nests suggests that tree availability rather than territoriality may determine where vultures nest. Furthermore, vultures can have large foraging ranges and some species nest colonially suggesting that nesting density is determined by the availability of trees with desired characteristics and is unlikely to be affected by over-crowding (Mateo-Tomas and Olea 2011, Jackson, Ruxton, and Houston 2008, Phipps et al. 2013, Kendall et al. 2014).

Issues such as elephant impact on trees and nesting disturbance have been considered as potential threats to vultures andit has been suggested that elephants may impact tree availability for nesting raptors in the Mara (Virani et al. 2010). The impact of elephants on tree-nesting vultures is not yet fully understood, although at high elephant densities, the number of suitable nesting trees are significantly diminished (Monadjem and Garcelon 2005). However, work in the Mara-Serengeti ecosystem suggests that while elephants may be able to maintain woodland density at a lower level, elephants were not the primary drivers in decreasing woodland density here (Dublin, Sinclair, and McGlade 1990). Woodland density in the Mara is lower now than in the 1980s, however as our estimates demonstrate, tree availability is still high. In addition, where breeding success for scavenging birds has been studied, rainfall has generally been found to be the primary factor determining nesting success rather than tree availability (Monadjem and Bamford 2009, Virani et al. 2012). Similarly, while nest disturbance can influence behavior and breeding success in cliff-nesting vultures, it is unlikely to be the determining factor in breeding success for tree-nesting species, which can easily move nests should disturbance arise (Arroyo and Razin 2006, Donazar, Hiraldo, and Bustamante 1993, Zuberogoitia et al. 2008). Finally, while nest disturbance could impact nesting success, it is unlikely to affect adult survival, which is more closely tied to population dynamics (Bamford et al. 2009).

Nesting preferences

While tree availability does not appear to be a limiting factor for nesting, understanding nesting preferences may assist in vulture conservation. In our study we found considerably more nests in the Masai Mara National Reserve than outside of it. This is consistent with similar studies of breeding vultures, which have reported that vultures tend to nest in protected areas, with Lappet-faced and White-headed vultures nesting exclusively in protected areas in Swaziland (Monadjem and Garcelon 2005, Bamford, Monadjem, and Hardy 2009).

Our results indicate that White-backed vultures tend to select, and in some cases prefer, tall trees (Bamford et al. 2009, Houston 1976, Herholdt and Anderson 2006). This is consistent with other studies that have indicated that White-backed vultures prefer tall trees and, in some cases, riparian areas which may be indicative of suitable tree availability (i.e. more tall trees along the river) rather than a specific characteristic being selected for, though characteristics can vary by area (Houston 1976, Monadjem and Garcelon 2005, Bamford, Monadjem, and Hardy 2009, Virani et al. 2010). Lappet-faced vultures are known to nest in short trees and to use *Acacia*, *Balanites*, and *Terminalia* trees though little work has been done on their nesting preferences (Mundy et al. 1992). In the Mara, Lappet-faced vultures appear to prefer shorter trees, particularly *Gardenia*, which offer wide tree tops for larger nests. Other common tree species used were *Balanites* and *Boscia*. In the Mara, we found no particular tree species or characteristic preferences for White-headed vulture nests, but *Olea*, *Boscia*, and *Acacia (Vachellia* or *Senegalia)* were the most common species of tree chosen. Tawny eagle showed no specific preferences in relation to tree height or diameter, but preferred *Euphorbia*, *Boscia*, and *Euclea* species.

Conclusion

Given that vultures are long-lived species, factors influencing adult survival are likely to be more important for population stability than breeding success (Bamford et al. 2009, Monadjem, Botha, and Murn 2013, Monadjem et al. 2014). We feel that the focus of future vulture conservation efforts should be on the major issues that impact adult survival and thus population growth. In this respect, poisoning appears to be the primary threat to most populations, particularly in East Africa (Murn and Botha 2017, Ogada 2014). Based on our findings, concerns related to tree availability or nesting disturbance are thus likely to be minor issues in comparison.

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Author contributions

CJK conceived of study, collected data, developed methods and wrote the paper. DR supervised the study and designed methods. PM analyzed data for analysis of tree availability. AM designed methods, analyzed the data and wrote parts of the paper.

Permits

Research was conducted under research permit NCST/5/002/R/448.

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Supplementary material

Appendix 1*: The number of trees recorded with nests of four avian scavengers in them and in a random sample of trees without nests in the Masai Mara National Reserve, Kenya*

Tree species	Number of trees with AWB nests	Number of trees with LFV nests	Number of trees with WHV nests	Number of trees with TE nests	Number of trees in random points
Vachellia (Acacia) abyssinica	0	0	0	0	3
Vachellia (Acacia) drepanolobium	0	0	0	0	4
Vachellia (Acacia) gerrardii	5	0	1	0	22
Vachellia (Acacia) kirkii	5	0	2	2	0
Vachellia (Acacia) nilotica	3	0	0	0	0
Senegalia (Acacia) senegal	1	0	0	0	0
Vachellia (Acacia) xanthophloea	7	1	0	0	11
Albizia gummifera	10	0	0	1	6

Balanites aegyptiaca	2	15	2	1	38
Boscia angustifolia	32	10	4	5	32
Clerodendrum buchananii	0	0	0	0	1
Commiphora africana	0	0	0	0	1
Diospyros abyssinica	3	0	0	0	13
Euclea divinorum	0	0	0	4	7
Euphorbia candelabrum	0	0	0	6	12
Ficus sp.	13	0	0	0	0
Ficus sycomorus	13	1	0	0	8
Ficus thonningii	1	0	0	0	4
Gardenia ternifolia	0	16	1	1	7
Kigelia africana	1	0	0	0	4
Lepisanthes senegalensis	1	0	0	0	5
Maytenus senegalensis	0	2	0	0	0
Olea europea	12	4	5	1	18
Warburgia	3	0	0	0	1

ugandensis					
Ziziphus mucronata	0	0	0	0	1
Unidentified	1	1	0	0	2
Total	**113**	**50**	**15**	**21**	**200**

Appendix 2*: The proportion of trees of a particular species used for nesting by four avian scavengers and the expected usage based on the proportions of trees in a random sample in the Masai Mara National Reserve, Kenya*

Tree species	Proportion used (AWB)	Proportion used (LFV)	Proportion used (WHV)	Proportion used (TE)	Proportion expected
Vachellia (Acacia) abyssinica	0.000	0.000	0.000	0.000	0.015
Vachellia (Acacia) drepanolobium	0.000	0.000	0.000	0.000	0.020
Vachellia (Acacia) gerrardii	0.044	0.000	0.067	0.000	0.110
Vachellia (Acacia) kirkii	0.044	0.000	0.133	0.095	0.000
Vachellia (Acacia) nilotica	0.027	0.000	0.000	0.000	0.000
Senegalia (Acacia) senegal	0.009	0.000	0.000	0.000	0.000
Vachellia (Acacia)	0.062	0.020	0.000	0.000	0.055

xanthophloea					
Albizia gummifera	0.088	0.000	0.000	0.048	0.030
Balanites aegyptiaca	0.018	0.300	0.133	0.048	0.190
Boscia angustifolia	0.283	0.200	0.267	0.238	0.160
Clerodendrum buchananii	0.000	0.000	0.000	0.000	0.005
Commiphora africana	0.000	0.000	0.000	0.000	0.005
Diospyros abyssinica	0.027	0.000	0.000	0.000	0.065
Euclea divinorum	0.000	0.000	0.000	0.190	0.035
Euphorbia candelabrum	0.000	0.000	0.000	0.286	0.060
Ficus sp.	0.115	0.000	0.000	0.000	0.000
Ficus sycomorus	0.115	0.020	0.000	0.000	0.040
Ficus thonningii	0.009	0.000	0.000	0.000	0.020
Gardenia ternifolia	0.000	0.320	0.067	0.048	0.035
Kigelia africana	0.009	0.000	0.000	0.000	0.020

Lepisanthes senegalensis	0.009	0.000	0.000	0.000	0.025
Maytenus senegalensis	0.000	0.040	0.000	0.000	0.000
Olea europea	0.106	0.080	0.333	0.048	0.090
Warburgia ugandensis	0.027	0.000	0.000	0.000	0.005
Ziziphus mucronata	0.000	0.000	0.000	0.000	0.005
Unidentified	0.009	0.020	0.000	0.000	0.010