Implications of farmland expansion for species abundance, richness and mean body mass in African raptor communities

Phil Shaw[1,2*], Micheal Kibuule[3], Dianah Nalwanga[4], George Kaphu[5], Michael Opige[4,6], Derek Pomeroy[3*]

[1] School of Biology, Sir Harold Mitchell Building, University of St Andrews, Fife, KY16 9TH, United Kingdom
[2] Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, PO Box 44, Kabale, Uganda
[3] Department of Zoology, Makerere University, PO Box 7298 Kampala, Uganda
[4] NatureUganda, PO Box 27034, Kampala, Uganda
[5] Uganda Wildlife Authority, PO Box 3530, Kampala, Uganda
[6] Ecological Trends Alliance, PO Box 36839, Kampala, Uganda

*Corresponding authors
E-mail addresses: ps61@st-andrews.ac.uk (P. Shaw), derek@infocom.co.ug (D. Pomeroy)

Abstract

Globally, conversion of natural habitats to farmland poses the greatest extinction risk to birds, its consequences being especially pervasive in the case of large predators and scavengers, whose declines may trigger extensive cascading effects. Human population growth in sub-Saharan Africa is expected to drive a vast expansion in agricultural land by 2050, largely at the expense of pastoral land and savanna. In East Africa, the greatest expanse of suitable land yet to be converted to agriculture lies mainly in South Sudan, DRC and Tanzania. To gauge the effects of land conversion on raptor populations in this region we used road survey data from neighbouring Uganda, from which we determined linear encounter rates (birds seen 100 km^{-1}; n = 33 species), and species richness (53 species). Encounter rates were much lower in pastoral land than in protected savanna (median difference: -41%; 23 species), and lower still in agricultural land (-90%; 24 species). These disparities were influenced by diet and body mass. For large eagles and vultures, encounter rates in agricultural land were 97% lower than in protected savanna (median of 12 species), whereas for smaller raptors they were 30% lower (12 species). Large, apex consumers were thus more vulnerable to farmland expansion, and this was reflected in the mean body mass of species encountered in savanna (1,740 g), pastoral (995 g) and agricultural land (856 g). Body mass differences remained significant when vultures were excluded. Since threat status is linked to body mass, encounter rates for globally threatened and near-threatened species likewise showed a more pronounced deficit in farmland than those of least concern. Accordingly, pastoral and agricultural transects were less species-rich (10.6 and 6.7 raptor species 100 km^{-1}, respectively) than savanna transects (13.2 species). Our findings suggest that the projected expansion of agricultural land in sub-Saharan Africa is likely to reduce raptor populations in pastoral land and savanna by c. 50% and 90%, respectively. We propose that conservation efforts focus on identifying the causes of raptor population deficits in farmland, and on safeguarding tracts of unprotected, intact savanna, together with existing protected areas.

Keywords: apex consumers; vultures; eagles; savanna; agricultural impacts; protected areas

1. Introduction

Land use conversion is considered to be the single biggest driver of biodiversity loss in the tropics (Foley et al. 2005, Jung et al. 2017). In particular, the expansion of cropped and pastoral land within natural ecosystems is the most important form of land conversion, by area (Lambin & Meyfroidt 2011). Farming is more damaging to wild nature than any other sector of human activity (Balmford et al. 2012) and poses the greatest extinction risk to birds, especially in developing countries (Green et al. 2005). In much of sub-Saharan Africa the expansion of agricultural habitats, particularly cultivated land, has occurred mainly at the expense of natural grassland, savanna and forests (Brink & Eva 2009), with profound effects on their ecological assemblages (Newbold et al. 2017). Similarly, the replacement of wild herbivore communities with domestic livestock has had substantial impacts on a range of ecosystem processes, contributing towards increased woody cover and a rise in herbivore methane emissions (Hempson et al. 2017).

While land use change has impacted severely on the extent, continuity and quality of terrestrial habitats, the loss of predators, scavengers and other apex consumers may have an equally pervasive influence on the natural world, due to the extensive cascading effects that follow their disappearance (Estes et al. 2011, Dirzo et al. 2014). In Africa, these effects include the potential loss of ecosystem services provided by vultures and other avian scavengers, which are likely to inhibit disease transmission, through the rapid disposal of carcasses (Ogada et al. 2012). The loss of this service in India has been described in a well-documented trophic cascade, wherein the collapse of vulture populations was followed by a substantial rise in the feral dog population, which in turn contributed to a $34 billion increase in healthcare costs associated with rabies treatment in humans (Sudarshan et al. 2007, Markandya et al. 2008).

For many African raptors the impacts of farmland conversion have been intensified through a range of anthropogenic effects, which include incidental and deliberate poisoning, linked mainly to the illegal killing of livestock predators and elephants (Otieno et al. 2010, Virani et al. 2011, Ogada 2014, Ogada et al. 2015, 2016, Monadjem et al. 2018). In West and Central Africa, large raptors are also killed for bushmeat (Buij et al. 2016), while trade in raptor body parts for traditional medicines is widespread, occurring in at least 19 African countries (McKean et al. 2013, Williams et al. 2014). Human disturbance can also adversely affect both tree- and cliff-nesting species (Borello & Borello 2002; Monadjem & Garcelon 2005; Bamford et al. 2009), while energy infrastructure poses a significant, growing threat to larger species, through collisions and electrocution (Jenkins et al. 2010, Rushworth & Krüger 2014, Kibuule & Pomeroy 2015).

The impacts of these pressures have attracted considerable attention, reflecting their scale, the graphic evidence they generate and their recent dramatic rise, particularly in the case of vulture poisoning (Ogada et al. 2016). In contrast, the effects of land use change on African raptor populations are more diffuse, and perhaps more difficult to quantify. Much of the transition to agriculture coincided with the colonial period, and hence pre-dates the standardised collection and analysis of biological survey data. Furthermore, for many observers the extent to which land use has changed may be obscured by shifting baseline syndrome, each generation viewing the conditions they encounter as the new norm, and focusing only on the extent to which these have changed over their own lifetime (Papworth et al. 2009).

While the effects of land use change on biodiversity may be difficult to quantify, its scale, and that of human population growth, are comparatively well documented. Between 1960 and 2016 the human population of sub-Saharan Africa increased by 0.8 billion (Canning et al. 2015, World Bank 2017a,b). During part of that period (1975–2000) the area of agricultural land in sub-Saharan Africa increased by 57%, mainly at the expense of natural vegetation, which contracted by 21%, with a loss of almost 5 million ha of forest and non-forest natural vegetation per annum (Brink & Eva 2009). The human population is projected to increase by a further 1.8 billion during 2016–2060 (Canning et al. 2015), generating an unprecedented surge in the demand for food. While the FAO has estimated that some 80% of this demand may be addressed through higher yields and increased cropping intensity (Bruinsma 2009), the shortfall will have to be met through farmland expansion. In sub-Saharan Africa the expected increase in arable land alone has been estimated at 64 million ha by 2050 (Bruinsma 2009).

Despite the geographic scale of land use conversion in Africa there have been few long-term studies quantifying its impacts on bird communities. Notable exceptions are the raptor road surveys conducted in West Africa (Thiollay 2006a,b,c) and Northern Botswana (Herremans & Herremans-Tonnoeyr 2000, Garbett et al. 2018), which reported substantial declines, both within protected areas (PAs) and farmland, and across a range of feeding guilds. Not surprisingly, raptor encounter rates in both regions were higher in PAs than in surrounding farmland, particularly for eagle and vulture species. These and other effects have been examined in West Africa by Buij et al. (2013), who concluded that while some Palearctic raptors may benefit from cropland expansion, the majority of Afrotropical and insectivorous Palearctic raptors are likely to decline in the face of further agricultural intensification. Declines are likely to be particularly severe among larger raptor species, reflecting the pattern of extinction risk evident among avian scavengers and mammalian predators; larger species being disproportionately threatened and among the first to disappear (Fritz et al. 2009, Di Marco et al. 2014, Dirzo et al. 2014, Ripple et al. 2014, Buechley & Şekercioğlu 2016).

In East Africa, the most extensive areas of land suitable for agricultural conversion, by virtue of being non-forested, unprotected and supporting a low human population density, lie in South Sudan, the Democratic Republic of the Congo (DRC) and Tanzania (Lambin & Meyfroidt 2011). As a step towards evaluating the likely impacts of farmland conversion on raptors, we assessed the abundance, species richness and mean body mass of raptors in relation to land use in neighbouring Uganda. In common with most African countries, Uganda has undergone significant changes in land use over recent decades. Between 1961 and 2005 the country saw little change in the area of protected savanna (Byaruhanga et al. 2001), but a 122% expansion in its agricultural land, mainly at the expense of pastoral land (from Langdale-Brown et al. 1964, Nakakaawa et al. 2011). Since cultivated land thus now accounts for a much higher percentage of land area in Uganda than in most neighbouring countries (World Bank 2017b), Uganda's raptor populations may exemplify the changes likely to arise elsewhere, as a result of further agricultural conversion.

Here, we examine disparities in each species' abundance within protected savanna, pastoral and agricultural land, and test the following predictions. First, based on published findings from southern and West Africa (e.g. Herremans & Herremans-Tonnoeyr 2000, Thiollay 2006c, Buij et al. 2013), we expected the majority of raptor species surveyed to be more abundant in protected savanna than in either farmland type. Second, we expected species richness (the number of species detected over a given distance) to be higher in protected savanna than in pastoral or agricultural land. Third, we predicted that disparities in encounter rates in relation to land use would be more pronounced in the case of large, resident raptors than for smaller, migratory species.

2. Methods

2.1 Data collection

We recorded the number of individuals of each diurnal raptor species seen while driving a series of transects along roads and tracks in Uganda, during January (86% of surveys), February (10%) and March (4%), 2008–2015 (Tables A1, A2). Owl species were likely to be substantially under-recorded, and hence were excluded from the survey. Forty transects, of 9–122 km in length (recorded by odometer), were surveyed at a mean of 33 km hr^{-1} on public roads, and 25 km hr^{-1} in National Parks. Most transects were surveyed once per annum over the eight-year period, and the total distance surveyed was 11,188 km.

The routes surveyed included public roads from Entebbe to Mbarara, Kampala and Murchison Falls NP, and from Soroti towards Moroto (Pomeroy et al. 2019). They also included a network of unpaved tracks within Murchison Falls, Queen Elizabeth, Kidepo Valley and Lake Mburo National Parks, and in Bugungu Wildlife Reserve, a buffer area for Murchison Falls NP (Figure A1).

Observation teams comprised a recorder plus 2–4 observers. In National Parks, and on some tracks outside of the parks, 1–2 'outside' observers watched from the cab roof or an open pick-up, to gain the widest possible view. 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. Observer configuration, as well as road surface and transect length, thus varied in relation to land use type (see Section 2.2.1).

We assigned each transect to one of three forms of land use: protected savanna, pastoral or agricultural land. Protected savanna comprised a mosaic of open and wooded grassland habitats within PAs. Pastoral land was often superficially similar to protected savanna in terms of vegetation structure and species composition, but lay outside of PAs, where large, wild herbivores have been largely or wholly replaced by livestock. Their replacement is likely to have had an adverse effect on the availability of carrion, and a positive effect on the density of woody cover (Hempson et al. 2017), in turn influencing prey resource availability for different raptor guilds. Agricultural land supported a wide range of crops (see Pomeroy et al*.* 2014, 2019), sometimes interspersed with small areas of pastoral land. Conversely, pastoral transects often included small areas of agricultural land. For logistical reasons, we were unable to survey raptors in forest land, which supports some of the species included in the study. For each transect we also estimated 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). Only a small proportion of transects (within PAs) had heavy tree cover or closed canopy, mainly comprising *Acacia* and *Combretum* species.

Whereas some of the birds encountered were identified while the vehicle was moving, in most cases we stopped to confirm the bird's identity, particularly for birds 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. Individuals of each species seen were assigned to one of four distance bands (0–100, 100–200, 200–500, >500 m), depending on their perpendicular distance from the transect. For further details see Pomeroy et al. (2019).

2.2 Data analysis

2.2.1 Encounter rates

On each survey of a given transect, we recorded the number of individuals of each species seen within 500 m on either side of the road. We used generalised linear mixed effects models (GLMMs) in the package glmmTMB (Brooks et al. 2017) in R (version 3.5.1; R Core Team 2018) to estimate species encounter rates in relation to land use, while controlling for the effects of other variables. In each model we entered the number of individuals of a given species recorded during one survey of a given transect as the dependent variable. The following variables were entered as fixed effects: the presence/absence of 'outside' observers (binary), land use category, altitude band (700–900, 950–1100, 1150–1400 m), rainfall band (800–950, 1000–1150, 1200–1400 mm) and tree cover (categorical). We specified transect length (log transformed) as an offset, and used a log-link function. Most transects were surveyed annually, yielding 226 transect-surveys in which the factors listed above were all recorded. To control for the effects of pseudo-replication, we entered 'transect identity' and 'year' as random terms.

Count data for scarce species typically follow a Poisson distribution, but one in which the amount of variation per sampling unit (e.g. per transect-survey) may be higher than expected, or over-dispersed (Linden and Mantyniemi 2011), in which case a negative binomial model may give an improved fit. We therefore fitted models with both a Poisson and a negative binomial distribution, calculating the variance for the latter either as $\varphi\mu$ ('NB1') or as $\mu(1+\mu/k)$ ('NB2') (Linden and Mantyniemi 2011, Brooks et al. 2017). For each of these three models we ran a zero-inflated and a non-zero-inflated version, yielding six model types (Table A3: Model 1). From these we selected the best fitting model for each species, based on Akaike's Information Criterion (AIC), using AICctab in the R package bblme (Bolker 2016). For the model selected, we used the R predict function to derive the number of encounters predicted for each transect-survey. We then calculated the predicted encounter rate for each transect-survey (from the length of the transect), and the mean encounter rate predicted for that species within each land use type.

Differences in encounter rates for a given species in each land use type could reflect variation in both its detectability and its abundance. We therefore compared detection patterns (the proportion of detections made in each distance band) of a given species in different land use types, e.g. contrasting the pattern of detections made in protected savanna with that in pastoral land. We applied Kruskal-Wallis tests to identify, then exclude, species whose detection patterns in one land use type differed significantly from that in another. Where fewer than 20 detections had been made in the two land use types being considered, we pooled observations for the relevant genus, and excluded the species in question if the detection patterns shown by members of its genus differed significantly between the two land use types being considered (Kruskal-Wallis test). Species retained for pair-wise land use comparisons are identified in Table A1.

The difference between the mean encounter rates predicted for a species in two land use types was expressed as a proportion of its encounter rate in protected savanna, in pairwise comparisons between savanna and either pastoral or agricultural land. Similarly, the difference in encounter rates between pastoral and agricultural land was expressed as a proportion of the rates recorded in the former. We used linear mixed-effects models to test whether these differences varied in relation to diet, mass, migratory status or threat status. Median body mass (g, log transformed) was extracted from del Hoyo et al*.* (2017) (Table A1). Diet (six categories: scavenger; generalist; or specialist in fish; invertebrates; fruit; or mammals/ reptiles/ snakes) was extracted from Brown et al*.* (1997) and del Hoyo et al*.* (2017). Migratory status (Palearctic migrant; Afrotropical migrant; resident) was based on Buij et al*.* (2013), and global threat status (threatened/near-threatened vs least concern) was obtained from BirdLife International (2018).

For each pair of land use types we entered the proportional difference in the species' encounter rate as the dependent variable. Since sample sizes were small, we limited each model to one fixed factor (median body mass, diet, migratory status or threat status). Because some genera (e.g. *Gyps*) were represented by multiple species, we included 'Genus' as a random effect (Table A3: Model 2). We selected the model with the lowest AIC score for each pairwise comparison. Probability estimates for the effects of each explanatory variable were calculated using the Kenward-Roger approximation (Halekoh & Højsgaard 2014).

2.2.2 Body mass

To further compare body mass differences in relation to land use, we calculated the total mass of all individuals seen on each survey of a given transect (using mass values given in Table A1), and divided this by the number of individuals, to give the mean mass of individuals seen per transect-survey. We assigned these values to 250 g intervals, to examine their frequency distribution in relation to land use. We then used a linear mixed-effects model to generate predicted values, specifying a natural log transformation of the mean mass as the dependent variable, and the following fixed factors: transect length (km, log transformed), the presence/absence of 'outside' observers (binary), land use category, tree cover, mean altitude band (m) and mean annual rainfall band (mm) (categorical) (Table A3: Model 3). 'Transect identity' and 'year' were entered as random terms, to control for the effects of pseudo-replication. The model yielded fitted, average body mass values for 220 transect surveys on which at least one raptor species had been recorded:

131 in protected savanna, 47 in pastoral land and 42 in agricultural land. We calculated the mean (±SE) predicted mass value for each land use type.

2.2.3 Species richness

To investigate the relationship between species richness and land use we plotted the cumulative number of species encountered during successive transect-surveys within each land use type, against the cumulative distance travelled. We excluded transect-surveys with missing data for tree cover or other factors. This approach shows the pattern of change in the number of 'new' species encountered over the (cumulative) distance surveyed, which totalled 5,031 km (protected savanna), 2,315 km (pastoral land) and 2,635 km (agricultural land). Since the pattern observed may have been influenced by factors other than land use, and involved the repeated sampling of transects, we further examined the relationship between species richness and land use using a linear mixed-effects model. In the model, we entered the number of species encountered on each transect-survey as the dependent variable, and the following variables as fixed effects: transect length (km, log transformed), the presence/absence of 'outside' observers (binary), land use, altitude, mean annual rainfall and tree cover (categorical) (Table A3: Model 4). Since we expected the number of species encountered to vary both in relation to land use and transect length, we included an interaction between these two variables, which improved the model fit (ΔAIC > 2). 'Transect identity' and 'year' were entered as random terms, to control for repeated sampling of the same transects and years. All (53) raptor species seen were included in this analysis (Table A4). To calculate the number of species predicted by the model we specified constant (modal) values for: 'outside' observers (present), altitude band (950–1100 m), rainfall band (1000–1150 mm) and tree cover ('light').

3. Results

3.1 Encounter rates in relation to land use

Over the eight survey years, 6,708 individuals of 53 raptor species were detected. Thirty-three species were seen in sufficient numbers to enable us to model encounter rates in relation to land use and other factors (Table A4). Of 23 species whose detection patterns (in relation to distance from the transect) were comparable in protected savanna and pastoral land (Table A1), 15 were less abundant in the latter. The median difference in the rate at which they were encountered was -41% (quartiles +40% to -80%; *n* = 23 species; Wilcoxon matched-pairs test: P = 0.088). A much greater disparity was evident between protected savanna and agricultural land; 19 out of 24 species were less abundant in the latter, and the median difference in their encounter rates was -90% (quartiles -31% to -100%; *n* = 24; Wilcoxon matched-pairs test: P < 0.003). Encounter rate differences between pastoral and agricultural land were also significant; 10 out of 14 species were less abundant in the latter, with a median difference of -52% (quartiles -2% to -83%; *n* = 14; Wilcoxon matched-pairs test: P = 0.025) (Fig. 1).

When the same comparisons were made with unmodelled data, median differences in encounter rates were broadly similar to those obtained from modelled data: a median of -48% between protected savanna and pastoral land, (quartiles +16% to -74%; *n* = 23 species; Wilcoxon matched-pairs test: P = 0.041); -88% between protected savanna and agricultural land (quartiles -45% to -98%; *n* = 24; Wilcoxon matched-pairs test: P < 0.001); and -41% between pastoral and agricultural land (quartiles -12% to -70%; *n* = 14; Wilcoxon matched-pairs test: P = 0.013) (Fig. 1).

In separate models, encounter rate differences for the same species in savanna and pastoral land were correlated with body mass and threat status. Heavier species and those of conservation concern showed a greater drop in abundance on pastoral land than lighter species and those of least concern. The first of these models (incorporating body mass) provided the better fit (Table 1,

Fig. 2). Similarly, encounter rate differences in savanna and agricultural land were significantly correlated with diet, body mass and threat status, with the former model (incorporating diet) providing the best fit (Table 1, Fig. 2) . Species specialising in predating small mammals or reptiles were significantly more abundant in agricultural land than in savanna, compared with generalist species (Table 1). Body mass, diet, migratory- and threat status had no significant influence on encounter rate disparities between pastoral and agricultural land.

3.2 Body mass in relation to land use

The mean body mass of all raptor individuals encountered during transect-surveys varied more widely in protected savanna than in pastoral or agricultural land, the two farmland types supporting a much more homogenous raptor community, with regards to size (Fig. 3). Predicted average body mass values for birds seen from transects through pastoral land (mean = 995±25.6 g(SE); n = 47 transect-surveys) and agricultural land (mean = 856±18.1 g; n = 42) were 43% and 51% lower than those seen in protected savanna (mean = 1,740±63.0 g; n = 131). Since vultures are heavier than most other raptors, and were more abundant in protected savanna, we re-examined the relationship after excluding vulture species from the model. The pattern observed was broadly similar, however, body mass averaging 933 g (±27.6 g; n = 47 transect-surveys) in pastoral, 824 g (±16.6 g; n = 42) in agricultural land and 1,332 g (±37.0 g (SE); n = 130) in protected savanna. Results from unmodelled data were similar with regards to body mass variation in relation to land use (Table A5).

Disparities in encounter rates between protected savanna and both pastoral and agricultural land were thus linked to body mass. To test this further, we examined encounter rate differences for small species (<1 kg) and large species (≥1 kg) within the three pairwise land use comparisons. Small species were more abundant (median difference: +44%; n = 10) and large species significantly less abundant in pastoral land than in protected savanna (median: -76%; n = 13; Kolmogorov-Smirnov test: D = 0.615; P < 0.03). Both size classes were less abundant in agricultural land than in protected savanna, but to differing degrees. The median disparity for small species (-30%; n = 12) was less pronounced than that for large species (-97%; n =12; Kolmogorov-Smirnov test: D = 0.667; P < 0.01). Body mass effects on encounter rate differences in pastoral and agricultural land were not significant (small species: -63%; large species: -40%).

In a linear mixed effects model restricted to large (≥1 kg) species, the disparity between encounter rates in protected savanna and pastoral land increased significantly in relation to body mass (disparity = -0.547*log(mass) + 3.712; n = 13 species; P<0.02). This indicates that the disparity widened by a further 18 percentage points for each 1 kg increase in body mass.

3.3 Threat status

Nine of the species examined were of global conservation concern, being listed as Critically Endangered (four species), Endangered (two), Vulnerable (one) or near-threatened (two species) (BirdLife International 2018). Species of global conservation concern were heavier on average (4,075 g; n = 9) than those of least concern (976 g; n = 21; Kolmogorov-Smirnov test: D = 0.794; P < 0.001). Since heavier species were significantly less abundant in farmland than in protected savanna, similar disparities were evident with respect to threat status. Species of conservation concern showed a significantly greater drop in encounter rates between protected savanna and pastoral land (median difference: -87%; n = 5), than those of least concern (median difference: -5%; n = 18 species; Kolmogorov-Smirnov test: D = 0.689; P = 0.049). Similarly, encounter rate differences between protected savanna and agricultural land were much greater for species of conservation concern (median difference: -100%; n = 8), than for those of least concern (median difference: -42%; n = 16 species; Kolmogorov-Smirnov test: D = 0.750; P = 0.005). Only one species of conservation concern was likely to have benefitted from farmland conversion; Hooded Vultures were recorded 58% more frequently in agricultural land than in pastoral land. Encounter rates for this species in pastoral and agricultural land were both higher than in protected savanna, however pairwise comparisons were confounded by differences in the species' detectability in the latter.

3.4 Species richness

We recorded 48, 42 and 31 diurnal raptor species in protected savanna, pastoral and agricultural land, respectively, partly reflecting differences in the cumulative distances surveyed in these land use types (Fig. 4A). Over the first 100 km surveyed, the number of species encountered had already begun to diverge, being 13.6 species (by interpolation) in savanna, 9.4 in pastoral land and 6.1 in agricultural land. By 2,000 km, disparities in species numbers were proportionally less pronounced: 45 and 38 species in savanna and pastoral land, 27 species in agricultural land. In protected savanna, species number levelled off after a cumulative survey distance of c. 3,500 km, but showed no indication of doing so within the (shorter) distances surveyed in pastoral and agricultural land (Fig. 4A).

A linear mixed-effects model was used to control for the effects of survey- and habitat variables, and for the repeated sampling of transects (Table A3: Model 4). This confirmed that the number of species encountered on each transect varied in relation to land use and length, yielding predicted totals of 13.2 species in protected savanna, 10.6 in pastoral land and 6.7 in agricultural land, on transects of 100 km (Fig. 4B).

4. Discussion

We show that raptor encounter rates were 41% lower in pastoral land and 90% lower in agricultural land than in protected savanna. In addition, encounter rates in agricultural land were 52% lower than in pastoral land, despite the latter being already depleted, mainly through the loss of large, scavenging species. This disparity is of particular relevance, since the 64 million ha expansion in agricultural land required to meet growing food demands by 2050 (Bruinsma 2009) is likely to be achieved mainly through the conversion of land already supporting pastoralism to some degree (Lambin & Meyfroidt 2011). Our findings suggest that such areas are likely to experience a median decline in raptor abundance of the order of 50% if converted to agriculture. In areas still largely comprising intact savanna, raptor abundance is likely to decline by a median of c. 90%, or higher in the case of large eagles and vultures.

Similar abundance patterns have been observed elsewhere in Africa. In West and southern Africa the relationship between raptor abundance and land use is influenced both by body size and migratory status; large, resident species are more sensitive to land use change than small Afrotropical or Palearctic migrants (Herremans & Herremans-Tonnoeyr 2000, Thiollay 2006c, Anadón et al. 2010, Buij et al. 2013). It has been suggested that non-breeding migrants are better able to tolerate the disturbance associated with farming activities than resident species, which tend to remain on their territories year-round, and hence avoid areas subject to disturbance when they are breeding. Furthermore, larger species are more likely to suffer from hunting pressure, through direct persecution (for bushmeat) and through the loss of their prey base (Thiollay 2006c) or of large trees in which to nest. Since large species tend to require larger territories, they are also less likely to persist in small fragments of suitable habitat. Our results were broadly consistent with these findings, in showing a link between abundance disparities, diet and body mass.

A more direct analysis of the effects of land conversion has been made in the Serengeti ecosystem, Tanzania, where Sinclair et al. (2002) compared bird species abundances in protected savanna with those in adjacent areas converted from savanna to cultivated land in the 1950s. Some 50 years later, insectivores and granivores/frugivores were 77% and 60% less common in the farmland plot than in the adjacent protected savanna. Furthermore, while the study recorded 104 individuals of 15 raptor species in protected savanna, only four individuals of three raptor species were recorded in the neighbouring farmland.

These deficits are broadly similar to those reported here, and consistent with findings reported by Child et al. (2009) in South Africa, in suggesting that African raptor species are particularly sensitive to farmland conversion. Child et al. (2009) showed that among nine functional bird groups examined, scavengers and raptors most often suffered a decrease in richness within agriculturally dominated landscapes.

An underlying assumption of the current study is that raptor populations within Uganda's four savanna national parks represent a baseline from which farmland communities have departed. Survey transects within these PAs overlapped extensively with those in farmland, in terms of altitude, and received a similar level of rainfall to those in pastoral land (1,019 vs 950 mm). Within agricultural areas, however, mean annual rainfall was slightly higher (1,178 mm), and the land perhaps more likely to have once supported a mosaic of savanna and forest (Langdale-Brown et al. 1964). In addition, the public roads surveyed lay mainly in the southern half of the country (Fig. 1A), and hence might not have accurately reflected raptor abundances further north, where there are larger, continuous expanses of pastoral land.

Disparities between encounter rates in savanna and farmland could have been magnified by the greater disturbance effects associated with public roads in farmland areas. Species deterred by traffic disturbance, housing and the higher human population densities associated with public roads may have been more abundant at greater distances from these roads. That is, our approach may have under-estimated species abundances in farmland, where road-related disturbance levels are likely to have been higher than in protected savanna, where traffic volumes and human numbers are low.

Our paired land use comparisons were restricted to species whose detectability did not differ significantly between the two land use types under comparison, and were made using values predicted from GLMMs, which controlled for the effects of potentially confounding variables, and for repeated sampling of transects. For heavier species and those of conservation concern, encounter-rate disparities between protected savanna and each farmland type were significantly more pronounced than among lighter species and those of least concern. Furthermore, surveys within protected savanna yielded more raptor species (over a given distance; Fig. 4), showing a wider variation in body mass (Fig. 3). The much greater uniformity in body mass evident in pastoral and agricultural land only partly reflected the near-absence of vulture species from these landscapes.

4.1 Conservation management

While African farming systems typically involve simpler, non-mechanised methods and fewer chemical treatments than in Europe and North America, their impacts on bird species adapted to savanna or wooded habitats can be profound (Sinclair et al. 2002, Child et al. 2009, Hulme et al. 2013, Renwick et al. 2014). Uganda is unusual within Africa, in that much of its land has already been converted to crop production, the impacts of which have recently become the focus of agri-environmental research (Hulme et al. 2013, Renwick et al. 2014). As in western countries, mitigation efforts are likely to follow either of two contrasting approaches: land sharing, in which low-yield, 'wildlife-friendly' farming is promoted, at the expense of semi-natural land; and land sparing, in which farmers strive for higher yields, while leaving aside larger fragments of semi-natural land (Hulme et al. 2013). Theoretically, land sparing should ensure that more of the original savanna is retained in perpetuity, affording a refuge for species poorly adapted to synanthropic conditions, and a benchmark against which to gauge the effects of human interventions elsewhere (Sinclair et al. 2002).

In this study, raptor abundance and species richness in agricultural land were such that typical land sharing measures are unlikely to prove effective in retaining or re-establishing viable populations, except in the case of synanthropic species. Thus, on land deemed suitable for farmland conversion, including large tracts of South Sudan, DRC, Tanzania and Mozambique (Lambin & Meyfroidt 2011), conservation efforts should focus instead on identifying and safeguarding the largest remaining expanses of unprotected, relatively intact savanna. Here, and within existing protected areas, efforts should focus on retaining intact raptor communities. In Uganda, such efforts would include the following. First, exclude or minimise anthropogenic disturbance of protected areas (e.g. pollution from an ongoing oil exploration programme in and around Murchison Falls NP). Second, allow pastoral areas bordering PAs to revert to savanna, particularly where they might form a bridge or corridor between PAs supporting globally threatened resident species. These might take the form of community-run conservancies or private game reserves, which have proved successful in boosting game populations elsewhere in East Africa and in southern Africa. Third, factors contributing to the observed disparities in raptor abundance among the three land use types examined here should be identified and addressed. Together, such initiatives could help to counteract the biological impoverishment associated with farmland expansion, and ensure the survival of intact raptor communities.

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6. References

Anadón, J.D., Sánchez-Zapata, J.A., Carrete, M., Donázar, J.A., Hiraldo, F., 2010. Large-scale human effects on an arid African raptor community. Animal Conservation 13, 495–504.

Balmford, A., Green, R., Phalan, B., 2012. What conservationists need to know about farming. Proc. R. Soc. B 279, 2714–2724.

Bamford, A.J., Monadjem, A., Hardy, I.C.W., 2009. Nesting habitat preference of the African white-backed vulture *Gyps africanus* and the effects of anthropogenic disturbance. Ibis 151, 51–62.

BirdLife International, 2018. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 31/01/2018

Bolker, B., R Development Core Team, 2016. bbmle: tools for general maximum likelihood estimation. R package version 1.0.18. https://CRAN.R-project.org/package=bbmle.

Borello, W.D., Borello, R.M., 2002. The breeding status and colony dynamics of Cape Vulture *Gyps coprotheres* in Botswana. Bird Conserv. Int. 12, 79-97.

Brink, A.B., Eva, H.D., 2009. Monitoring 25 years of land cover change dynamics in Africa: a sample based remote sensing approach. Applied Geography 29, 501–512

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated Generalized Linear Mixed Modeling. The R Journal 9(2): 378–400.

https://journal.r-project.org/archive/2017/RJ-2017-066/index.html.

Brown, L.H., Urban, E.K., Newman, K., 1997. The Birds of Africa. Volume I. Academic Press: London, UK

Bruinsma, J., 2009. The Resource Outlook to 2050: By How Much Do Land, Water and Crop Yields Need to Increase by 2050? Expert Meeting on How to Feed the World in 2050. FAO, Rome

Buechley, E.R., Şekercioğlu, C.H., 2016. The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biol. Conserv. 198, 220–228

Buij, R., Croes, B.M., Gort, G., Komdeur, J., 2013. The role of breeding range, diet, mobility and body size in associations of raptor communities and land-use in a West African savanna. Biol. Conserv. 166, 231–246

Buij, R., Nikolaus, G., Whytock, R., Ingram, D., Ogada, D., 2016. Trade of threatened vultures and other raptors for fetish and bushmeat in West and Central Africa. Oryx, 50(4), 606-616. doi:10.1017/S0030605315000514

Byaruhanga, A., Kasoma, P., Pomeroy, D., 2001. Important Bird Areas in Uganda. East Africa Natural History Society, Kampala.

Canning, D., Raja, S., Yazbeck, A.S., 2015. Africa's Demographic Transition: Dividend or Disaster? Overview booklet. Africa Development Forum series. World Bank: Washington, DC. License: Creative Commons Attribution CC BY 3.0 IGO

Carrete, M., Tella, J.L., Blanco, G., Bertellotti, M., 2009. Effects of habitat degradation on the abundance, richness and diversity of raptors across Neotropical biomes. Biol. Conserv. 142, 2002–2011

Child, M.F., Cumming, G.S., Amano, T., 2009. Assessing the broad-scale impact of agriculturally transformed and protected area landscapes on avian taxonomic and functional richness. Biol. Conserv. 142, 2593–2601

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), 2017. Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/ in June 2017.

Di Marco, M., Boitani, L., Mallon, D., Hoffmann, M., Iacucci, A., Meijaard, E., Visconti, P., Schipper, J., Rondinini, C., 2014. A Retrospective Evaluation of the Global Decline of Carnivores and Ungulates. Conservation Biology 28(4): 1109–1118.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G. Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401-406. DOI: 10.1126/science Birds, Body Size and the Threat of Extinction

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T, Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011., Trophic Downgrading of Planet Earth. Science 333 (6040), 301-306 DOI: 10.1126/science.1205106

Fischer, G., Shah, M., 2010., Farmland Investments and Food Security, Statistical Annex. Report Prepared under World-Bank-IIASA Contract, (Intl Inst Appl Syst Anal, Laxenburg, Austria).

Foley, J., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574.

Fritz, S.A., Bininda-Emonds, O.R.P., Purvis, A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* 12: 538–549.

Garbett, R., Herremans, M., Maude, G., Reading, R.P., Amar, A., 2018., Raptor population trends in northern Botswana: A re-survey of road transects after 20 years. Biological Conservation 224: 87–99.

Government of Uganda, 1967. Atlas of Uganda 2nd edition. Department of Lands and Surveys, Entebbe, Uganda.

Green, R.E. Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the Fate of Wild Nature. Science 307, 550-555

Halekoh, U., Højsgaard, S., 2014. A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package pbkrtest. Journal of Statistical Software 59(9), 1–32

Hempson, G.P., Archibald, S, Bond, W.J. 2017. The consequences of replacing wildlife with livestock in Africa. Scientific Reports 7: 17196 DOI:10.1038/s41598-017-17348-4

Herremans, M, Herremans-Tonnoeyr, D., 2000. Land use and the conservation status of raptors in Botswana. Biol. Conserv. 94, 31–41

Hulme, M.F., Vickery, J.A, Green, R.E, Phalan, B., Chamberlain, D.E., Pomeroy, D.E., Nalwanga, D., Mushabe, D., Katebaka, R., Bolwig, S., Atkinson, P.W. 2013 Conserving the Birds of Uganda's Banana-Coffee Arc: Land Sparing and Land Sharing Compared. PLoS ONE 8(2): e54597. doi:10.1371/journal.pone.0054597

Jenkins, A.R., Smallie, J.J., Diamond, M., 2010. Avian collisions with power lines: a global review of causes and mitigation with a South African perspective. Bird Conserv. Int. 20, 263-278

Jung, M., Hill, S.L.L., Platts, P.J., Marchant, R., Siebert, S., Fournier, A., Munyekenye, F.B., Purvis, A., Burgess, N.D., Newbold, T., 2017, Local factors mediate the response of biodiversity to land use on two African mountains. Anim. Conserv, 20, 370–381. doi:10.1111/acv.12327

Kibuule, M., Pomeroy, D., 2015. Avian mortality rates on a power line near Kampala, Uganda. Scopus 34, 52–55

Lambin, E.F., Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. PNAS 108(9): 3465–3472

Langdale-Brown, I., Osmaston, H.A., Wilson, J.G., 1964. The Vegetation of Uganda and its bearing on land-use. Government of Uganda, Entebbe, Uganda

Linden, A., Mantyniemi, S., 2011. Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 92(7), 1414–1421.

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline – an appraisal of the human health and other benefits of vultures in India. Ecological Economics 67, 194–204.

McKean, S., Mander, M., Diederichs, N., Ntuli, L., Mavundla, K., Williams, V., Wakelin, J., 2013. The impact of traditional use on vultures in South Africa. Vulture News, 65, 15–36

Monadjem, A., Garcelon, D.K., 2005. Nesting distribution of vultures in relation to land use in Swaziland. Biodiversity and Conservation 14, 2079–2093

Monadjem, A., Kane, A., Botha, A., Kelly, C., Murn, C., 2018. Spatially explicit poisoning risk affects survival rates of an obligate scavenger. Scientific Reports 8: 4364 DOI:10.1038/s41598-018-22632-y

Nakakaawa, C.A., Vedeld, P.O., Aune, J.B., 2011. Spatial and temporal land use and carbon stock changes in Uganda: implications for a future REDD strategy. Mitig Adapt Strateg Glob Change 16, 25–62

Newbold, T., Boakes, E.H., Hill, S.L.L., Harfoot, M.B.J., Collen, B., 2017. The present and future effects of land use on ecological assemblages in tropical grasslands and savannas in Africa. Oikos doi: 10.1111/oik.04338

Ogada, D.L. 2014. The power of poison: pesticide poisoning of Africa's wildlife. Annals of the New York Academy of Sciences, 1322, 1–20.

Ogada, D.L., Torchin, M.E., Kinnaird, M.F. & Ezenwa, V.O., 2012 Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. Conservation Biology, 26: 453–460.

Ogada, D., Shaw, P., Beyers, R.L., Buij, R., Murn, C., Thiollay, J.M., Beale, C.M., Holdo, R.M., Pomeroy, D., Baker, N., Krüger, S.C., Botha, A., Virani, M.Z., Monadjem, A., Sinclair, A.R.E., 2015. Another Continental Vulture Crisis: Africa's Vultures Collapsing toward Extinction. Conservation Letters 9, 89-97. DOI: 10.1111/conl.12182

Ogada, D., Botha, A., Shaw, P., 2016. Ivory poachers and poison; drivers of Africa's declining vulture populations. Oryx 50(4), 593–596 DOI: https://doi.org/10.1017/S0030605315001209

Otieno, P.O., Lalah, J.O., Virani, M., Jondiko, I.O., Schramm, K.W., 2010. Carbofuran and its toxic metabolites provide forensic evidence for furadan exposure in vultures (*Gyps africanus*) in Kenya. Bulletin of Environmental Contamination and Toxicology, 84, 536–544.

Papworth, S.K., Rist, J., Coad, L., Milner-Gulland, E.J., 2009. Evidence for shifting baseline syndrome in conservation. Conservation Letters 2, 93–100.

Pomeroy, D., Shaw, P., Opige, M., Kaphu, G., Ogada, D.I., Virani, M.Z. 2014. Vulture populations in Uganda: using road survey data to measure both densities and encounter rates within protected and unprotected areas. Bird Conservation International 25(4): 399-414. DOI: 10.1017/S095927091400029X

Pomeroy, D., Kibuule, M., Nalwanga, D., Kaphu, G., Shaw, P., 2019. Densities and population sizes of raptors in Uganda's conservation areas. Ostrich. DOI: 10.2989/00306525.2018.1508083

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Renwick, A.R., Vickery, J.A., Potts, S.G., Bolwig, S., Nalwangae, D., Pomeroy, D.E., Mushabee, D., Atkinsona, P.W., 2014. Achieving production and conservation simultaneously in tropical agricultural landscapes. Agriculture, Ecosystems and Environment 192, 130–134.

Ripple, W.J. et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. (doi:10.1126/science.1241484)

Rushworth, I., Krüger, S. 2014 Wind farms threaten southern Africa's cliff-nesting vultures. Ostrich 85(1): 13-23. DOI: 10.2989/00306525.2014.913211

Sánchez-Zapata, J.A., Carrete, M., Gravilov, A., Sklyarenko, S., Ceballos, O., Donázar, J.A., Hiraldo, F., 2003. Land use changes and raptor conservation in steppe habitats of Eastern Kazakhstan. Biol. Conserv. 111, 71–77.

Sinclair, A.R.E., Mduma, S.A.R., Arcese, P., 2002. Protected areas as biodiversity benchmarks for human impact: agriculture and the Serengeti avifauna. Proc. Roy. Soc. B 269, 2401–2405.

Sudarshan, M.K., Madhusudana, S.N., Mahendra, B.J., Rao, N.S.N, Ashwath Narayana, D.H., Abdul Rahman, S., Meslin, F.-X., Lobo, D., Ravikumar, K., Gangaboraiah, 2007. Assessing the burden of human rabies in India: results of a national multi-center epidemiological survey. International Journal of Infectious Disease 11: 29–35.

Thiollay, J.M., 2006a. Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment. Bird Conservation International, 16, 353–365.

Thiollay, J.M., 2006b. The decline of raptors in West Africa: long-term assessment and the role of protected areas. Ibis 148, 240-254.

Thiollay, J.M., 2006c. Large bird declines with increasing human pressure in savanna woodland (Burkina Faso). Biodiversity & Conservation 15, 2085–2108.

Virani, M.Z., Kendall, C., Njoroge, P., Thomsett, S., 2011. Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. Biol. Conserv., 144, 746-752.

Williams, V.L., Cunningham, A.B., Kemp, A.C., Bruyns, R.K., 2014 Risks to Birds Traded for African Traditional Medicine: A Quantitative Assessment. PLoS ONE 9(8): e105397. doi:10.1371/journal.pone.0105397

World Bank, 2017a. https://data.worldbank.org/indicator/SP.POP.GROW?name_desc=false Downloaded 05/09/2017

World Bank, 2017b. https://data.worldbank.org/region/sub-saharan-africa. Downloaded 18/12/2017

Table 1
Variables associated with differences in raptor encounter rates within pairs of land use types. A negative effect, e.g. with respect to body mass, for ‘Savanna vs Pastoral’, indicates that the mean body mass of species detected on pastoral transects was lower than on protected savanna transects. Since sample sizes were low, potential explanatory variables (body mass, migratory status, threat status and diet) were examined in separate models. Parameters from models showing statistically significant effects are shown below, the best fitting model being that with the lowest AIC value (ΔAIC = 0.00). Differences in species encounter rates on pastoral vs agricultural transects showed no significant relationship with the four variables examined

Model	*n* species	ΔAIC	Term	LRT	P	Condition	Effect	SE	P
Savanna vs Pastoral:	23	0.00	Intercept				4.054	0.936	<0.001
full dataset			Log body mass	15.466	<0.001		-0.591	0.132	<0.001
	23	8.15	Intercept				0.092	0.195	0.643
			Threat status	4.527	<0.040	Cons. concern[1]	-0.894	0.418	0.044
Savanna vs Pastoral:	21	0.00	Intercept				4.197	1.109	0.002
excluding vultures[2]			Log body mass	12.036	<0.001		-0.614	0.160	0.003
Savanna vs Agricultural:	24	0.00	Intercept				-0.528	0.333	0.136
full dataset			Diet	11.922	0.018	Generalist	-	-	-
						Fish	0.442	0.953	0.650
						Invertebrates	-0.462	0.714	0.528
						Reptiles/ mammals	1.358	0.518	0.021
						Carrion	-0.458	0.609	0.465
	24	2.68	Intercept				3.358	1.098	0.007
			Log body mass	8.544	<0.004		-0.525	0.155	0.003
	24	5.70	Intercept				-0.142	0.248	0.579
			Threat status	4.197	<0.050	Cons. concern	-0.493	0.241	0.070
Savanna vs Agricultural:	20	0.00	Intercept				-0.528	0.362	0.171
excluding vultures			Diet	8.583	0.035	Generalist	-	-	-
						Fish	-0.442	1.036	0.678
						Invertebrates	-0.462	0.776	0.563
						Reptiles/ mammals	1.358	0.563	0.034
	20	2.88	Intercept				3.952	1.429	0.014
			Log body mass	6.442	<0.020		-0.620	0.212	0.010

[1] Conservation concern: species classed as globally threatened or near-threatened
[2] Excluding scavenging vulture species

Figure legends

Fig. 1

Differences in linear encounter rates (individuals 100 km^{-1} of transect) in relation to land use. Each column shows the median percentage difference in encounter rates for raptor species present in two land use types. Filled columns show estimates derived from GLMMs; unfilled columns show estimates from unmodelled data. Thus, modelled encounter rates for 23 species were 41% lower in pastoral land than in protected savanna. Error bars show upper and lower quartiles. Figures above the columns show the number of species included in each pair-wise comparison. Species showing significant differences in their detection patterns within the land use types in question were excluded from the comparison (see text)

Fig. 2

Pair-wise comparisons between the number of individuals encountered 100 km^{-1} in protected savanna versus: (A) pastoral land and (B) agricultural land, in relation to body mass. Each point represents one species. A negative percentage value when comparing protected savanna with e.g., pastoral land, indicates that correspondingly fewer individuals were seen in the latter. Globally threatened or near-threatened species (black symbols) tended to be heavier and showed a greater drop in abundance than most species of least concern (grey symbols). Diamond symbols indicate scavenging vultures; circles indicate other raptor species

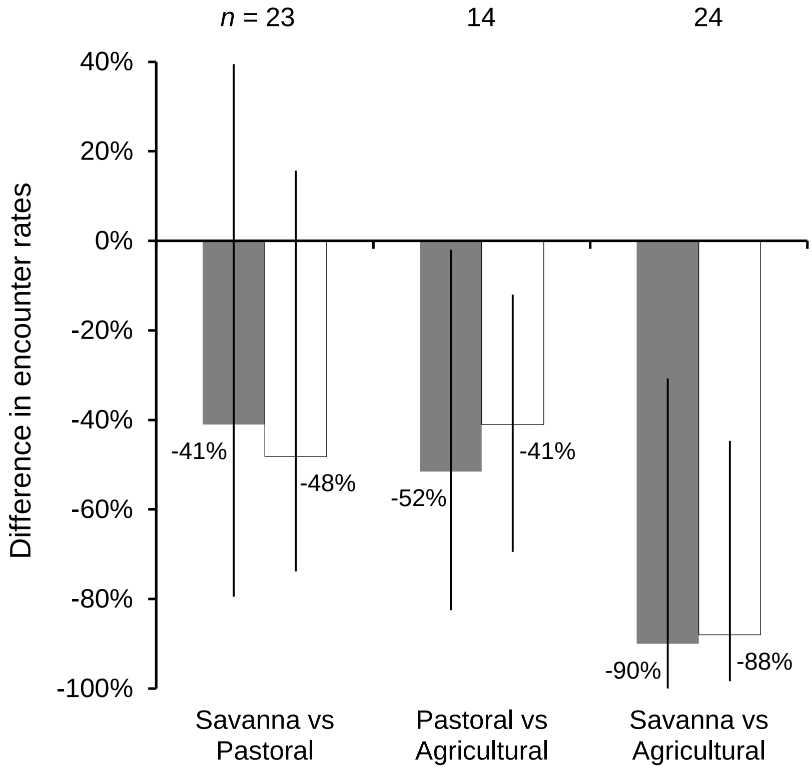
Fig. 3

Variation in the mean body mass of raptor species encountered during transect-surveys in: A. protected savanna (n = 131 transect-surveys); B. pastoral land (n = 47); and C. agricultural land (n = 42). Each column represents the number of transect-surveys on which the mean body mass recorded fell within a given 250 g interval. Since the number of transect-surveys varied between land use types, frequencies have been scaled to a value of 1.0. The mean body mass of raptors encountered within protected savanna was higher and much more variable than in pastoral or agricultural land, illustrating the greater size uniformity within farmland habitats

Fig. 4

The number of raptor species encountered in relation to distance surveyed within protected savanna (solid line), pastoral (dashed line) and agricultural land (dotted line). A). The cumulative number of species encountered in relation to the cumulative distance travelled during successive transect-surveys. B). The relationship between transect length and the number of raptor species encountered. Points indicate the mean number of species predicted from multiple surveys of transects within protected savanna (●), pastoral (●) and agricultural land (○). Error bars show ±1 SE. Fitted lines are the product of a linear mixed effects model controlling for the effects of other variables, and for repeated sampling of transects (see text)

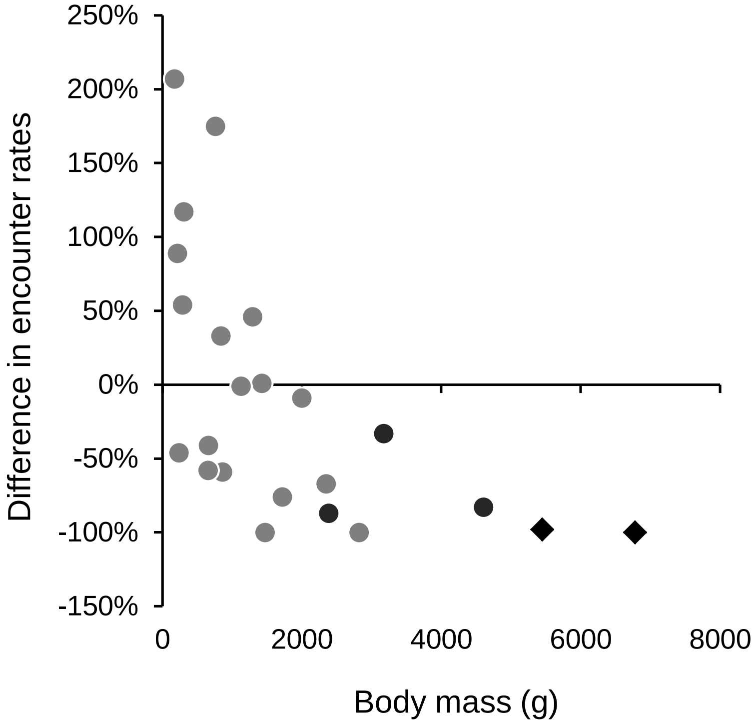
Fig. 1



n = 23
14
24
40%
20%
0%
-20%
-40%
-60%
-80%
-100%
Difference in encounter rates
-41%
-48%
-52%
-41%
-90%
-88%
Savanna vs Pastoral
Pastoral vs Agricultural
Savanna vs Agricultural

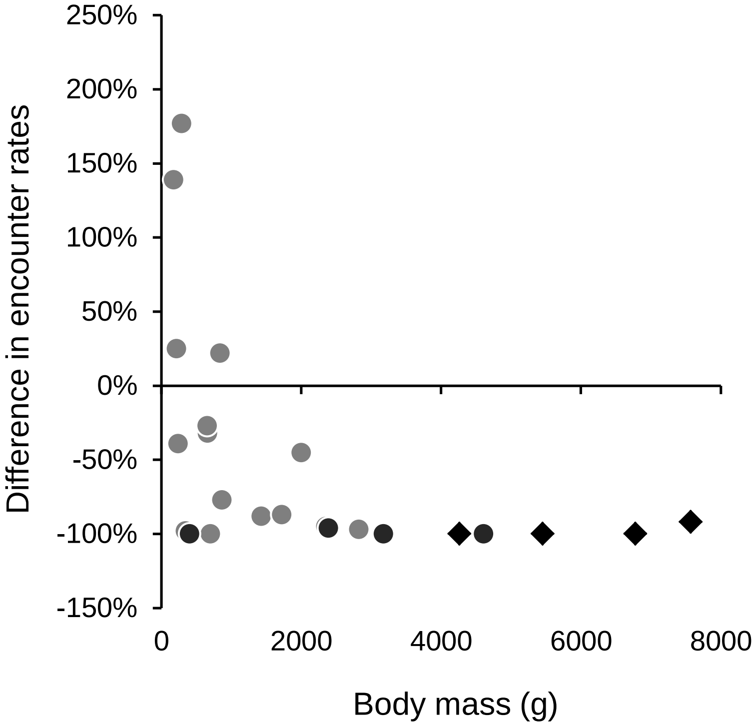
Fig. 2

A



Difference in encounter rates
250%
200%
150%
100%
50%
0%
-50%
-100%
-150%
0
2000
4000
6000
8000
Body mass (g)

B



Difference in encounter rates
250%
200%
150%
100%
50%
0%
-50%
-100%
-150%
0
2000
4000
6000
8000
Body mass (g)

Fig. 3

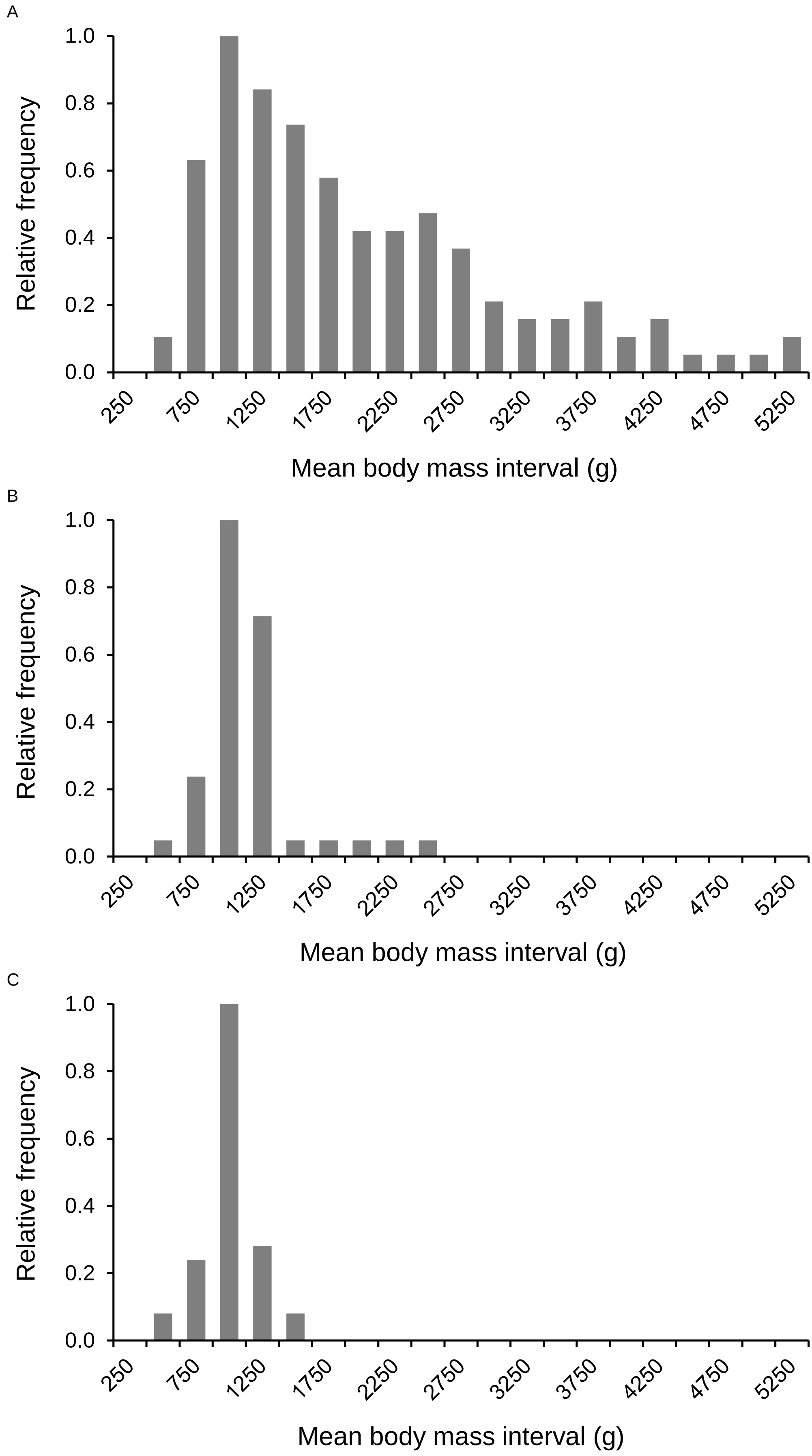
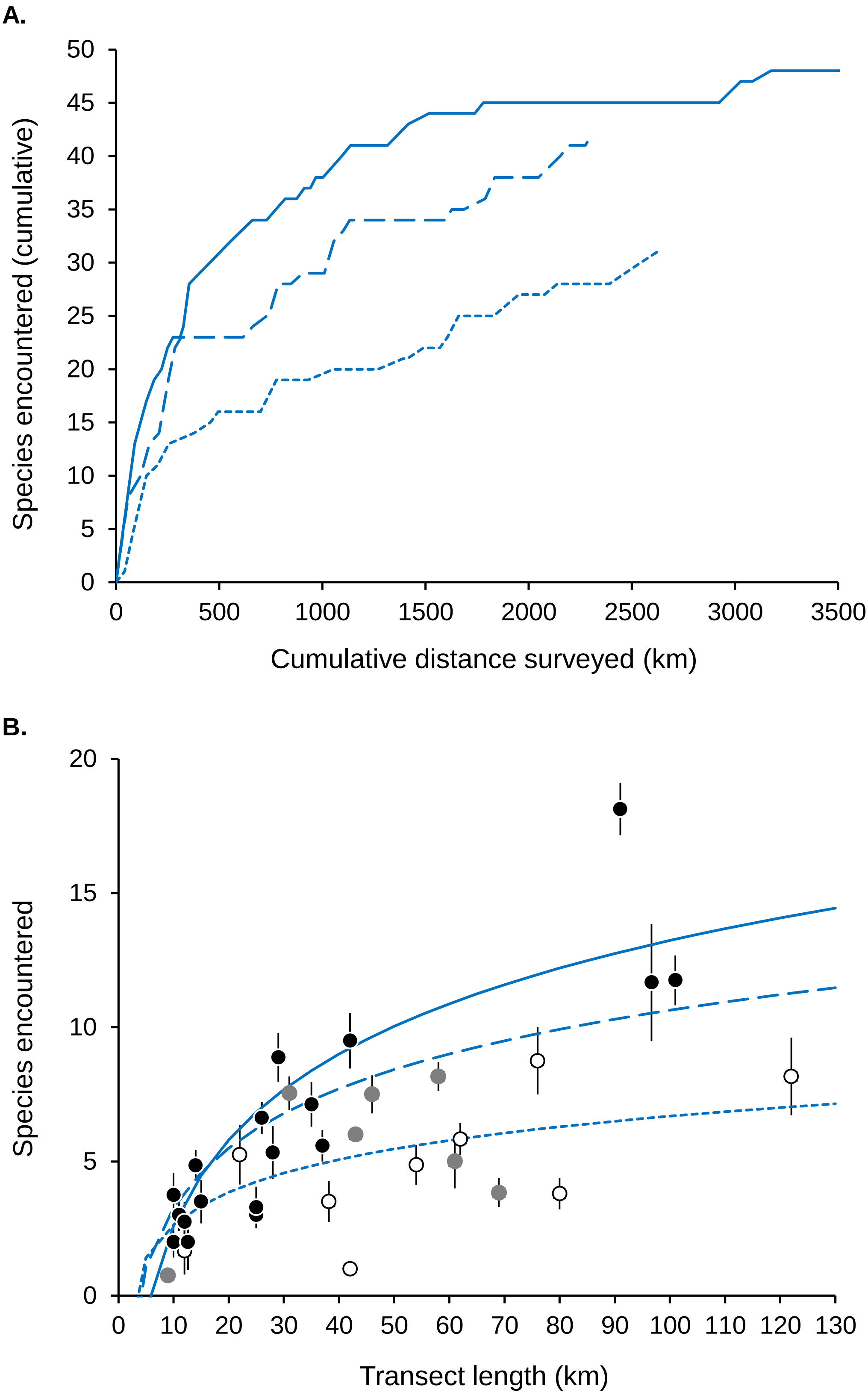

A
Relative frequency
1.0
0.8
0.6
0.4
0.2
0.0
250
750
1250
1750
2250
2750
3250
3750
4250
4750
5250
Mean body mass interval (g)
B
Relative frequency
1.0
0.8
0.6
0.4
0.2
0.0
250
750
1250
1750
2250
2750
3250
3750
4250
4750
5250
Mean body mass interval (g)
C
Relative frequency
1.0
0.8
0.6
0.4
0.2
0.0
250
750
1250
1750
2250
2750
3250
3750
4250
4750
5250
Mean body mass interval (g)

Fig. 4


A.
Species encountered (cumulative)
0
5
10
15
20
25
30
35
40
45
50
0
500
1000
1500
2000
2500
3000
3500
Cumulative distance surveyed (km)
B.
Species encountered
0
5
10
15
20
0
10
20
30
40
50
60
70
80
90
100
110
120
130
Transect length (km)

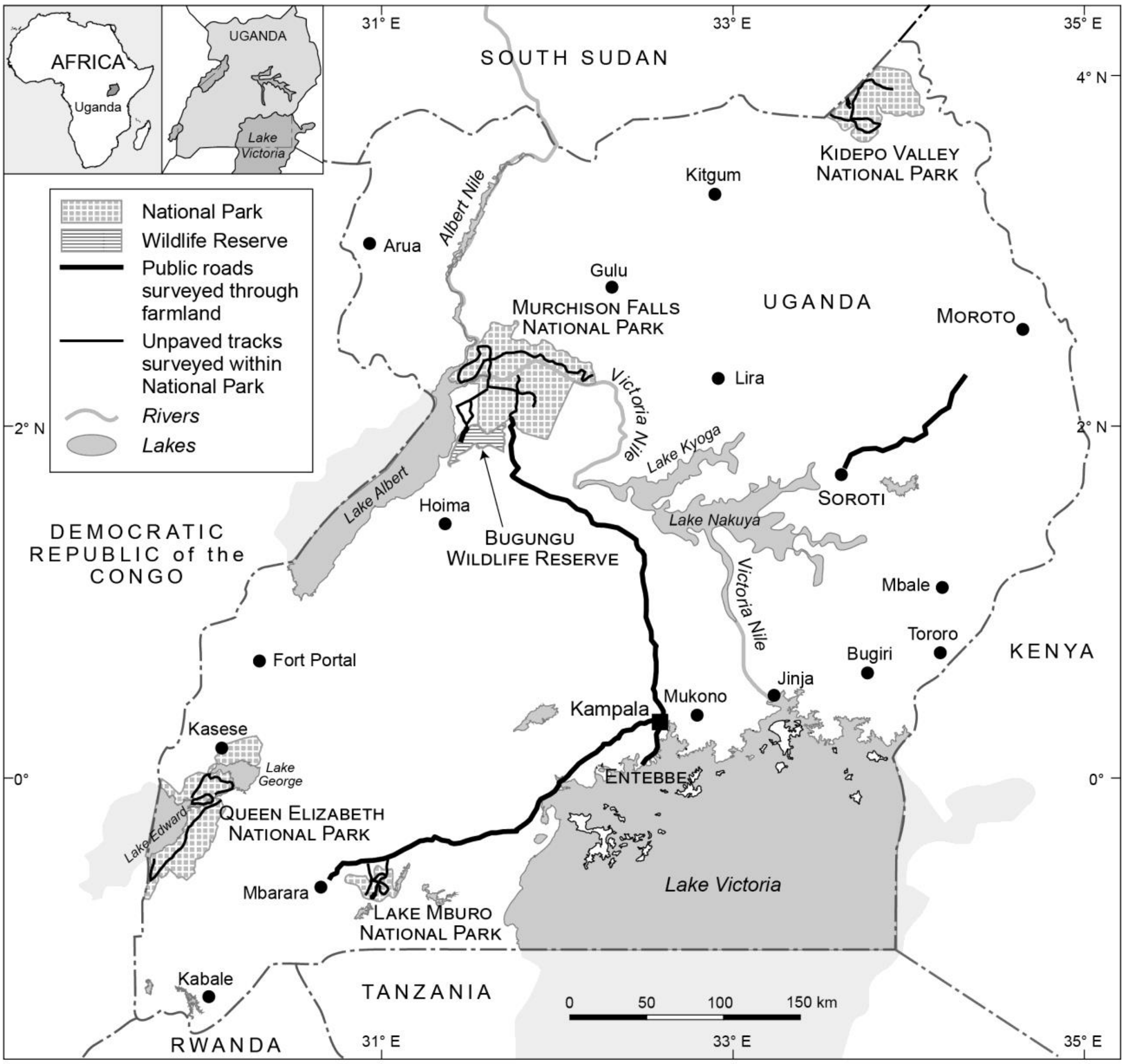


Figure A1 Routes surveyed during annual road counts, 2008–2015. Black lines indicate public roads surveyed through farmland, and unpaved tracks surveyed within four National Parks. Reproduced from *Ostrich* (2019) 90(1): 25-36 with permission © NISC (Pty) Ltd

Table A1 Diurnal raptor species recorded within 500 m of driven line transects in Uganda during 2008–2015. Species whose encounter rates were included in pair-wise comparisons between land use types, e.g. Savanna versus Pastoral land, are indicated.

Species		Threat status[1]	Mass (g)[2]	Diet[3]	Migratory status[4]	Savanna vs Pastoral[5]	Pastoral vs Agri.	Savanna vs Agri.
African hawk-eagle	*Aquila spilogaster*	lc	1,425	G	AS	Y		Y
steppe eagle	*Aquila nipalensis*	EN	3,175	G	P	Y		Y
tawny eagle	*Aquila rapax*	lc	2,350	G	AS	Y	Y	Y
Verreaux's eagle	*Aquila verreauxii*	lc	4,012	MR	AS			
black-chested snake-eagle	*Circaetus pectoralis*	lc	1,719	MR	AS	Y		Y
brown snake-eagle	*Circaetus cinereus*	lc	2,000	MR	AS	Y	Y	Y
short-toed snake-eagle	*Circaetus gallicus*	lc	1,700	MR	P			
western banded snake-eagle	*Circaetus cinerascens*	lc	1,126	MR	AS	Y		
lesser spotted eagle	*Clanga pomarina*	lc	1,475	G	P			
African fish-eagle	*Haliaeetus vocifer*	lc	2,821	F	AS	Y		Y
booted eagle	*Hieraaetus pennatus*	lc	842	G	P			
Wahlberg's eagle	*Hieraaetus wahlbergi*	lc	838	G	AM	Y	Y	Y
long-crested eagle	*Lophaetus occipitalis*	lc	1,291	MR	AS	Y	Y	
martial eagle	*Polemaetus bellicosus*	VU	4,605	G	AS	Y		Y
crowned eagle	*Stephanoaetus coronatus*	NT	3,674	MR	AS			
bateleur	*Terathopius ecaudatus*	NT	2,385	G	AS	Y	Y	Y
african hobby	*Falco cuvieri*	lc	178	Br	AS			
common kestrel	*Falco tinnunculus*	lc	214	G	ASP	Y		Y
fox kestrel	*Falco alopex*	lc	275	G	AS			
grey kestrel	*Falco ardosiaceus*	lc	239	G	AS	Y	Y	Y
lanner falcon	*Falco biarmicus*	lc	658	Br	AS			
lesser kestrel	*Falco naumanni*	lc	152	I	P			
red-necked falcon	*Falco ruficollis*	lc	203	Br	AS			
african marsh-harrier	*Circus ranivorus*	lc	486	G	AS			
Montagu's harrier	*Circus pygargus*	lc	308	G	P	Y	Y	
pallid harrier	*Circus macrourus*	NT	401	G	P			Y
western marsh-harrier	*Circus aeruginosus*	lc	659	G	P	Y		Y
African goshawk	*Accipiter tachiro*	lc	282	G	AS			
black sparrowhawk	*Accipiter melanoleucus*	lc	638	Br	AS			
little sparrowhawk	*Accipiter minullus*	lc	83	Br	AS			
shikra	*Accipiter badius*	lc	172	MR	AS	Y	Y	Y
grasshopper buzzard	*Butastur rufipennis*	lc	340	I	AM		Y	Y
augur buzzard	*Buteo augur*	lc	1,110	G	AS			
Eurasian buzzard	*Buteo buteo*	lc	863	MR	P	Y		Y
red-necked buzzard	*Buteo auguralis*	lc	654	G	AM			
lizard buzzard	*Kaupifalco monogrammicus*	lc	288	MR	AS	Y		Y
bat hawk	*Macheiramphus alcinus*	lc	625	Bt	AS			
dark chanting-goshawk	*Melierax metabates*	lc	759	G	AS	Y	Y	
eastern chanting-goshawk	*Melierax poliopterus*	lc	643	G	AS			
pale chanting-goshawk	*Melierax canorus*	lc	811	G	AS			

Species		Threat status[1]	Mass (g)[2]	Diet[3]	Migratory status[4]	Savanna vs Pastoral[5]	Pastoral vs Agri.	Savanna vs Agri.
gabar goshawk	*Micronisus gabar*	lc	168	Br	AS			
European honey-buzzard	*Pernis apivorus*	lc	698	I	P		Y	Y
African harrier-hawk	*Polyboroides typus*	lc	653	G	AS	Y	Y	Y
black-winged kite	*Elanus caeruleus*	lc	259	MR	AS		Y	Y
black kite	*Milvus migrans*	lc	847	S	AMP			
osprey	*Pandion haliaetus*	lc	1,510	F	P			
palm-nut vulture	*Gypohierax angolensis*	lc	1,470	V	AS	Y		
Rüppell's vulture	*Gyps rueppelli*	CR	7,570	S	AS			Y
white-backed vulture	*Gyps africanus*	CR	5,450	S	AS	Y		Y
hooded vulture	*Necrosyrtes monachus*	CR	2,050	S	AS		Y	
Egyptian vulture	*Neophron percnopterus*	EN	2,000	S	ASP			
lappet-faced vulture	*Torgos tracheliotos*	EN	6,780	S	AS	Y		Y
white-headed vulture	*Trigonoceps occipitalis*	CR	4,260	S	AS			Y

[1] lc = least concern; NT = near-threatened; VU = Vulnerable; EN = Endangered; CR = Critically endangered. BirdLife International (2018)

[2] Median of values given in del Hoyo et al. (2017).

[3] Extracted from Brown et al. (1997), del Hoyo et al. (2017). S = scavenger; G = generalist, Br = bird specialist; Bt = bats; F = fish; I = invertebrates; MR= mammals/reptiles/snakes; V = vegetarian (fruit)

[4] Migratory status: AM = Afrotropical migrant; AS = Afrotropical, sedentary; P = Palearctic migrant; ASP = Afrotropical, sedentary, but Palearctic migrants also occur; AMP = Afrotropical migrant, Palearctic migrants also occur. Adapted from Buij et al. (2013).

[5] Species whose encounter rates were included in a pairwise comparison between Savanna and Pastoral land, i.e. their detection patterns, with respect to distance from the transect, did not differ significantly between these two land use types.

Table A2 Transect details. A. Combined distance and number of transects surveyed in each year and land use type. Figures include repeat surveys of some transects, i.e. 'out and back'. B. The number of surveys made of each transect in each year of study. Adapted from *Ostrich* (2019) 90(1): 25-36 with permission © NISC (Pty) Ltd

Table A2A

Year	Agricultural			Pastoral			Savanna			Total
	Kms	% Effort[1]	No.	Kms	% Effort	No.	Kms	% Effort	No.	Kms
2008	110	12%	3	9	1%	1	784	87%	22	903
2009	22	7%	1	0	0%	0	309	93%	9	331
2010	568	29%	10	463	24%	10	896	46%	22	1,927
2011	519	32%	9	394	24%	9	706	44%	19	1,619
2012	556	32%	10	394	23%	8	776	45%	21	1,726
2013	507	30%	8	394	23%	8	779	46%	21	1,680
2014	482	39%	8	363	29%	7	405	32%	16	1,250
2015	595	34%	10	394	22%	8	763	44%	21	1,752
Total:	3,359	30%		2,411	22%		5,418	48%		11,188

[1] The distance surveyed within land use type, expressed as a percentage of the total distance surveyed in that year

Table A2B

		Year							
Land use	Transect identifier	2008	2009	2010	2011	2012	2013	2014	2015
Agricultural	2			1	1	2	1		1
	7			1	1	1	1	1	1
	24			2	2	2	2	2	2
	38	1	1	1	1	1	1	1	1
	39			1	1	1	1	1	1
	41	1		1	1	1	1	1	2
	44			1	1	1	1	1	1
	68	1		1	1	1		1	1
	72			1					
Pastoral	1			2	1	1	1	1	1
	12			1	1	1	1	1	1
	17			1	1				
	21			1	1				
	28			2	2	2	2	2	2
	32			2	2	2	2	1	2
	66	1		1	1	1	1	1	1
	70					1	1	1	1
Savanna	3	1	1	1	1	1	1	1	1
	8	1	1	1	1	1	1	1	1
	9	1	1			1	1	1	
	13	1	1	1	2	2	2	2	2
	18	2	1	1	1	2	2	1	2
	22	1	1	1	1	1	1	1	1
	25	1	1	1	1	1	1	1	1
	29	1	1	1	1	1	1	1	1
	33	1			1	1	1	1	1
	35	2	1	1	1	2	2	2	2
	43	1		1	1	1	1		1
	45	2		2	2	2	2		2
	47	1		1	1	1	1		1
	49			1					
	50			1					
	51			1					
	52			1					
	53			1					
	54	1		1	1	1	1	1	1
	56	1		1	1	1	1	1	1
	58	1			1	1		1	1
	60			2			1	1	1
	61	2		1	2	1	1		1

Table A3 Models used to examine raptor encounter rates in relation to land use, body mass, threat- and migratory status

Model	Dependent variable	Fixed effects	Offsets	Interaction terms	Random factors	Distributions	Sample sizes
1	Individuals encountered[1]	Outside observers + Land use + Altitude + Rainfall + Tree cover	Transect length (log transformed)	None	Survey year + Transect identity	Zero-inflated and non-zero-inflated Poisson and Negative binomial (NB1, NB2)	226 transect-surveys, 35 transects, 8 years
2	Percentage difference in a species' encounter rates in two land use types[2]	One of the following in each model: Body mass (log transformed); Diet; Migratory status; Threat status	None	None	Genus		23 species (Savanna vs Pastoral land) 14 species (Pastoral vs Agricultural land) 24 species (Savanna vs Agricultural land)
3	Mean body mass (log transformed) of birds encountered [3]	Transect length (log transformed) + Outside observers + Land use + Tree cover + Altitude + Rainfall	None	None	Survey year + Transect identity		220[4] transect-surveys, 35 transects, 8 years
4	Raptor species number	Transect length (log transformed) + Outside observers + Land use + Tree cover + Altitude + Rainfall	None	Transect length* Land use	Survey year + Transect identity		226 transect-surveys, 35 transects, 8 years

[1] The number of individuals encountered on each transect-survey

[2] The difference between the mean fitted encounter rate for a species in two land use types, expressed as a proportion of its encounter rate in protected savanna (in pairwise comparisons between savanna and either pastoral or agricultural land) or pastoral land (in pairwise comparisons between pastoral and agricultural land)

[3] A natural log transformation of the mean body mass of individuals of all species encountered on a given transect survey

[4] Six transect-surveys on which no raptors were seen have been excluded

Table A4 Unmodelled and modelled encounter rates (birds seen 100 km^{-1}) for 53 and 33 raptor species, respectively. Modelled encounter rates are the rates predicted from GLMMs, after controlling for the effects of variation in transect length, the presence of outside observers, land use, altitude, rainfall and tree cover, and the repeated sampling of the same transects and years. Differences in the sample sizes from which modelled and unmodelled estimates were drawn reflect missing values for some of the variables used in the models. Encounter rates were modelled only for species with at least 10 sightings

		Unmodelled encounter rates				Modelled encounter rates							
Species		***n*[1]**	**Savanna**	**Pastoral**	**Agricultural**	***n*[1]**	**Savanna**	**SE**	**Pastoral**	**SE**	**Agricultural**	**SE**
African hawk-eagle	*Aquila spilogaster*	29	0.30	0.33	0.15	22	0.28	0.024	0.28	0.019	0.03	0.004
steppe eagle	*Aquila nipalensis*	84	1.33	0.50	0.00	84	1.03	0.317	0.69	0.242	0.00	0.000
tawny eagle	*Aquila rapax*	163	2.49	0.83	0.24	159	3.49	0.345	1.17	0.258	0.16	0.039
Verreaux's eagle	*Aquila verreauxii*	1	0.02	0.00	0.00	1	-	-	-	-	-	-
black-chested snake-eagle	*Circaetus pectoralis*	42	0.63	0.21	0.09	39	0.68	0.037	0.16	0.050	0.09	0.032
brown snake-eagle	*Circaetus cinereus*	150	1.66	1.29	0.86	128	1.33	0.038	1.22	0.054	0.73	0.087
short-toed snake-eagle	*Circaetus gallicus*	22	0.33	0.04	0.09	17	-	-	-	-	-	-
western banded snake-eagle	*Circaetus cinerascens*	27	0.24	0.50	0.06	24	0.43	0.132	0.43	0.084	0.02	0.003
lesser spotted eagle	*Clanga pomarina*	8	0.13	0.04	0.00	8	-	-	-	-	-	-
African fish-eagle	*Haliaeetus vocifer*	142	2.49	0.04	0.18	135	3.12	0.451	0.00	0.000	0.08	0.014
booted eagle	*Hieraaetus pennatus*	12	0.17	0.04	0.06	12	0.21	0.064	0.04	0.017	0.08	0.058
Wahlberg's eagle	*Hieraaetus wahlbergi*	104	0.54	1.49	1.16	91	0.81	0.048	1.08	0.099	1.00	0.107
long-crested eagle	*Lophaetus occipitalis*	313	2.79	2.74	2.86	290	1.92	0.143	2.81	0.153	2.82	0.186
martial eagle	*Polemaetus bellicosus*	38	0.65	0.12	0.00	35	0.65	0.034	0.11	0.013	0.00	0.000
crowned eagle	*Stephanoaetus coronatus*	2	0.04	0.00	0.00	2	-	-	-	-	-	-
bateleur	*Terathopius ecaudatus*	458	7.66	1.37	0.30	444	8.73	0.218	1.12	0.035	0.35	0.012
african hobby	*Falco cuvieri*	7	0.02	0.04	0.15	7	-	-	-	-	-	-
common kestrel	*Falco tinnunculus*	30	0.28	0.29	0.24	25	0.18	0.013	0.34	0.036	0.22	0.028
fox kestrel	*Falco alopex*	2	0.02	0.04	0.00	2	-	-	-	-	-	-

Species		Unmodelled encounter rates				Modelled encounter rates						
		n[1]	Savanna	Pastoral	Agricultural	n[1]	Savanna	SE	Pastoral	SE	Agricultural	SE
grey kestrel	*Falco ardosiaceus*	160	1.96	1.00	0.89	149	1.70	0.195	0.91	0.064	1.03	0.142
lanner falcon	*Falco biarmicus*	6	0.00	0.25	0.00	6	-	-	-	-	-	-
lesser kestrel	*Falco naumanni*	10	0.09	0.21	0.00	10	-	-	-	-	-	-
red-necked falcon	*Falco ruficollis*	22	0.37	0.08	0.00	20	-	-	-	-	-	-
african marsh-harrier	*Circus ranivorus*	16	0.15	0.00	0.24	14	0.18	0.041	0.00	0.000	0.25	0.053
Montagu's harrier	*Circus pygargus*	54	0.63	0.75	0.06	50	0.39	0.053	0.85	0.137	0.11	0.018
pallid harrier	*Circus macrourus*	29	0.35	0.37	0.03	24	0.18	0.034	0.54	0.092	0.00	0.000
western marsh-harrier	*Circus aeruginosus*	38	0.44	0.25	0.24	33	0.39	0.038	0.23	0.021	0.26	0.031
African goshawk	*Accipiter tachiro*	9	0.11	0.04	0.06	9	-	-	-	-	-	-
black sparrowhawk	*Accipiter melanoleucus*	3	0.04	0.00	0.03	3	-	-	-	-	-	-
little sparrowhawk	*Accipiter minullus*	5	0.09	0.00	0.00	5	-	-	-	-	-	-
shikra	*Accipiter badius*	64	0.35	0.87	0.71	57	0.30	0.013	0.93	0.088	0.72	0.052
grasshopper buzzard	*Butastur rufipennis*	883	15.76	0.71	0.36	872	21.85	2.486	1.20	0.225	0.34	0.025
augur buzzard	*Buteo augur*	4	0.00	0.12	0.03	3	-	-	-	-	-	-
Eurasian buzzard	*Buteo buteo*	35	0.48	0.25	0.09	34	0.54	0.070	0.22	0.030	0.13	0.020
red-necked buzzard	*Buteo auguralis*	1	0.02	0.00	0.00	1	-	-	-	-	-	-
lizard buzzard	*Kaupifalco monogrammicus*	98	0.52	1.00	1.37	88	0.57	0.052	0.88	0.101	1.59	0.301
bat hawk	*Macheiramphus alcinus*	1	0.02	0.00	0.00	1	-	-	-	-	-	-
dark chanting-goshawk	*Melierax metabates*	123	0.92	2.03	0.71	107	1.08	0.110	2.98	0.718	0.34	0.141
eastern chanting-goshawk	*Melierax poliopterus*	1	0.02	0.00	0.00	1	-	-	-	-	-	-
pale chanting-goshawk	*Melierax canorus*	2	0.00	0.04	0.03	2	-	-	-	-	-	-
gabar goshawk	*Micronisus gabar*	9	0.07	0.08	0.09	9	-	-	-	-	-	-
European honey-buzzard	*Pernis apivorus*	152	2.33	1.04	0.03	141	2.71	0.239	1.09	0.134	0.00	0.000
African harrier-hawk	*Polyboroides typus*	56	0.65	0.33	0.39	55	0.69	0.032	0.29	0.017	0.50	0.021

Species		Unmodelled encounter rates				Modelled encounter rates						
		n[1]	Savanna	Pastoral	Agricultural	*n*[1]	Savanna	SE	Pastoral	SE	Agricultural	SE
black-winged kite	*Elanus caeruleus*	126	0.50	2.53	1.13	111	0.31	0.053	2.88	0.533	1.07	0.223
black kite	*Milvus migrans*	2253	8.80	21.82	37.21	2138	9.31	1.178	25.08	1.408	45.48	7.365
osprey	*Pandion haliaetus*	17	0.28	0.04	0.03	16	-	-	-	-	-	-
palm-nut vulture	*Gypohierax angolensis*	86	1.40	0.00	0.30	84	0.77	0.083	0.00	0.000	0.49	0.070
Rüppell's vulture	*Gyps rueppelli*	101	1.72	0.29	0.03	92	1.49	0.173	0.00	0.000	0.12	0.012
white-backed vulture	*Gyps africanus*	494	9.08	0.08	0.00	473	10.39	1.110	0.25	0.034	0.00	0.000
hooded vulture	*Necrosyrtes monachus*	134	0.46	1.33	2.29	110	0.29	0.023	1.38	0.132	2.18	0.257
Egyptian vulture	*Neophron percnopterus*	1	0.00	0.04	0.00	1	-	-	-	-	-	-
lappet-faced vulture	*Torgos tracheliotos*	48	0.89	0.00	0.00	45	0.83	0.088	0.00	0.000	0.00	0.000
white-headed vulture	*Trigonoceps occipitalis*	33	0.48	0.29	0.00	24	0.24	0.018	0.80	0.090	0.00	0.000

[1] Number of encounters recorded

Table A5 **A.** The mean body mass of all individuals of (53) raptor species encountered during transect-surveys through protected savanna, pastoral and agricultural land, calculated from unmodelled data. The mean body mass was calculated for each transect-survey, from the number of individuals seen per species, and the species' median mass (Table A1; from del Hoyo et al. 2017). Mean body mass was much higher in savanna than in pastoral or agricultural land, and these differences remained when vulture species were excluded.

B. Pairwise comparisons of encounter rates for large (>1 kg) vs small species, in relation to land use, using unmodelled data. Each comparison shows the median difference in encounter rates between protected savanna and either pastoral or agricultural land. A negative value indicates that the encounter rate in savanna was higher. Large species showed a significantly greater drop in abundance than smaller species

A.

	All species			Excluding vultures		
Land use type	Mean mass (g)	SE	n[1]	Mean mass (g)	SE	n[1]
Protected savanna	1,898	99.89	131	1,395	52.35	130
Pastoral land	1,033	53.29	47	956	46.10	47
Agricultural land	880	34.38	42	847	33.10	42

[1] The number of transect-surveys conducted in each land use type

B.

Comparison	Body mass	Median difference	n[1]	Kolmogorov-Smirnov: D	P
Savanna vs Pastoral	Large[2]	-67%	13	0.692	0.009
	Small	+12%	10		
Savanna vs Agricultural	Large	-97%	12	0.583	0.034
	Small	-43%	12		

[1] The number of species compared

[2] 'Large' species: > 1 kg