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Densities and population sizes of raptors in Uganda's conservation areas

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Projected increases in Africa's human population over the next 40 years point to further, large-scale conversion of natural habitats into farmland, with far-reaching consequences for raptor species, some of which are now largely restricted to protected areas (PAs). To assess the importance of PAs for raptors in Uganda, we conducted an annual road survey through savanna, pastoral and agricultural land during 2008–2015. Here, we present density estimates for 34 diurnal raptor species, 17 of which were encountered largely or entirely within PAs. These included seven out of eight globally threatened or near-threatened species surveyed. Based mainly on published demographic values, we converted density estimates (birds 100 km^{-2}) to numbers of adult pairs, for 10 resident, savanna-dependent species. We then estimated adult population sizes within conservation areas (individual PAs and clusters of contiguous PAs), based on the area of savanna in each site. This suggested that two threatened residents, Martial Eagle *Polemaetus bellicosus* and Lappet-faced Vulture *Torgos tracheliotos*, have national breeding populations of just 53–75 and 74–105 pairs, respectively. A third species, White-headed Vulture *Trigonoceps occipitalis*, may have a breeding population of just 22–32 pairs. In each case, at least 90% of pairs are thought to reside within Uganda's five largest conservation areas. In three cases our estimates of pair density were markedly lower than in other studies, while in six cases they were broadly consistent with published findings, often derived using more intensive survey methods. Further work is required to determine the accuracy of our estimates for individual conservation areas, and to assess the long-term viability of Uganda's threatened raptor populations.

Densités et taille des populations de rapaces dans les zones de conservation de l'Ouganda

Les augmentations prévues de la population humaine en Afrique au cours des 40 prochaines années indiquent une conversion à grande échelle des habitats naturels en terres agricoles, avec de lourdes conséquences pour les espèces de rapaces, dont certaines sont maintenant largement limitées aux aires protégées (AP). Pour évaluer l'importance des aires protégées pour les rapaces en Ouganda, nous avons effectué un suivi annuel moyennant des transects routiers à travers les terres de savane, pastorales et agricoles durant la période 2008–2015. Ici, nous présentons des estimations de densité pour 34 espèces de rapaces diurnes, dont 17 ont été rencontrées en grande partie ou entièrement dans les AP. Parmi celles-ci, sept sur huit espèces menacées ou quasi menacées à l'échelle mondiale ont été recensées. Sur la base des valeurs démographiques publiées, nous avons converti les estimations de densité (oiseaux 100 km^{-2}) en nombres de couples d'adultes, pour 10 espèces sédentaires, dépendantes de la savane. Nous avons ensuite estimé la taille des populations adultes dans les aires de conservation (aires protégées individuelles et groupes d'aires protégées contiguës), en fonction de la superficie de savane de chaque site. Cela suggère que deux espèces sédentaires menacées, l'Aigle martial *Polemaetus ellicosus* et le Vautour Oricou *Torgos tracheliotos*, ont respectivement des des populations reproductrices de 53–75 et 74–105 couples. Une troisième espèce, le vautour à tête blanche, *Trigonoceps occipitalis*, peut avoir une population reproductrice de seulement 22–32 couples. Dans chaque cas, au moins 90% des couples présents dans les cinq plus grandes zones de conservation de l'Ouganda. Dans trois cas, nos estimations de la densité de couples étaient nettement plus faibles que dans d'autres études, alors que dans six cas, elles étaient largement conformes aux résultats publiés, provenant de méthodes d'enquête plus intensives. Des travaux supplémentaires sont nécessaires pour déterminer l'exactitude de nos estimations pour chaque zone de conservation et pour évaluer la viabilité à long terme des populations de rapaces menacées de l'Ouganda.

Keywords: African raptors, eagles, protected areas, raptor abundance, savanna, vultures

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Introduction

Many African raptor species are suffering regional or continent-wide declines, driven by a wide range of factors (Thiollay 2006a, 2006b, 2007; Virani et al. 2011; Ogada et al. 2015). Species at greatest risk are those most affected by illegal poisoning, the bushmeat trade, killing for traditional 'medicines', or through collisions with energy infrastructure (Jenkins et al. 2010; Otieno et al. 2010; Virani et al. 2011; McKean et al. 2013; Ogada 2014; Ogada et al. 2015, 2016; Buij et al. 2016). Since vulnerability to these threats often coincides within species, some African raptors now face a perfect storm of adverse conditions.

For slow-breeding, resident species dependent on natural habitats, the on-going expansion of farmland and the degradation of rangelands present further, more pervasive threats, spanning much of Africa. During 1975–2000 almost 5 million ha of forest and non-forest natural vegetation was destroyed annually in sub-Saharan Africa, resulting in a 21% reduction in natural vegetation and a 57% increase in the area of agricultural land (Brink and Eva 2009). This expansion coincided with a rise in the human population, which increased by 0.8 billion during 1960–2016, and is projected to increase by a further 1.8 billion by 2060 (Canning et al. 2015; World Bank 2017a, 2017b). The conversion of savanna, forest and other natural habitats into pastoral and agricultural land is thus set to continue, with far-reaching consequences for most African raptors, and for other savanna-dependent species.

The scale and nature of these changes are important, since many African raptors are more abundant in open- or wooded savanna, than in the farmland habitats that often replace them (Herremans and Herremans-Tonnoeyr 2000; Thiollay 2006c, 2007; Anadón et al. 2010; Buij et al. 2013; Pomeroy et al. 2014). Furthermore, since much of Africa's remaining natural and semi-natural land is now confined to protected areas (PAs), the global populations and ranges of many of its larger, resident raptors are likely to have become highly fragmented.

To fully appreciate the implications of farmland conversion for such species it is important to determine the degree to which they are dependent on protected areas, their density within savanna, and hence the number of pairs each PA is capable of supporting. In a detailed case study, Murn et al. (2016) applied this approach to the White-headed Vulture *Trigonoceps occipitalis*, a species now largely confined to PAs throughout its global range. Their findings highlight the fragmentary nature of the species' global distribution, showing that 78% of occupied PAs are each likely to support fewer than five breeding pairs. Furthermore, most of the PAs supporting larger breeding populations (of at least 20 breeding pairs) were separated from other occupied PAs by at least 100 km (Murn et al. 2016). The insights provided by this approach are key to understanding the population status of Africa's PA-dependent raptors more fully.

One country that has already experienced the transition to a predominantly agricultural landscape is Uganda, whose human population increased by a factor of six during 1960–2016 (World Bank 2017c), coinciding with an expansion in agricultural land over the same period (FAO 2018). To investigate the size and distribution of Uganda's raptor populations, and their dependence on PAs, we conducted a series of annual road surveys spanning 2008–2015. Here, we present abundance estimates for each raptor species within protected savanna, pastoral land and agricultural land, where sample sizes permit. We identify species that were particularly dependent on protected savanna; that is, species we found only in protected savanna, or whose density in savanna was much greater than in pastoral or agricultural land. Based on published demographic values, we estimate the number of adult pairs likely to reside in each protected area, and compare these estimates with breeding densities from elsewhere in Africa. We also examine habitat associations of each species, as a guide to their management within PAs.

Methods

We recorded the number of individuals of each diurnal raptor species seen whilst driving a series of transects along roads and tracks in Uganda during January (86% of surveys), February (10%) or March (4%) during 2008–2015. Since owl species were likely to be substantially under-counted they were excluded from the survey. Transects were of 9–122 km in length (recorded by odometer), and in most cases were surveyed repeatedly over the eight-year period, normally only once each year. The total distance surveyed was 11 188 km (Supplementary Table S1), at a mean of 33 km h^{-1} on public roads (SD = 11.6; n = 44 transect-years), and 25 km h^{-1} in National Parks (SD = 8.9; n = 57 transect-years). Observation teams comprised a recorder plus 2–4 observers. In National Parks, and on some tracks outside of the parks, observers gained the widest possible view from the cab roof or by standing behind the cab (in an open pick-up). We refer to these as 'outside observers'. Most transects were surveyed between 09:00 and 17:00, when soaring birds were more likely to be in the air, and hence more visible. Both flying and perched individuals were counted.

Transects followed a network of unpaved tracks in Uganda's four main savanna National Parks (Murchison Falls, Queen Elizabeth, Kidepo Valley and Lake Mburo NPs) and in Bugungu Wildlife Reserve, a buffer area for Murchison Falls NP. They also included public roads from Entebbe to Mbarara, Entebbe to Murchison Falls NP, and from Soroti towards Moroto (Figure 1). Although some birds were identified while the vehicle was moving, we stopped to confirm the identity of most birds seen, particularly those in groups. Rarely, additional raptors were seen as a result of stopping, and were included in the count. Time spent stationary was included in the transect duration.

Each transect was assigned to one of three land-use categories: savanna, pastoral land or agricultural land. Savanna transects followed unpaved tracks through open- or wooded grassland within the protected areas named above. Pastoral transects were on public roads through vegetation that was often superficially similar in structure and species composition to that of natural, protected savanna, but lay outside of protected areas, where wild

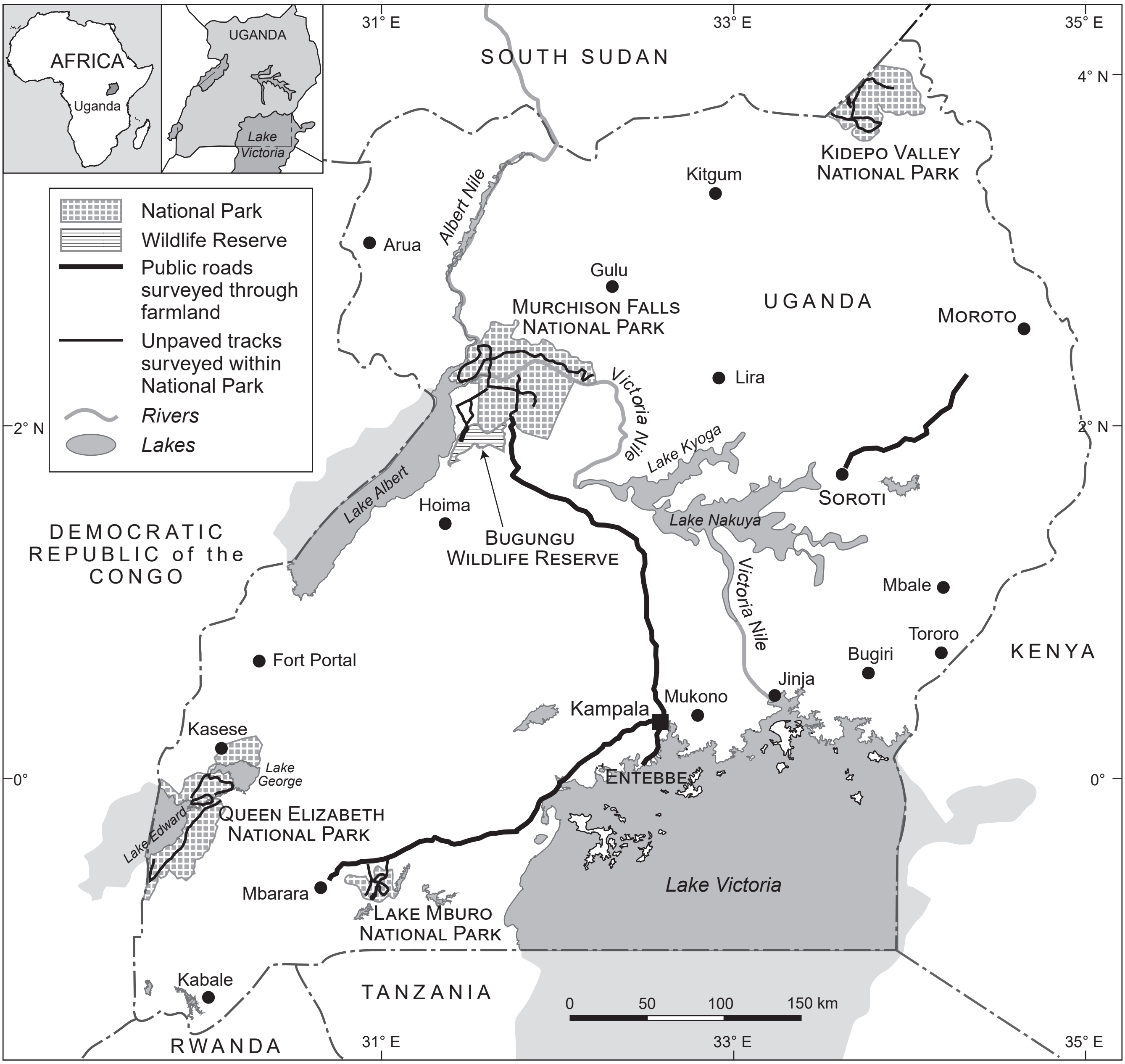

Figure 1: Routes surveyed during annual road counts, 2008–2015. Black lines indicate public roads surveyed through farmland, and unpaved tracks surveyed within four National Parks

herbivores were largely or wholly replaced by livestock. Agricultural transects also followed public roads, but through land supporting a range of crops, almost all of them in small fields, typically interspersed with patches of non-native trees, e.g. *Eucalyptus* species. Most pastoral transects included small areas of agricultural land and vice versa. Both of these transect types included human settlements, mainly small trading centres. For each transect we also recorded the mean altitude (from topographical maps), mean annual rainfall (from Government of Uganda 1967) and tree cover. The latter was defined as: open grassland, light tree cover, heavy tree cover, or closed canopy (i.e. forest). A small proportion of transects within PAs were predominantly tree covered, dominated by acacia (*Senegalia* and *Vachellia* spp.) and *Combretum* spp.

The migratory status of each species was defined as: resident, Palearctic migrant, or Afrotropical migrant (after Buij et al. 2013). Two species, Black Kite *Milvus migrans* and Common Kestrel *Falco tinnunculus*, have both migratory and resident populations in East Africa (Zimmerman et al. 1996; Brown et al. 1997).

Abundance estimates

The perpendicular distance of each bird from the road or track (when first seen) was estimated and assigned to one of four distance bands: 0–100, 100–200, 200–500 and >500 m. Detections made in the furthest band were subsequently discarded, since its outer limit was not defined. Four key functions (half-normal, hazard-rate, uniform and negative-exponential) were applied, using Distance V6.0, Release 2 (Thomas et al. 2010). Since the negative-exponential function is no longer recommended (Thomas et al. 2010), we selected from among the three remaining functions, using Akaike's Information Criterion (AIC), lower AIC values indicating an improved fit, requiring fewer parameters. For each species we used a Kruskal–Wallis test to determine whether the proportion of sightings made in each distance band varied significantly in relation to land use. If so, we applied a conventional distance sampling (CDS) model to data from each land-use type separately. Otherwise, we used multiple covariate distance sampling (MCDS; Marques et al. 2007; Thomas et al. 2010), stratifying by land use.

The public roads surveyed within agricultural and pastoral land were closely associated with homesteads, villages and trading centres, and supported a moderate volume of traffic. These factors almost certainly reduced the roadside densities of some raptors, while boosting numbers of synanthropic species. Since density estimates derived from agricultural and pastoral transects were unlikely to have been representative of these forms of land use generally, we did not attempt to estimate population sizes within agricultural or pastoral land. In contrast, density estimates derived from transects through protected savanna were much less likely to have been influenced by these confounds, since people and infrastructure were virtually absent, traffic was both scarce and slower-moving, and roadkill less evident than on public roads. We therefore estimated species' population sizes within protected areas by multiplying their density in protected savanna by the area of this land-use type in Uganda.

Land use estimates were provided by the National Biodiversity Data Bank, using data extracted from WCS and eCountability (2016). Estimates were obtained by first summing the area of all land classed either as moist or dry savanna, and adding 50% of the land area classed either as forest–savanna mosaic or as seasonal wetland. This calculation was made for 646 PAs of three types: National Parks, Wildlife Reserves and Forest Reserves (Supplementary Table S4). A further 66 Forest Reserves (each of less than 1 km^2) were excluded, since most of these were known to have been converted to agricultural production or to exotic tree plantations (National Biodiversity Data Bank *in litt*.). Of the 646 PAs considered, some were contiguous with other PAs, yielding more extensive blocks of savanna than they would have, had they been surrounded by farmland. We therefore identified clusters of contiguous PAs, and calculated the total area of savanna within each cluster, rather than treating its component PAs as separate sites. Eleven such clusters, encompassing 33 PAs, were included in our final list. Hereafter, we refer to both isolated PAs and clusters of contiguous PAs as 'conservation areas' (CAs) (Supplementary Table S4). An additional site designation, 'Community Wildlife Management Areas', was excluded from the analysis, since these largely comprise pastoral land, and typically support only sparse populations of natural prey (DP pers. obs.).

We identified species that showed a strong affinity for protected savanna, and hence for conservation areas, based on the species' much higher density in savanna compared with pastoral and agricultural land (from Table 1). Each species was scored as follows: (1) species encountered only in protected savanna (during this study), or too few encounters recorded in pastoral or agricultural land to be able to estimate densities in these land-use types; (2) species whose density in protected savanna was at least four times that in pastoral or agricultural land; and (3) all remaining species.

For resident species in categories 1 or 2 we estimated the number of pairs likely to reside in each CA as follows. First, we estimated the number of individuals present of all ages, from the species' density in savanna and the total area of savanna present. We used published estimates from study populations to estimate the proportion of birds likely to be adult, and hence of breeding age. Where published demographic values were lacking, we assumed that adults accounted for 65% of the population, this being the mean percentage for the five species for which published estimates were available. For each species we estimated the number of pairs of adults likely to be present, in two scenarios: where all adults were paired; and where 75% of adults were paired. We further assumed that small CAs, with sufficient savanna to support only a single pair of a given species, would be occupied only intermittently. Following Murn et al. (2016), we took a conservative approach to estimating the number of breeding pairs present, by excluding CAs where the amount of savanna was less than double that required to support one pair of the target species.

Habitat associations

We investigated the relationship between the number of individuals encountered on each survey of a given transect, and potential explanatory variables, using generalised linear mixed models (GLMMs). These were fitted using the *glmer* function in the lme4 package in R 3.0.1 (R Development Core Team 2016). Each case in the data set represented one transect-year, i.e. one survey of a given transect in a given year. The explanatory variables included were: land-use type; transect length; mean altitude; mean annual rainfall; tree cover category; and the presence of 'outside' observers. Since multiple surveys were made from each transect, sometimes in the same year, we specified 'transect identity' and 'year' as random terms in each model.

In most cases, few or no individuals of a given species were encountered in a given transect-year. Hence, the distribution of the dependent variable (the number of individuals encountered) was often highly skewed. We therefore examined the relationship between the number of individuals encountered and potential explanatory variables using two model structures. First, we identified explanatory variables associated with the presence/absence of a given species, specifying a binomial error distribution. In the second model we restricted the data set to cases where at least one individual of the target species had been recorded, and specified a Poisson error distribution. For each model type, minimal models were derived through stepwise

Table 1: Density estimates (birds 100 km^{-2}) in relation to land use. Figures are presented only for species–land use combinations yielding sufficient encounters with which to estimate density using Distance sampling

Species	Land use[a]	*n*[b]	Model[c]	Detection function	Adjustments[d]	ESW[e]	Density	Confidence limits
African Hawk-eagle *Aquila spilogaster*	Savanna	16	CDS	Uniform		500	0.29	(0.16–0.54)
Steppe Eagle	Savanna	72	MCDS	Half normal		193	3.40	(1.27–9.13)
A. nipalensis	Pastoral	12	MCDS	Half normal		102	2.51	(0.55–11.32)
Tawny Eagle	Savanna	135	MCDS	Half normal		226	5.46	(3.67–8.13)
A. rapax	Pastoral	20	MCDS	Half normal		243	1.76	(0.92–3.36)
Black-chested Snake-eagle *Circaetus pectoralis*	Savanna	34	CDS	Uniform	Cos. 1	291	1.07	(0.63–1.80)
Brown Snake-eagle	Agricultural	27	CDS	Half normal		241	1.75	(0.96–3.19)
C. cinereus	Savanna	90	CDS	Half normal		206	3.99	(2.87–5.55)
	Pastoral	30	CDS	Uniform	Cos. 1	251	2.55	(1.47–4.42)
Short-toed Snake-eagle *C. gallicus*	Savanna	18	CDS	Half normal		294	0.56	(0.25–1.25)
Western Banded Snake-eagle	Savanna	13	MCDS	Half normal		142	0.84	(0.38–1.85)
C. cinerascens	Pastoral	12	MCDS	Half normal		181	1.41	(0.62–3.23)
African Fish-eagle *Haliaeetus vocifer*	Savanna	135	MCDS	Half normal		199	6.19	(4.39–8.72)
Wahlberg's Eagle	Agricultural	34	MCDS	Half normal		176	3.01	(1.63–5.56)
Hieraaetus wahlbergi	Savanna	29	CDS	Uniform	Cos. 1	256	1.04	(0.64–1.68)
	Pastoral	36	MCDS	Half normal		193	3.97	(1.80–8.76)
Long-crested Eagle	Agricultural	94	MCDS	Half normal		124	11.56	(8.37–15.96)
Lophaetus occipitalis	Savanna	151	MCDS	Half normal		164	8.42	(6.03–11.76)
	Pastoral	92	MCDS	Half normal		135	10.15	(7.23–14.23)
Martial Eagle *Polemaetus bellicosus*	Savanna	35	MCDS	Half normal		189	1.70	(1.06–2.71)
Bateleur	Savanna	415	MCDS	Half normal	Cos. 2	197	19.29	(15.27–24.35)
Terathopius ecaudatus	Pastoral	33	MCDS	Half normal	Cos. 2	215	3.28	(1.48–7.24)
Common Kestrel *Falco tinnunculus*	Savanna	15	MCDS	Half normal		302	0.45	(0.17–1.22)
Grey Kestrel	Agricultural	29	MCDS	Half normal		107	4.24	(2.39–7.51)
F. ardosiaceus	Savanna	106	MCDS	Half normal		113	8.54	(5.82–12.52)
	Pastoral	23	MCDS	Half normal		73	6.69	(3.60–12.44)
Red-necked Falcon *F. ruficollis*	Savanna	20	MCDS	Half normal		152	1.19	(0.56–2.54)
Montagu's Harrier	Savanna	34	MCDS	Half normal		147	2.11	(1.14–3.91)
Circus pygargus	Pastoral	18	MCDS	Half normal		206	1.87	(0.75–4.65)
Pallid Harrier	Savanna	19	MCDS	Half normal		155	1.12	(0.50–2.49)
C. macrourus	Pastoral	9	MCDS	Half normal		334	0.58	(0.20–1.66)
Western Marsh-harrier *C. aeruginosus*	Savanna	24	MCDS	Half normal		216	1.02	(0.58–1.76)
Shikra	Agricultural	22	CDS	Uniform	Cos. 1	108	3.19	(1.64–6.21)
Accipiter badius	Savanna	19	CDS	Uniform	Cos. 1	127	1.37	(0.67–2.80)
	Pastoral	20	CDS	Uniform	Cos. 1	103	4.15	(2.42–7.09)
Grasshopper Buzzard	Agricultural	8	MCDS	Half normal		163	0.76	(0.23–2.50)
Butastur rufipennis	Savanna	852	MCDS	Half normal		136	57.10	(41.73–78.12)
	Pastoral	14	MCDS	Half normal		171	1.75	(0.73–4.18)
Eurasian Buzzard *Buteo buteo*	Savanna	26	MCDS	Half normal		137	1.74	(0.95–3.17)
Lizard Buzzard	Agricultural	50	CDS	Uniform	S. poly. 2	88	8.88	(5.58–14.20)
Kaupifalco monogrammicus	Savanna	29	CDS	Uniform	S. poly. 2	92	2.88	(1.72–4.82)
	Pastoral	27	CDS	Uniform	S. poly. 2	121	4.75	(2.72–8.27)
Dark Chanting-goshawk	Agricultural	24	MCDS	Half normal		239	1.57	(0.64–3.87)
Melierax metabates	Savanna	50	MCDS	Half normal		143	3.19	(2.09–4.87)
	Pastoral	49	MCDS	Half normal		172	6.09	(3.03–12.24)
European Honey-buzzard	Savanna	126	MCDS	Half normal		150	7.66	(5.12–11.44)
Pernis apivorus	Pastoral	25	MCDS	Half normal		155	3.25	(1.58–7.54)
African Harrier-hawk	Agricultural	13	MCDS	Half normal		210	0.97	(0.41–2.28)
Polyboroides typus	Savanna	35	MCDS	Half normal		159	2.01	(1.24–3.26)
Black-winged Kite	Agricultural	35	MCDS	Half normal		92	5.92	(3.28–10.68)
Elanus caeruleus	Savanna	26	MCDS	Half normal		80	2.98	(1.34–6.61)
	Pastoral	61	MCDS	Half normal		160	8.16	(3.97–16.76)

Table 1: (cont.)

Species	Land use[a]	n[b]	Model[c]	Detection function	Adjustments[d]	ESW[e]	Density	Confidence limits
Black Kite	Agricultural	1 233	MCDS	Half normal		149	129.45	(91.12–183.70)
Milvus migrans	Savanna	477	MCDS	Half normal	Cos. 2	179	24.31	(16.65–35.50)
	Pastoral	518	MCDS	Half normal		171	64.60	(53.31–78.29)
Osprey *Pandion haliaetus*	Savanna	15	MCDS	Half normal		302	0.45	(0.20–1.03)
Palm-nut Vulture *Gypohierax angolensis*	Savanna	72	CDS	Uniform	S. poly. 2	96	6.86	(4.19–11.23)
White-backed Vulture *Gyps africanus*	Savanna	445	MCDS	Half normal		271	15.04	(10.12–22.33)
Gyps spp.	Savanna	585	MCDS	Half normal		271	19.74	(13.29–29.33)
Rüppell's Vulture *G. rueppelli*	Savanna	139	MCDS	Half normal		271	4.71	(3.17–6.99)
Hooded Vulture	Agricultural	76	CDS	Half normal		112	10.59	(4.91–22.81)
Necrosyrtes monachus	Savanna	25	CDS	Uniform		500	0.46	(0.17–1.20)
	Pastoral	32	CDS	Half normal		116	5.86	(2.54–13.55)
Lappet-faced Vulture *Torgos tracheliotos*	Savanna	48	CDS	Half normal		200	2.19	(1.21–3.94)
White-headed Vulture *Trigonoceps occipitalis*	Savanna	26	MCDS	Half normal		227	1.05	(0.56–1.96)

[a] Land-use types: savanna transects followed unpaved tracks through open- or wooded grassland within PAs; pastoral transects were on public roads through vegetation that was often superficially similar to that of savanna, but lay outside of PAs; agricultural transects also followed public roads, but through land supporting crops. See Methods for further details

[b] Number of encounters recorded in this land-use type

[c] Model type: CDS = conventional distance sampling, MCDS = multiple covariate distance sampling

[d] Adjustments: Cos = cosine, S. poly. = simple polynomial

[e] Effective strip width (m)

elimination of the least significant explanatory variable, as recommended by Crawley (2005). Final models were those with the lowest AIC value.

Results

Population densities

Densities were estimated for 34 raptor species; 12 in arable land, 18 in pastoral land and for all 34 in protected savanna (Table 1). Fifteen (44%) of the 34 species were encountered only in savanna, or else so sparsely in farmland that it was not possible to estimate their densities there. Of those species for which density estimates could be made in pastoral or agricultural land, two occurred at much lower densities (<25%) than they attained in savanna. Thus, 17 raptor species appeared to be almost exclusively associated with savanna, and were therefore largely or wholly restricted to conservation areas. Our density and population estimates for one species, African Fish Eagle *Haliaeetus vocifer*, were likely to have been misleading, because the species is closely associated with linear aquatic features (rivers and lake shores), and is widespread in (unprotected) freshwater habitats. Consequently, we have excluded this species from further abundance analyses, leaving 16 'savanna-dependent' species (Table 2). Note, however, that the confidence limits associated with these density estimates were typically wide, showing extensive overlap for a given species in savanna and pastoral or agricultural land (Table 1).

Fragmentation effects

Based on land-use data provided by WCS and eCountability (2016), we estimated that savanna habitats covered 22 308 km^2 in Uganda in 2010, all of it within CAs. We have used this figure to estimate the number of individuals present in Uganda's CAs, for each of the 16 savanna-dependent species, by multiplying the total area of protected savanna (above) by each species' density within savanna (Table 2). This approach is likely to have over-estimated population sizes, however, because our savanna area figure includes many small fragments. Of the 624 CAs identified, 49% contained less than 1 km^2 of savanna, and were therefore unlikely to support even a single pair of the species in question. Conversely, the five largest CAs each contained >1 000 km^2 of savanna, and together accounted for 63% of the total area of protected savanna.

Fragmentation of the available habitat is likely to impact mainly on resident species, particularly those defending large, year-round breeding territories, and colony-nesters requiring very extensive areas of savanna in which to forage (e.g. *Gyps* spp.). Of the 16 savanna-dependent species, 10 are resident in Uganda and are known or likely to breed there. Based on estimates of the proportion of adult birds in the population, and assuming that 75%–100% of adults were paired, at least half of these species are likely to have breeding populations of fewer than 100 pairs (Table 3). They include Martial Eagle *Polemaetus bellicosus* (53–75 pairs), Lappet-faced Vulture *Torgos tracheliotos* (74–105 pairs) and White-headed Vulture (22–32 pairs). In

Table 2: Raptor species recorded only, or much more frequently, in protected savanna than in pastoral or agricultural land. The combined number of individuals present in conservation areas (CAs) has been estimated from the species' population density in savanna, and the total area of savanna within the CA network

Species	Dependency score[a]	Global threat status[b]	Migratory status[c]	Individuals in CA network	Confidence limits
African Hawk-eagle	1	LC	R	65	(35–121)
Black-chested Snake-eagle	1	LC	R	238	(141–401)
Short-toed Snake-eagle	1	LC	PM	125	(55–278)
Martial Eagle	1	VU	R	379	(237–604)
Bateleur	2	NT	R	4 302	(3 406–5 433)
Common Kestrel	1	LC	RPM	101	(37–272)
Red-necked Falcon	1	LC	R	267	(126–565)
Western Marsh-harrier	1	LC	PM	227	(130–393)
Grasshopper Buzzard	2	LC	AM	12 737	(9 308–17 427)
Eurasian Buzzard	1	LC	PM	388	(212–708)
Osprey	1	LC	PM	101	(44–230)
Palm-nut Vulture	1	LC	R	1 530	(934–2 505)
White-backed Vulture	1	CR	R	3 354	(2 257–4 982)
Rüppell's Vulture	1	CR	R	1 050	(707–1 560)
Lappet-faced Vulture	1	EN	R	489	(271–880)
White-headed Vulture	1	CR	R	233	(124–436)

[a] Dependency on protected savanna was scored as: 1 = species only recorded in savanna, or encounters in pastoral and agricultural land too few to support density estimation in these land-use types; 2 = highest density attained in pastoral or agricultural land was ≤25% of density in savanna. Species whose density in pastoral or agricultural land was >25% of their density in savanna have been excluded

[b] Global threat status: LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered (source: BirdLife International 2018)

[c] Migratory status in Uganda: AM = Afrotropical migrant; R = resident; RPM = both resident individuals and Palearctic migrants present; PM = Palearctic migrant

each case, at least 90% of pairs are likely to reside within the five largest CAs (Table 3).

To gauge the effects of fragmentation on species' populations we compared the numbers of adult pairs estimated using the above approach (Table 3), with the number derived by multiplying pair density by the total area of savanna in Uganda (Table 2). That is, we compared population estimates that take account of resource fragmentation, with those in which fragmentation was disregarded. Not surprisingly, national estimates for the 10 resident, savanna-dependent species were all lower when fragmentation was taken into account, by a median of 41% (quartiles: 30%–48%) (Figure 2).

Habitat associations

Binomial GLMMs indicated that 11 species were more likely to be detected from savanna transects than from pastoral or agricultural transects (Table 4, Supplementary Table S2). A further three species were more likely to be detected from savanna or pastoral transects, when the data from these were pooled, suggesting that the species were attracted by features common to both but missing from agricultural land. Of these 14 species, five are classed as globally threatened and one as near-threatened. Not surprisingly, this group includes the larger, resident eagles (Martial Eagle and Bateleur *Terathopius ecaudatus*) as well as three vulture species (White-backed *G. africanus*, Rüppell's *G. rueppelli* and White-headed Vulture). Land-use preferences of a fourth species, Lappet-faced Vulture, could not be modelled in the same way, due to its absence from pastoral and agricultural transects. Among nine species that were more likely to be detected from pastoral transects, or from pastoral and agricultural transects in combination, only one (Hooded Vulture *Necrosyrtes monachus*) is globally threatened (Table 4). Thus, seven out of eight globally threatened or near-threatened species were significantly associated with, or restricted to, protected savanna.

In GLMMs fitted with a Poisson error distribution, and restricted to cases where the target species was seen, four species (Steppe Eagle *Aquila nipalensis*, Tawny Eagle *A. rapax*, Bateleur and Grey Kestrel *F. ardosiaceus*) were more abundant on savanna transects than elsewhere. Only one species (White-headed Vulture) was more abundant on pastoral transects, and one (Hooded Vulture) on pastoral–agricultural transects combined (Table 4).

Five species were more likely to be encountered on transects where tree cover was absent or light, while two were positively associated with denser tree cover. Similarly, four species were more abundant where tree cover was absent, while two were more abundant in denser tree cover. The latter included Rüppell's Vulture, which, although more often seen from transects in open or lightly-wooded grassland, occurred in larger numbers when encountered in more wooded habitat (Table 4).

Discussion

Driven line transects are one of the most widely used methods for measuring raptor abundance in Africa.

Table 3: Estimates of the number of adult pairs present in Uganda's conservation areas (CAs), for resident raptor species highly dependent on savanna habitats

Species	Proportion assumed adult[a]	Source[b]	Area pair^{-1} (km^2)	Total pairs, assuming:		Occupied CAs[d]	Number of CAs likely to support[d]:			Percentage pairs in five largest CAs[d]
				75% adults paired	100% adults paired		<5 pairs	5–20 pairs	>20 pairs	
African Hawk-eagle	0.65	1	–[c]	3	5	2	2	0	0	100
Black-chested Snake-eagle	0.65	1	288–384	30	42	5	3	2	0	98–100
Martial Eagle	0.65	1	181–241	53	75	7	2	5	0	93–96
Bateleur	0.65	2, 3	16–21	862	1 191	54	39	8	7	73–75
Red-necked Falcon	0.65	1	257–342	34	49	6	3	2	0	96–97
Palm-nut Vulture	0.55	2, 4	53–71	222	307	15	8	2	5	84–86
White-backed Vulture	0.80	2, 5	17–22	828	1 145	54	39	8	7	73–76
Rüppell's Vulture	0.80	6	53–71	222	307	15	8	2	5	84–86
Lappet-faced Vulture	0.66	7	138–184	74	105	9	4	4	1	91–93
White-headed Vulture	0.54	8	354–472	22	32	5	3	2	0	100

[a] The proportion of individuals assumed to be adult, and hence of breeding age

[b] Sources used for estimating the proportion of adult birds in the population. 1, Mean of estimates for five species for which published sources were available; 2, Brown et al. (1997); 3, Watson (1990a); 4, Kemp and Kirwan (2018); 5, Anderson (2000), Murn et al. (2002), Monadjem et al. (2012); 6, assumed to be as for White-backed Vulture; 7, Mundy et al. (1992); 8, Murn et al. (2016)

[c] Density extremely low; estimated area required per pair likely to be misleading

[d] Assuming 75% of adults are in pairs

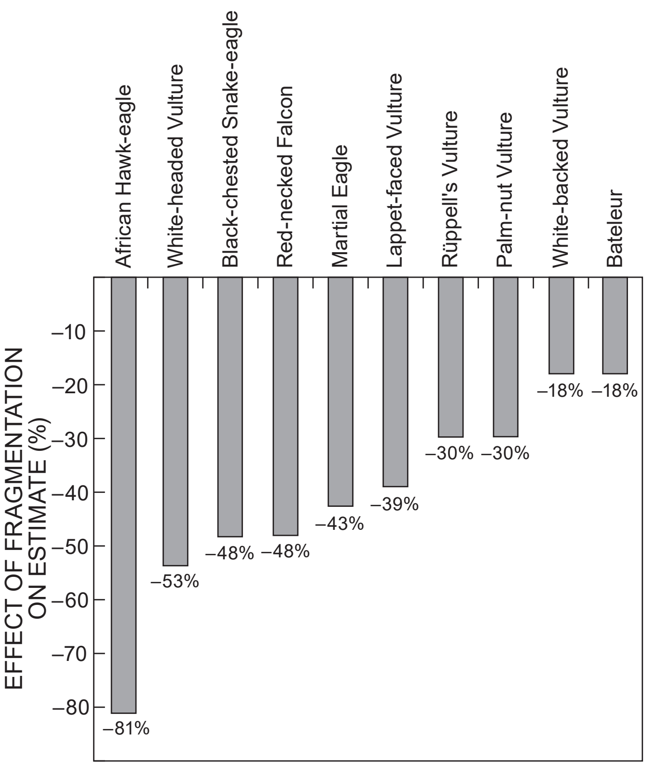

Figure 2: The effects of habitat fragmentation on population estimates for 10 resident, savanna-dependent species. Population sizes were estimated in two ways: (1) by multiplying the combined area of protected savanna in all conservation areas (CAs) by the species' density in that habitat; and (2) by multiplying the area of protected savanna in each CA by the species' density, but excluding CAs with too little savanna to support at least one pair of the species in question. Population estimates were 41% lower (median; quartiles: 28%–48%) when sites with insufficient savanna were excluded (2), than when all protected savanna was treated as a single block (1)

However, they tend to yield a biased estimate of bird density, because conditions adjacent to roads and tracks will often differ from those in the wider landscape. Here, transects on public roads running through pastoral and agricultural land were associated with moderate levels of traffic disturbance, infrastructure development, housing and vegetation changes, and were considered unlikely to yield raptor densities representative of these two land-use types. In particular, species deterred by these factors may have been more abundant at greater distances from public roads within pastoral and agricultural land. If so, our figures may tend to over-estimate any differences between these land-use types and the densities attained in protected savanna, where the level of bias associated with (unpaved) survey routes was likely to have been lower, and the roadside densities we recorded were more likely to have been representative of protected savanna generally. Nonetheless, we note that foot transects consistently yield higher raptor densities than driven transects, particularly of smaller species (DP pers. obs.).

Pomeroy et al. (2014) estimated population densities and sizes of six vulture species in Uganda, using data from the first six years of the survey described here, i.e. during 2008–2013. Not surprisingly, their density estimates within protected savanna were similar to those presented here. However, their population estimates differed substantially, for two reasons. First, using an earlier land-cover data set, they estimated that the area of savanna within Uganda's PA network was much lower (9 573 km^2) than the figure used in this study (22 308 km^2). The latter was drawn from a more recent and, we believe, more accurate assessment (WCS and eCountability 2016). Second, Pomeroy et al. (2014) treated all savanna as a single block when estimating national population sizes, ignoring the effects of fragmentation, illustrated here in Figure 2.

We estimated the number of adult pairs of each resident, savanna-dependent species likely to reside within

Table 4: The influence of land use and tree cover on the likelihood of a species being encountered on a given transect (Binomial models), and on the number of individuals recorded (Poisson models). The latter were restricted to surveys of transects in which at least one individual of the target species was seen. For effect sizes, see Supplementary Table S2. Globally threatened and near-threatened species are shown in bold and bold-italics, respectively

Explanatory variable	Model type	Species' presence or abundance positively associated with:			
		Savanna	Savanna–Pastoral	Pastoral	Pastoral–Agricultural
Land use	Binomial (presence/ absence)	**Steppe Eagle**** African Fish-eagle*** **Martial Eagle***** ***Bateleur***** Red-necked Falcon* Western Marsh-harrier⁺ Grasshopper Buzzard** European Honey-buzzard** **White-backed Vulture***** **Rüppell's Vulture*** **White-headed Vulture****	Brown Snake-eagle* Montagu's Harrier* Eurasian Buzzard⁺	Tawny Eagle⁺ W. Banded Snake-eagle⁺ Dark Chanting-goshawk⁺	Wahlberg's Eagle* Long-crested Eagle** Shikra** Black-winged Kite⁺ Black Kite*** **Hooded Vulture****
Land use	Poisson (abundance)	**Steppe Eagle**** Tawny Eagle* ***Bateleur⁺*** Grey Kestrel***	-	**White-headed Vulture****	**Hooded Vulture****
Feature	Model type	Open grassland–light tree cover		Heavy tree cover–closed canopy	
Tree cover	Binomial (presence/ absence)	Red-necked Falcon⁺ Montagu's Harrier* Western Marsh-harrier** Black-winged Kite⁺ **Rüppell's Vulture***		Wahlberg's Eagle** Bateleur*	
Tree cover	Poisson (abundance)	**Steppe Eagle***** Grey Kestrel* Grasshopper Buzzard** European Honey-buzzard*		**Rüppell's Vulture**** **Hooded Vulture****	

⁺ $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Uganda's conservation areas. Although in some species immatures may also form pairs, we have focused on adult pairs, which are more likely to attempt to breed, and to do so successfully. We therefore estimated the proportion of birds likely to be adult and paired, and then calculated the area of savanna available to each adult pair. We used this value to exclude sites in which the amount of savanna available was likely to be too small to support a single adult pair. Since it would have been impractical to try to assess the age of each bird seen, the proportion of adults in the population was estimated from published findings. In the absence of these data we assumed that 65% of the population were adult, this being the median value for those species for which data were available. We further assumed that, for resident, savanna-dependent species, 75%–100% of adults were paired (Table 3). Since the upper figure is probably attained only rarely, we have used the lower figure when discussing the 10 species largely confined to conservation areas.

Our estimates of the numbers of adult pairs present within conservation areas could prove conservative, given that most of the 10 savanna-dependent species are likely to be capable, to some degree, of exploiting adjacent pastoral land, or of regularly crossing farmland to reach other, nearby conservation areas. If so, some of the sites we rejected as being too small to accommodate a given species may be occupied, and hence the species may prove to be more abundant than our estimates suggest.

Vultures

Murn et al. (2016) demonstrated the value of using nest densities and demographic parameters to refine estimates of the global population size of White-headed Vulture, a species highly dependent on Africa's PA network. They estimated a global population of 5 475–5 493 birds, much lower than a long-standing estimate of 7 000–12 000 birds (Mundy et al. 1992), and more precise than the population size category in which the species is currently placed by BirdLife International (2018): 2 500–9 999 mature individuals.

Here, we estimated that the area of savanna available to White-headed Vulture pairs in Uganda averaged 472 km^2 $pair^{-1}$; slightly higher than the value used by Murn et al. (2016) for East African populations (400 km^2 $pair^{-1}$), based on their density in the Serengeti ecosystem (Pennycuick 1976). Murn et al. (2016) estimated that Uganda's PA series was likely to support 12.2 breeding pairs of White-headed Vulture, distributed across 13 sites. Since they assumed that only 75% of pairs attempt to breed in any given year, this translates into 16.3 pairs (breeding and non-breeding); fewer than the 22 pairs (in five conservation areas) estimated here (Table 3). This disparity may stem from differences in the area figures used in the two studies. Murn et al. (2016) assumed that each PA consisted entirely of suitable habitat, but that land close to the PA boundary was likely to be less suitable than core areas (following Herremans and Herremans-Tonnoeyr 2000). Their population estimates were thus based on the entire area of the site (rather than the area of savanna present), from which they subtracted a fixed area (50 km^2), to account for likely boundary effects. In contrast, our estimates were based on the amount of savanna present, which accounted for 72% of the land within conservation areas, the remainder comprising less suitable habitat, including wetlands and rain forest. Furthermore, we measured the combined area of savanna within clusters of contiguous sites, whereas Murn et al. (2016) treated each site as a discrete area, rejecting PAs that were individually too small to support White-headed Vulture pairs, even where they were contiguous with other savanna sites.

In this study, White-headed Vultures were significantly more likely to be detected from savanna transects than from pastoral or agricultural transects, but were significantly more abundant on pastoral transects (Table 4). This finding is likely to prove misleading, however, as it is based partly on a count of seven birds seen once on a single pastoral transect; all (26) other sightings were made on savanna transects, involving lower numbers per transect.

Lappet-faced Vultures are largely confined to conservation areas, which we estimate to hold some 74 pairs, distributed among nine CAs, with ~93% of pairs residing in the five largest CAs. These figures are derived from the area of savanna available per pair, which we estimated at 184 km^2. This figure is a little higher than estimates derived from nest counts made during aerial surveys in Swaziland (147 km^2 pair^{-1}; from Monadjem and Garcelon 2005; Bamford et al. 2009) and Zululand, South Africa (149 km^2 pair^{-1}; from Bamford et al. 2009) (Supplementary Table S3). Equivalent estimates from other PAs vary widely, however, from 256 km^2 pair^{-1} in Kruger NP, South Africa (Murn et al. 2013) to just 43 km^2 pair^{-1} in the Serengeti ecosystem (Pennycuick 1976), where carcass availability was presumably much higher.

Uganda's conservation areas are also likely to support the equivalent of 828 and 222 pairs of White-backed and Rüppell's Vultures, at a density of one pair per 22 km^2 and 71 km^2, respectively. For White-backed Vulture, similar densities have been reported from aerial counts of nests in Hwange NP, Zimbabwe (27 km^2 pair^{-1}; Howells and Hustler 1984), Linyanti, Botswana (23 km^2 pair^{-1}; Bamford et al. 2009) and Kruger NP (22 and 32 km^2 pair^{-1}; Monadjem et al. 2012; Murn et al. 2013). However, much higher densities have been reported from aerial counts of tree colonies in Swaziland (2 km^2 pair^{-1}; Bamford et al. 2009), Zululand (5 km^2 pair^{-1}; Bamford et al. 2009) and Kimberley, South Africa (1.7 km^2 pair^{-1}; Murn et al. 2017). While Virani et al. (2010) reported similarly high densities (0.7–2.8 km^2 pair^{-1}) from a ground-based survey in Masai Mara GR, Kenya, they noted that the (mainly riverine) areas they sampled were unlikely to be representative of the entire Masai Mara ecosystem. No comparable density estimates were found for Rüppell's Vulture.

The population of Palm-nut Vulture *Gypohierax angolensis* in Uganda's conservation areas is likely to include some 222 pairs, occupying 15 CAs. We estimate that the amount of savanna available per pair was 71 km^2, suggesting that suitable habitat is very patchily distributed. A much lower area requirement, of 2 km^2 pair^{-1}, has been reported from Côte d'Ivoire, but was considered exceptional (Brown et al. 1997).

Eagles

Uganda's conservation areas encompass sufficient savanna to support some 53 pairs of Martial Eagle, across seven CAs. Our estimate of the mean area available pair^{-1} (241 km^2) was higher than in the Masai Mara (120 km^2 pair^{-1}; Ong 2000), Hwange NP (133 km^2; Hustler and Howells 1987) and Kruger NP: 108–194 km^2 pair^{-1} (Snelling 1970; Herholdt and Kemp 1997; van Eeden et al. 2017), but lower than in Tsavo East NP, Kenya, where Smeenk (1974) recorded a density equivalent to 300 km^2 pair^{-1}. Not surprisingly, lower densities have been recorded in desert or semi-desert habitat: Kalahari Gemsbok NP, South Africa supported 20–30 pairs (at 320–480 km^2 pair^{-1}) in 1988–1994, dropping to just nine breeding pairs (889 km^2 pair^{-1}) by 2011–2012 (Herholdt and Kemp 1997; Amar et al. 2016).

The mean area of protected savanna available to Bateleur pairs (21 km^2 pair^{-1}) was much lower than has been reported from Kenya (170 km^2 pair^{-1}; Brown et al. 1997), but closer to that recorded in Kruger NP: 3.1 nests 100 km^{-2}; equivalent to 32 km^2 nest^{-1} (Watson 1990a, 1990b). When adjusted to account for non-breeding pairs (16% of pairs p.a.; Watson 1990b), the area available to each pair will have been lower, averaging 27 km^2 pair^{-1}, i.e. closer to our estimate. Nonetheless, we feel that our population estimate for Uganda's conservation areas (862 pairs in 54 CAs) should perhaps be treated with caution.

Density estimates for African Hawk-eagle *A. spilogaster* in southern Africa range between 19 and 33 km^2 pair^{-1} in Kruger NP and Matobo, Zimbabwe (Snelling 1970; Steyn 1975), and 18–59 km^2 pair^{-1} in Hwange NP (Hustler and Howells 1988). Similarly, in East Africa, Smeenk (1974) reported an average territory size of 56 km^2 pair^{-1} in Tsavo East NP. In contrast, our density estimate was extremely low, despite the species being widespread in East Africa, including Uganda. We recorded a density of just 0.29 birds 100 km^{-2}, suggesting that suitable habitat was very patchily distributed, or that the species was substantially under-recorded from driven line transects. Reasons for the disparity between our figures and those derived from more intensive studies thus remain unclear.

In tropical Africa, Black-chested Snake-eagle *Circaetus pectoralis* and its congeners occur at low densities, each pair requiring 'several hundred km^2' (Brown et al. 1997). This suggests that our very low density estimate (384 km^2 pair^{-1}) may be broadly accurate, yielding a population estimate of ~30 pairs, in the five largest CAs.

Red-necked Falcon Falco ruficollis

Our Red-necked Falcon density estimate (342 km^2 pair^{-1}) differed markedly from published estimates. Nests have been found as little as 1.3–3.2 km apart in Zambia and 1.9–15.5 km apart in South Africa, although these spacings were regarded as exceptional (Tarboton 2001). Inter-nest distances of 3–10 km, indicating densities of 7–78 km^2 pair^{-1}, are regarded as being more typical in southern Africa (Tarboton 2001), while a density of 167 km^2 pair^{-1} has been recorded in the central Namib (Brown 1988). Our low density estimate suggests that conditions appropriate for the species are extremely patchily distributed in Uganda's conservation areas. This may reflect the species' association with Borassus Palm *Borassus aethiopum*, which is generally scarce in most of Uganda (DP pers. obs.).

Conclusions

Road surveys within four of Uganda's National Parks yielded raptor densities that were, in most cases, broadly comparable with published estimates from other studies, most of which involved ground-based or aerial surveys of occupied nests (Supplementary Table S3). For Uganda's globally threatened species at least, further work is required to determine whether the estimates presented here accurately reflect the numbers of adult pairs present within the National Parks surveyed; and whether they are equally applicable to other forms of PA, as well as to smaller conservation areas generally. There is also a pressing need to assess the viability of threatened raptor species particularly dependent on Uganda's conservation areas, namely Martial Eagle and Lappet-faced, White-headed, Rüppell's and White-backed Vultures. Breeding populations of the first three species are both sparse and fragmented, placing their long-term viability in Uganda in doubt. While the breeding status of the two *Gyps* vultures is unclear, there is strong evidence that they can make long-distance movements within Uganda (Pomeroy 2008), and are likely to be part of a regional meta-population. This will need to be so for all species with fragmented populations if they are to survive in the long term. Much more needs to be known of the populations and movements of these five species, to help secure their Ugandan populations in perpetuity.

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