IBIS
international journal of avian science
Ibis (2020) doi: 10.1111/ibi.12836

Variation in monthly sizes of home-ranges of Hooded Vultures *Necrosyrtes monachus* in western, eastern and southern Africa

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Tracking studies are often used to inform conservation plans and actions. However, species have frequently only been tracked in one or a few localities, whereas space use can be remarkably flexible, especially in long-lived species with advanced learning abilities. We assessed variability in space use in the Critically Endangered Hooded Vulture *Necrosyrtes monachus* by pooling movement data from three populations across the species' sub-Saharan range (in South Africa, Botswana, Ethiopia, Kenya, The Gambia and Mozambique). We estimated minimum convex polygons and kernel density estimators (KDEs) and compared monthly home-range sizes between breeding and non-breeding seasons, age-classes and subspecies, accounting for uneven sampling within groups. Mean (± sd) monthly home-range sizes (95% KDEs) for adult Hooded Vultures from southern (12 453 ± 21 188 km^2, $n = 82$) and eastern Africa (3735 ± 3652 km^2, $n = 24$) were 103 and 31 times larger than those of conspecifics from western Africa (121 ± 98 km^2, $n = 48$). This may relate partly to subspecific differences, and individuals with small home-ranges in western Africa and Ethiopia were trapped in urban environments. Regional variation in space use by Hooded Vultures may be linked to flexibility in feeding behaviour (degree of commensalism) which may arise in response to resource availability and persecution in different areas. Age-class also affected monthly home-range sizes, with immature birds generally having larger monthly home-range size estimates than

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adults. Our results highlight the flexibility of Hooded Vultures in terms of their home-range sizes and suggest that home-range sizes differ between populations and individuals, depending on the extent of human commensalism. Our results also reaffirm the importance of international co-operation in conservation efforts aimed at protecting this wide-ranging, non-migratory species.

Keywords: kernel density estimate, minimum convex polygon, monthly home-range size estimate, vulture.

The 22 obligate scavenger vulture species worldwide perform a vital ecological function by consuming carrion and other organic waste (Buechley & Şekercioğlu 2016, Plaza & Lambertucci 2017). Vultures are ecologically important (Markandya *et al.* 2008, Margalida & Colomer 2012, Grilli *et al.* 2019) and culturally significant (McKean *et al.* 2013, Williams *et al.* 2014, Buij *et al.* 2016) but their use in traditional medicine (Saidu & Buij 2013, Boakye *et al.* 2019) has, along with poisoning and persecution (Ogada & Buij 2011, Garbett *et al.* 2018, Dabone *et al.* 2019), contributed to population declines for most African vulture species (Ogada *et al.* 2012, 2016, Buechley & Şekercioğlu 2016, Botha *et al.* 2017). Among those with the worst conservation status is the Critically Endangered Hooded Vulture *Necrosyrtes monachus*, which has experienced population declines of over 80% in some areas over the last three generations (Ogada & Buij 2011, Ogada *et al.* 2016, BirdLife International 2017).

Due to their ecological importance and poor conservation status, there has been a growing research interest in vultures, which has been partially aided by tracking technology. Patterns in space use reflect the ecological requirements of a species (Sutherland 1998), and so movement ecology and home-range studies are increasingly being used as tools to assist in species conservation (Fraser *et al.* 2018). This is especially important for mobile species whose conservation needs may have been overlooked by nature conservation authorities to date (Runge *et al.* 2014).

Old World vultures generally have very large home-ranges. For example, over a 6-month period, the cumulative minimum convex polygon (MCP) size of three immature Bearded Vultures *Gypaetus barbatus* was 10 999 km^2 (Krüger & Amar 2017). Over a cumulative 6- to 20-month period, the mean MCP sizes of five adult and two immature Cape Vultures *Gyps coprotheres* were 21 320 km^2 and 482 276 km^2, respectively (Bamford *et al.* 2007). The large home-ranges of Old World vultures may be attributed to their obligate scavenging lifestyle and the need to search large areas for food, which is unpredictable in space and time.

However, movement strategies may be surprisingly flexible within and between individuals and populations (Austin *et al.* 2004, Börger *et al.* 2006a, Saïd *et al.* 2009) and this plasticity may depend both on an individual's specializations in the use of resources and on environmental factors (Schlaich 2019). For example, in the Hooded Vulture, such environmental factors may include the spatial and temporal predictability of food, and local cultural beliefs, where the latter may partially dictate levels of persecution. These two factors (resource predictability and persecution) combined may result in varied levels of commensalism throughout the species' range. Hooded Vultures' movements may also differ depending on life-history traits, such as age-class and whether the bird is breeding. Given their dire conservation status and the fact that research in Africa is still lacking, we believed there was a need for further investigation into the movement ecology of Hooded Vultures.

Historically, breeding Hooded Vultures were believed to have small home-ranges (Ferguson-Lees & Christie 2001). The commensal relationship Hooded Vultures have with people in certain areas (Shelley & Buckley 1872, Anderson 1999, Ogada & Buij 2011) may result in smaller home-ranges. However, non-breeding adults and immatures have been shown to range over larger distances (Steyn 1982, Kemp *et al.* 2018). For example, a Hooded Vulture that was initially ringed as an immature in northern Zimbabwe was found 180 km from the initial ringing location, 21 years later (Paijmans *et al.* 2017), and four adult birds radiotagged in northern Botswana had relatively large home-ranges, with 95% kernel density estimators (KDEs) that varied from 1329 km^2 in the dry (breeding) season to 6498 km^2 in the wet (non-breeding) season (Reading *et al.* 2019). Thus, we might expect the home-ranges of Hooded Vultures to be within the same order of magnitude as those of other African vulture species. To our knowledge, only one published study has used telemetry to gather movement data on this species (Reading *et al.* 2019).

A primary aim of our study was to determine which factors affect monthly home-range size of Hooded Vultures. Adult Hooded Vultures visit their nests throughout the year (Thompson *et al.* 2017), so we hypothesized that age-class may affect home-range size and we predicted that adults would have smaller home-ranges compared with immatures. Second, non-breeding adult Cape and Bearded Vultures use larger home-ranges than breeding adults do (Krüger *et al.* 2014, Pfeiffer *et al.* 2015) so we hypothesized that non-breeding adults would use larger home-ranges compared with breeding adults. Unfortunately, we were unable to sex sufficient individuals to account for behavioural differences between the sexes. Third, we looked at three interrelated variables: subspecies, region and commensalism. There are two recognized subspecies of Hooded Vultures, *N. m. monachus* and *N. m. pileatus* (Fig. 1a), which differ in their degree of commensalism (Forsman 2016, Kemp *et al.* 2018). North of the equator, the species is at its most abundant, living in close association with human settlements (Chapin 1932, Allan 1996, Anderson 1999, Thiollay 2007, Jallow *et al.* 2016, Mullié *et al.* 2017, Henriques *et al.* 2018). South of the equator, Hooded Vultures are more likely to be found in protected areas, where they seem to depend less on food associated with humans (Anderson 1999), although signs of commensalism have been observed in these populations, too: Hooded Vultures feed on:

- Food scraps from tourists on Hot Air Balloon Safaris in Kenya (M.Z.V., D.O., K.L.B. pers. obs., and E. Reson *in litt*.)
- Food provided to crocodiles at crocodile farms in Botswana and South Africa (R.P.R., G.M., P.H., L.J.T. pers. obs.)
- Food provided at supplementary feeding sites in South Africa (L.J.T. pers. obs).
- Abattoir offal in Ethiopia (E.R.B. pers. obs.).

However, these may represent rare cases that, for the majority of the population, are unlikely to contribute much to the birds' diet. Predictability of food has been shown to drive the foraging dynamics and movements of various avian species, including Egyptian Vultures *Neophron percnopterus* (Van Overveld *et al.* 2018), Bald Eagles *Haliaeetus leucocephalus* (Turrin *et al.* 2015) and White Storks *Ciconia ciconia* (Flack *et al.* 2016, Rotics *et al.* 2017). We therefore hypothesized that 'subspecies' may affect home-range size of Hooded Vultures. We predicted that *N. m. pileatus* individuals, being generally less commensal, would have larger home-ranges than *N. m. monachus* individuals. Note that the subspecies to which our study birds belonged was determined based on trapping location, rather than genetic analysis. As our 30 study birds came from western, eastern and southern Africa, where the degree of commensalism of Hooded Vultures and the predictability of food in space and time vary, we hypothesized that 'region' may affect Hooded Vulture home-range size. We predicted that Hooded Vultures from western Africa would therefore have smaller home-ranges than those of their eastern and southern African conspecifics.

The number of months during which our study birds were tracked differed among individuals. We were also interested in determining how we could minimize tracking periods for individuals of endangered species, such as African vultures and therefore a secondary aim was to determine the minimum tracking period needed to accurately assess and compare home-range size estimates. When deciding whether to fit their study birds with a permanent or 'breakaway' harness (where the latter are designed to fall off after a limited time, Kenward 1985), raptor biologists must take into account the minimum time period necessary to answer their questions, as well as ethical concerns, which may be heightened by the conservation status of the study species. We predicted that at least 12 months' worth of movement data would be necessary to overcome differences in terms of season and breeding period, to estimate the home-range size of Hooded Vultures accurately.

METHODS

Trapping and marking

Thirty Hooded Vultures were caught in six countries between 26 September 2013 and 28 June 2017 (Table 1, Table S1). These birds were trapped by field teams working in different countries for their own independent studies, and we have pooled the resulting movement data. Trapping

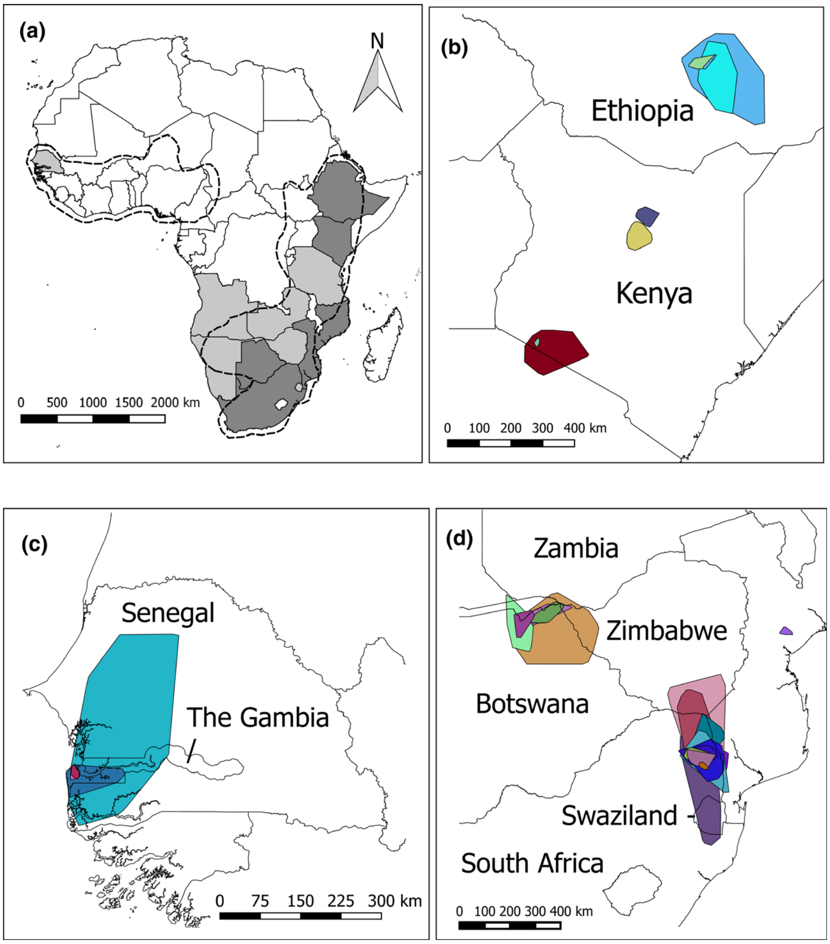

Figure 1. (a) Six African countries in which our 30 Hooded Vultures *Necrosyrtes monachus* were caught and tagged: The Gambia, Ethiopia, Kenya, Mozambique, Botswana and South Africa (shown in dark grey), and the additional seven countries into which their estimated home-ranges (100% MCPs) extended: Senegal, Tanzania, Zambia, Zimbabwe, Swaziland, Angola and Namibia (in light grey). The dashed lines delineate the ranges of *N. m. monachus* in the north and *N. m. pileatus* in the south (based on Kemp *et al.* 2018). We also present home-range estimates (cumulative 100% MCPs) of the Hooded Vultures tagged in (b) eastern Africa, (c) western Africa and (d) southern Africa. The various shades/colours denote different individuals.

locations in Botswana, Kenya, Mozambique and South Africa were within nature reserves. Those in Ethiopia were at abattoirs. In The Gambia, birds were trapped using supplementary feeding in a low-density human settlement area and at a nature reserve, where the daily feeding of caged Spotted Hyaenas *Crocuta crocuta* and a nearby abattoir attract hundreds of Hooded Vultures. Capture techniques included: removal of nestlings from the nest by hand, padded leg-hold traps (Bloom *et al.* 2007), cannon nets (*sensu* Garbett *et al.* 2018), noose carpets, and strings of monofilament nooses positioned around and over bait (Kendall *et al.* 2013). Each individual was fitted with GPS-GSM or solar Argos Platform Terminal Transmitter (PTT) units using a backpack harness. These units ranged from 20 to 45 g, comprising 0.9–3.4% of an individual's mass (1.8 ± 0.6%, mean ± sd, $n = 17$, Tables 1 and Table S1). Units were manufactured by Microwave Telemetry Inc. (Columbia, MD, USA), North Star Science and Technology, LLC (Oakton, VA, USA), KoEco Inc. (GPS-GSM, South Korea), Wildlife Computers Inc. (Redmond, WA, USA) or Made-byTheo (Theo Gerrits at www.madebytheo.nl) (see Table 1 and Table S1).

Age and sex determination

Hooded Vultures that were captured in the nest (Table 1 and Table S1) were classed as 'nestlings'

Table 1. Summary information for the study birds and their transmitters.

Field	No. of categories	Categories (*n*)
Study birds		
Individual	n/a	30 individuals
Sex	3	Female (5), male (6), unsexed (19)
Mass of bird (g)	n/a	Ranged from 1230 to 2800 g. Seven birds were not weighed.
Age when tagged	3	Adult (10), immature (17), nestling (3)
Trapping location/method		
Country	6	Botswana (5), Ethiopia (4), Kenya (4), Mozambique (1), South Africa (12), The Gambia (4)
Trapping method	4	Cannon nets (5), padded leg-hold traps (4), nooses (18), hand-grabbed (3)
Date tagged	n/a	26 September 2013 to 28 June 2017
Tag information		
Unit type	5	KoEco (2), MTI (17), NSTI (7), MadeByTheo (2), Wildlife Computers (2)
Unit mass (g)	7	20 g (2), 27 g (2), 30 g (16), 35 g (2), 40 g (2), 45 g (5), NA (1)
Unit mass (%)	n/a	0.9–3.5%
Duty cycle	8	a (4), b (8), c (7), d (2), e (2), f (3), g (2), h (2)
Duration (months)	n/a	1–48 months
No. of fixes (total)	n/a	61 to 147 443
Mean fixes/month	n/a	113 to 21 126

when they were tagged, up until the month in which they fledged (as determined by inspecting monthly movements). When they fledged, they were classed as 'immatures' (i.e. pre-definitive, *sensu* Clarke & Pyle 2015). Hooded Vultures that were in adult plumage when they were tagged (Finch-Davies & Kemp 1980) were classed as 'adults.'

Hooded Vultures are sexually monomorphic (Steyn 1982), and we present data for sex only when sex determination was performed by molecular DNA analysis (Table 1 and Table S1). To obtain DNA samples for molecular sexing, when each bird was captured, either blood was obtained from the base of a feather shaft or a tiny volume of blood was drawn from the brachial vein or from a talon using a sterile needle, blotted onto collection paper, and stored in an Eppendorf tube. Blood samples were then sent for avian DNA sexing either to Molecular Diagnostic Services in South Africa or to Moncton University in Canada. As we knew the sex of so few of our study birds, we excluded this information from our statistical analyses.

Data processing

Data analyses were performed in R version 3.6.1 (R Core Team 2019) and all graphs were produced using the R package *ggplot2* (Wickham 2009). Satellite tracking data were inspected visually in the open-source geographical information system software QGIS version 2.8 (QGIS Development Team, 2019). Fixes identified as outliers (e.g. those located over oceans, or >300 km from locations taken 1 h previously) were manually removed, and all 2D fixes were removed. Movement data were delineated by individual and month. We did not exclude data collected in the first few weeks after deployment (following Holland *et al.* 2017), as there is no evidence to suggest that transmitters negatively affect birds' flying ability (Barron *et al.* 2010).

Quantifying home-ranges

Local *xy* co-ordinates were transformed to 1984WGS and then projected to UTM37N (for Ethiopia), UTM28N (for The Gambia), UTM37S (for Kenya), UTM35S (for Botswana) and UTM36S (for South Africa and Mozambique), using the R packages *sp* (Pebesma & Bivand 2005) and *rgdal* (Bivand *et al.* 2016). For each bird and each monthly and cumulative-monthly file, we estimated home-range size using both MCP and KDE with the R package *adehabitatHR* (Calenge 2006). For the latter method, we used fixed kernel estimators (i.e. smoothing factors are fixed over the plane) (Worton 1989) and the h_{ref} algorithm, with a grid size set at 100 m. We included both methods here for comparative purposes. We subsampled the data to hourly fixes for Botswana and Kenya (see Fig. S1 and Table S2).

As we were interested in comparing monthly home-range size of Hooded Vultures between and within individuals, we use the term 'home-range' size to mean our assessment of the size of the ecological neighbourhoods of individual Hooded Vultures.

Quantifying commensalism

We calculated the proportion of each individual's fixes that was spent in urban areas. This was determined by plotting the fixes for each respective Hooded Vulture on the S2 prototype LC 20-m map of Africa 2016 (ESACCI 2017) and using the Point Sampling Tool (version 0.5.2) plug-in (Jurgiel 2018), in QGIS (QGIS Development Team 2019), to find the corresponding land cover for each location. The 20-m-resolution map includes the following land cover types: trees, shrubs, grassland, cropland, vegetation that is aquatic or regularly flooded, vegetation that is sparse or lichen mosses, bare areas, built-up areas, snow and/or ice, and open water. For the purpose of this study, we categorized fixes as falling either in 'built-up' (i.e. urban) areas or not, and we converted this to a percentage of time spent in urban areas as a proxy for how 'commensal' each individual is.

Statistical analyses

To address our primary aim of determining which factors affect monthly home-range size of Hooded Vultures, we defined a set of candidate *a priori* models (Table S3) following Burnham and Anderson (2002). We then performed a generalized linear mixed-effects analysis using the R package *lme4* (Bates *et al.* 2015) to determine the effects of various predictor variables on the monthly home-range size of Hooded Vultures. We conducted three separate analyses, with our respective continuous response variables being monthly home-ranges, in the form of (i) 100% MCP (km^2) representing the maximum area of activity, (ii) 95% kernel (km^2) estimating the majority of the home-range area and (iii) the 50% kernel (km^2) estimating the core use area (Worton 1989, Krüger & Amar 2017). We included predictors with possible biological importance in the global model regardless of whether they were statistically significant (Cheng *et al.* 2010); predictor variables were the same for all three response variables. We began with a baseline model, which included only the random effect 'Individual', and then we added models that included only each respective fixed effect. We then tested models with additive effects of each of the predictor variables, as well as one global model, which contained all three fixed effects. To avoid overfitting, we excluded interaction terms from our models. We excluded any monthly home-range estimates that were calculated with fewer than 10 fixes (Börger *et al.* 2006b), and thus six bird-months of data in total were excluded.

Fixed effects included: 'Age-class' ('immature' or 'adult'; the monthly home-range estimates for the three nestlings were discarded), 'Breeding season' ('breeding' or 'non-breeding' (Table S4; Van Someren 1956; Elgood *et al.* 1994; Dowsett-Lemaire & Dowsett 2014; Steyn 1982; Tarboton & Allan 1984; Thompson *et al.* 2017; Brown *et al.* 1982), where breeding was the period between courtship and nest building to fledging (*sensu* Krüger *et al.* 2014)), 'Subspecies' (either '*monachus*' or '*pileatus*', depending on the tagging location) and 'Region' (i.e. 'western' (The Gambia), 'eastern' (Kenya and Ethiopia) or 'southern' (South Africa, Botswana and Mozambique) Africa, depending on the tagging location (Fig. 1)). As 'Region' is nested within 'Subspecies', we compared two models containing only these respective fixed effects and 'Individual' (the individual's name) as a random effect, and found that the model containing 'Subspecies' had a lower corrected Akaike information criterion (AICc) than that containing 'Region'. We therefore excluded 'Region' as a fixed effect from our candidate models. A list of all candidate models is given in Table S3. Throughout their range, Hooded Vultures exhibit behavioural plasticity as a human-commensal, and as the level of commensalism would be confounded with both 'Subspecies' and 'Region', we decided not to include 'Commensal' as a fixed effect in our candidate models. 'Individual' was included as a random effect to control for repeated measures.

Visual inspections of residual plots showed no deviations from normality or homoscedasticity. The best approximating models were chosen according to differences in AICc values between each candidate model and the best approximating model (ΔAICc), and on their corrected Akaike weights (AICcWt), produced using the R package *AICcmodavg* (Mazerolle 2016), following

Wagenmakers and Farrell (2004) and Burnham and Anderson (2002). Models with ΔAICc < 2 were averaged for multimodel inference using the *MuMIn* package (Bartoń, 2016) in R version 3.6.1 (R Core Team 2019).

Assessing robustness of home-range estimates

To address our second aim of establishing the minimum tracking period necessary to confidently estimate home-range size for Hooded Vultures, we defined 'cumulative monthly home-range size' as home-range estimates made for each successive month of the bird's data, including all data from that month, and all previous months. That is, for each individual, we calculated home-ranges for (i) month 1 only, (ii) months 1 and 2, (iii) months 1, 2 and 3, (iv) all the way up to months 1, 2, 3 … and *n*, where *n* is the total number of months a particular individual was tracked for. We standardized between- and within-individual variation in cumulative monthly home-range size estimates by calculating monthly increases in cumulative home-range size for a particular individual as a percentage of the previous month's cumulative home-range size. MCPs could only increase or stay constant with successive months, for KDEs the monthly change could be positive or negative, and so we squared this change to result in a positive value for 50% and 95% KDEs. We used a piecewise linear regression model (a breakpoint regression, Thompson 2020) with the R package *lme4* (Bates *et al.* 2014) to objectively estimate the number of months at which an asymptote in cumulative home-range size was reached. Theoretically, at this point, additional months of tracking data would not significantly increase the cumulative monthly home-range size estimates for our study birds.

RESULTS

The 30 study birds were caught in six countries, spread across eastern, western and southern Africa, and their monthly home-range estimates extended into an additional seven countries (Fig. 1a). There was great variation in home-range size within each of the three respective populations from which our birds were drawn (Fig. 1b–d).

Monthly home-ranges for Hooded Vultures of different sexes, subspecies, age-classes and regions are shown in Figure 2(a)–(d), respectively. Mean monthly home-ranges of adult birds tagged in southern, eastern and western Africa are presented in Table 2.

Quantifying commensalism

The proportion of time that Hooded Vultures were found in urban vs. non-urban areas was greatest in birds in Ethiopia and The Gambia (eastern and western Africa, respectively). In contrast, Hooded Vultures in South Africa, Botswana, Kenya and Mozambique spent very little time in urban areas (Table 3).

Body mass (g) was recorded at the time of tagging for 23 of the 30 study birds; these masses ranged from 1230 to 2800 g, with an overall mean (± sd) of 1955 (± 372) g, *n* = 23 (Tables 1 and Table S1). Hooded Vultures from western Africa (*N. m. monachus*, 1649 ± 211 g, *n* = 4) were lighter than conspecifics from eastern (*N. m. pileatus*, 2023 ± 138 g, *n* = 4) and southern Africa (*N. m. pileatus*, 2014 ± 426 g, *n* = 15).

Statistical analyses

For none of the three response variables (100% MCP, 95% KDE and 50% KDE) in our generalized linear mixed model (GLMM) was there conclusive evidence for any of the approximating models for monthly home-ranges of Hooded Vultures. We therefore, for each response variable, performed model averaging of those models for which ΔAICc < 2. For each of the three response variables, the averaged model contained the fixed effects 'Age-class' and 'Subspecies', and the best approximating model for 95% KDE also included 'Breeding season' (Tables S5 and S6). For the sake of brevity, we discuss the results only for the 95% KDE. 'Subspecies' affected monthly home-range size, with individuals from the *N. m. pileatus* subspecies having monthly home-ranges that were 8348 km^2 larger than those of individuals from the *N. m. monachus* subspecies (Fig. 2b, Table S6). Immature birds had home-ranges that were 2755 km^2 larger than those of adults. Home-ranges were slightly larger (728 km^2) during the breeding season than during the non-breeding season (Table S6). To prevent overfitting we excluded interaction terms (such as the interaction of age-class and breeding season) from our models, although this interaction term may have provided more clarity on whether

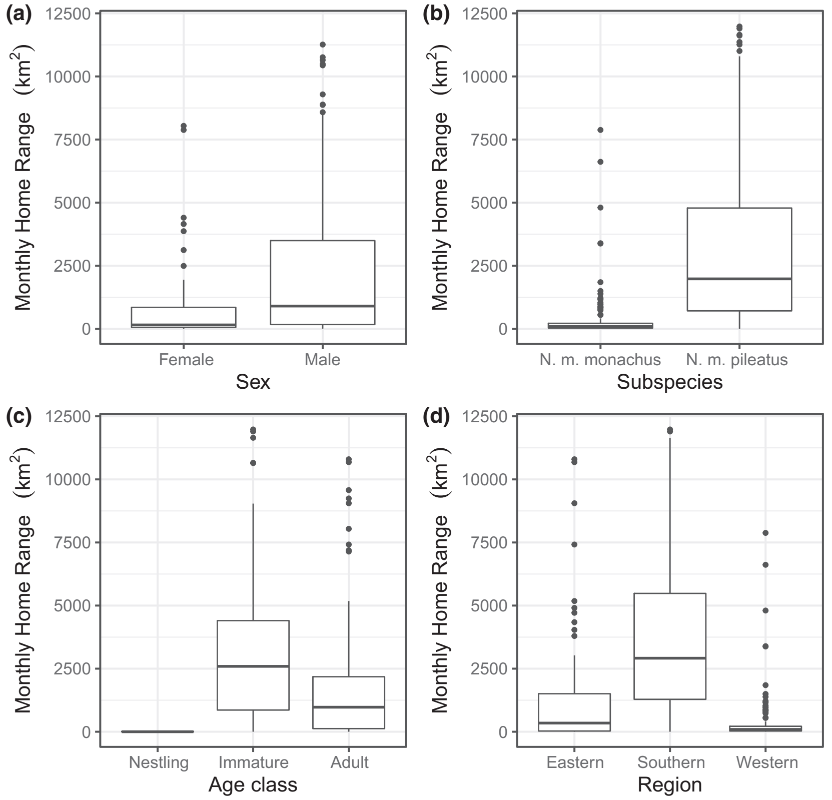

Figure 2. Monthly home-range size estimates (95% KDE, km^2) for Hooded Vultures *Necrosyrtes monachus* of different (a) sexes, (b) subspecies, (c) age-classes and (d) African regions. Boxes contain the 25th to 75th percentiles, and medians are shown with the thick lines. Whiskers show the minimum and maximum values, and outliers are shown with dots.

Table 2. Mean (± sd) of monthly home-range estimates (km^2) for adult Hooded Vultures from western (The Gambia), eastern (Ethiopia and Kenya) and southern Africa (Botswana, South Africa and Mozambique).

Region	100% MCP	50% KDE	95% KDE
Western Africa	65 ± 26 (48)	20 ± 24 (48)	121 ± 98 (48)
Eastern Africa	3698 ± 3961 (24)	527 ± 592 (24)	3735 ± 3652 (24)
Southern Africa	9965 ± 16 093 (82)	2188 ± 4055 (82)	12 453 ± 21 188 (82)

Note that we only used data for Hooded Vultures that we could confidently age as adults, that is, five birds from southern Africa, four from eastern Africa and one from western Africa. The number of 'bird-months' is shown in parentheses.

the movements of post-dependence immature birds (which should not have been affected by breeding season) were confounding this result. Re-running our models with the inclusion of this interaction term ('age-class' × 'breeding season') suggested that this was likely to be the case, that in fact immature Hooded Vultures did have larger home-ranges than adults during the breeding season; however, we focused on our initial results, due to issues with overfitting.

Assessing robustness of home-range estimates

When cumulative 100% MCP was plotted against 'month of study', the slope of the line was positive and large up to and including 8 months, after which the slope tended towards zero. Our piecewise regression analyses produced breakpoints for each of our three estimates of cumulative home-range size (Table 4).

Table 3. Mean percentage of time (%, as determined by the proportion of fixes) that Hooded Vultures (*n*) in different countries spent in urban areas.

Country	%	*n*	Range
Ethiopia	19.9	4	11.2–30.2
The Gambia	15.5	4	9.5–20.2
Botswana	0.4	4	0.0–0.9
Kenya	0.3	4	0.0–0.6
South Africa	0.2	12	0.0–0.6
Mozambique	0[a]	1	0.0

[a] The value for the bird from Mozambique is not a mean, as it represents just one individual.

Table 4. Estimated breakpoints (95% confidence interval, and number of bird-months) for three estimates of home-range size in relation to cumulative monthly home-range size of Hooded Vultures.

Home-range estimate	Breakpoint (month)	95% confidence interval	Number of bird-months
100% MCP	8.08	8.08–8.22	586
50% KDE	6.89	6.49–7.11	586
95% KDE	7.36	7.15–7.36	586

DISCUSSION

This is the first Pan-African study on the movement ecology of any African vulture species. Our results show large differences in monthly home-range size estimates between Hooded Vultures of different age-classes and subspecies, where the latter may be primarily related to feeding habits associated with different levels of commensalism with humans. Due to the imbalance in age-classes of tracked birds between study sites, regions and subspecies, our ability to disentangle additive and nested effects of all these variables is limited. That said, we found ecologically sensible statistical effects for ‘age-class’ and ‘subspecies’, which we discuss in more detail in the remainder of the discussion.

Age-class

Age-class was the most important of the three predictor variables (age-class, breeding season and subspecies) accounting for variability in Hooded Vulture home-range size. Although the effect size for age-class is smaller than that for subspecies, age-class accounted for more variability compared with subspecies. We caution that for all three predictor variables, the standard errors of the mean (sem) were substantial relative to the estimate sizes (Table S6). Immature Hooded Vultures had monthly home-ranges that were generally much larger than those of adults, in line with studies on other vulture species (Phipps *et al.* 2013, Krüger *et al.* 2014). This may be because adult Hooded Vultures visit and are somewhat ‘attached’ to their nests year round (Thompson *et al.* 2017), whereas immatures may not be spatially constrained in this way. Furthermore, immature Hooded Vultures may range more widely because they are seeking foraging areas away from adult conspecifics, where they may compete with other vultures (Mundy *et al.* 1992, Bamford *et al.* 2007). In Bearded Vultures, the exploratory and dispersive movements of recently fledged birds resulted in home-ranges that were larger than those of breeding adults (Krüger *et al.* 2014, López-López *et al.* 2014, Krüger & Amar 2017). In contrast, monthly home-ranges of adult California Condors *Gymnogyps californianus* were significantly larger than those of immatures, which typically spend their first 2 years near natal areas (Rivers *et al.* 2014).

Breeding season

We were surprised to find that monthly home-ranges (95% KDE) of Hooded Vultures were slightly larger in the breeding season than in the non-breeding season. This is in contrast to the findings of Krüger *et al.* (2014) and Pfeiffer *et al.* (2015), who found that non-breeding adult Bearded and Cape Vultures use larger home-ranges than breeding adults. Interestingly, ‘breeding season’ was not included in the best (averaged) approximating model for 50% KDE and 100% MCP, suggesting it did not affect these two estimates of monthly home-range size. We did not have enough data from adult Hooded Vultures of known sex to compare home-range sizes between the sexes in the breeding and non-breeding seasons, and we therefore encourage those studying sexually monomorphic species to confirm the sex of their study animals through molecular DNA analysis.

Subspecies, region and commensalism

As expected, Hooded Vultures in western Africa had much smaller monthly home-ranges than their conspecifics in eastern and southern Africa. This is probably because their food in western African towns is more predictable in space and time, and they are more commensal than their conspecifics (Shelley & Buckley 1872, Anderson 1999). Hooded Vultures in eastern and southern Africa mostly occur in rural areas, where food resources are patchily distributed, necessitating foraging over wider areas, which results in larger home-ranges. Of the three African regions, the vultures that spent the most time in urban areas were those in western Africa, although, despite their reputation as strongly commensal birds, the majority of their time was still spent in rural areas. We were surprised to find that our four Gambian study birds (*N. m. monachus*, the subspecies generally regarded as more commensal) spent less time in urban areas than did the four birds we caught in Ethiopia (*N. m. pileatus*, the subspecies viewed as less commensal). This may be because not all of the birds from The Gambia were caught in urban areas, whereas all four birds trapped in Ethiopia were caught in an urban area. It was also interesting to find a stark difference in the proportion of time that birds from Kenya and Ethiopia, both eastern African countries, spent in urban areas. In terms of their degree of commensalism, Hooded Vultures from Ethiopia are more similar to conspecifics from western Africa, whereas those from Kenya are more similar to birds from southern Africa.

We found great variation in monthly home-range size estimates of Hooded Vultures, even within a subspecies (*N. m. pileatus*), both between regional populations (eastern versus southern African) and within a region (Kenya versus Ethiopia) (Fig. 1). This suggests there is substantial flexibility in home-range size and commensalism within a region and within a subspecies, even if one subspecies is more commensal. Ideally, in assessing an individual's level of commensalism, its movement data should be ground-truthed to determine whether each feeding event occurred at a 'light' or 'heavy' feeding station (*sensu* Monsarrat *et al.* 2013) or the food resulted from hunting/culling activities (Mateo-Tomás & Olea 2010) or from natural deaths (predation or disease). Mullié *et al.* (2017) suggested that Hooded Vultures probably adapt their feeding behaviour to local differences in people's attitudes towards them. We believe that a lack of persecution from people will facilitate a greater degree of commensalism in Hooded Vultures. If one were to try to tease apart the contribution of developmental plasticity and phenotypic flexibility to Hooded Vulture feeding behaviour and consequent home-range size, one would ideally trap birds at a variety of sites, in the same country, and take samples for genetic analysis.

We caution that the movements of the Hooded Vultures we tracked in eastern, western and southern Africa may not be representative of conspecifics throughout the whole of those regions. For example, the birds trapped in The Gambia and in South Africa are very close to the limits of this species' range. We further highlight that unequal sampling (e.g. of age-classes across populations, regions and subspecies) may influence the apparent importance of predictor variables. Despite its large effect size, the support for the effect of 'subspecies' is only weak to moderate (based on AICc). We would expect the effect of 'subspecies' (and also 'region') to be resolved better in a more balanced study design. Similarly, although our analyses provide statistical support for the idea that there are regional differences in home-range size related to commensalism, this support is still limited.

CONCLUSIONS

Hooded Vultures are non-migratory, and yet the monthly home-ranges of our study birds overlapped international borders, highlighting the need for international collaboration of all stakeholders involved in vulture conservation (Phipps *et al.* 2013). Our breakpoint regression analyses suggested that 7–8 months of tracking data are sufficient to give reliable estimates of 50% KDE, 95% KDE and 100% MCP for Hooded Vultures. This supports the idea that one can obtain good estimates of home-range size without long-term tracking, and so breakaway harnesses can be used. In terms of the conservation implications of our study, our analyses show that immature Hooded Vultures, and individuals of the *N. m. pileatus* subspecies, range over wider areas, highlighting that they may be at greater risk of threats than adults and individuals of the *N. m. monachus* subspecies. The greatest threat to African vultures is poisoning (Ogada *et al.* 2016, Botha *et al.* 2017), which may occur over vast areas. Travelling more widely may expose an individual to more threats, particularly to more poisoned carcasses, as the further an individual travels, the greater the chances of encountering poisoned baits. Currently, data on age-classes and sex of poisoned Hooded Vultures are generally lacking from the African Wildlife Poisoning Database. We encourage those who attend poisoning scenes to record the age-classes of poisoned birds, and to take samples for molecular DNA sexing if possible.

The high degree of commensalism observed in Hooded Vultures from The Gambia and Ethiopia has ramifications in terms of reduced ecosystem services in rural areas in those two countries, as well as possible exposure of the birds to a wider range of threats, as the habitats they occupy are more heterogeneous. Governments of Hooded Vulture range states are encouraged to develop and enact national vulture multi-species action plans, with specific management interventions aimed at addressing local threats, in accordance with recommendations outlined in the Multi-species Action Plan to Conserve African-Eurasian Vultures (Botha *et al.* 2017).

We thank everyone who allowed us to work on their land, and who assisted with fieldwork. In particular, we thank A. Daka, S. Seyfu and the Bale Mountain Lodge in Ethiopia; M. Odino in Kenya; D. Kenny, J. Bradley, T. David, M. Keiteretse and B. Those in Botswana; M. L. Kassama, M. J. Jallow, F. Mendy, and Makasutu and Madiana Lodge in The Gambia; Boise State University volunteers and Gorongosa National Park in Mozambique; Kenya Bird of Prey Trust, Northern Rangelands Trust, Melako and Jaldesa conservancies, the Senior Warden of Masai Mara National Reserve, A. Tira and M. Braun in Kenya; and A. Bosch, J. P. Davies, J. 'Trigger' Eksteen, B. Havemann, D. Joubert, R. Loon, D. Pietersen, C. Rowles, C. T. Downs, Phalaborwa Mining Co., Sefapane Lodge, Cleveland Private Game Reserve, Timbavati Private Nature Reserve, Selati Game Reserve, Olifants River Private Game Reserve and SANParks, in South Africa. F. Dowsett-Lemaire and R. Dowsett assisted with dates for breeding seasons. We thank the contributors to the West African Bird DataBase at www.wabdab.org, managed by U. Liedén, T. J. Wacher and J. Brouwer. R. van Eeden and G. Tate helped with R code. Fieldwork was conducted with permission from SANParks (no permit no. associated), the government of The Gambia (permit no. 2014 AHG21/01(26)), Ethiopia's Wildlife Conservation Authority (no permit no. associated), Botswana's Department of Wildlife and National Parks (EWT8/36/4XXXIV(16)), Kenya's National Commission for Science, Technology and Innovation (NACOSTI/P/16/31214/9467 and 15965), Mozambique's Dept. of Scientific Services in Gorongosa (PNG/DSCi/C75/2017), and South Africa's LEDET (permit no. ZA/LP/HO/2937) and MTPA (permits MPB. 5557 and MPB. 5581). This paper is Hawk Mountain Sanctuary contribution to conservation science number 325. We are grateful to W. Vansteelant, R. Kimball and three anonymous reviewers for constructive comments, which greatly improved the manuscript.

FUNDING

We are grateful for funding and support from AZA Conservation Grant Fund, Bowling for Rhinos, Denver Zoo, Detroit Zoo, GreenMatter, San Diego Zoo Global, National Geographic Society, Raptors Botswana, The Wallace Research Foundation, The Rufford Foundation (ref. 18421-1, 21859-2), a Fulbright Fellowship, the Wilderness Wildlife Trust, and the National Research Foundation (ZA, no. 99494). R. Calder (Wildlife Computers Inc.) kindly donated two prototype PTT units.

AUTHOR CONTRIBUTIONS

K.L.B. and L.J.T. conceived and designed the study. Funding acquisition was done by all co-authors. Fieldwork was conducted by K.L.B., L.J.T., M.J.B., A.J.B., K.W., W.N., E.R.B., R.R., R.A.G., P.H., G.M., M.Z.V., S.T., D.O. and C.R.B. L.J.T. analysed the data and wrote the original draft. Subsequent revisions benefitted from contributions from K.L.B., L.J.T., E.R.B., R.R., C.R.B., R.A.G., D.O., W.N. and A.J.B.. All authors approved the final manuscript.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

ETHICS APPROVAL

Ethical approval was granted by SANParks' Animal Use and Care Committee (13-11), the University of KwaZulu-Natal Animal Ethics Subcommittee (AREC/094/015PD), the University of Cape Town Faculty of Science Animal Ethics Committee (2015/V6/AA) and the San Diego Zoo Global (IACUC approval no. A3675-01).

DATA AVAILABILITY STATEMENT

The raw data analysed in this study are archived on Movebank (http://www.movebank.org) as part of the 'Hooded Vulture Africa', 'Hooded Vulture Peregrine Fund KoEco Kenya', 'northern Kenya vulture project' and 'Hooded vulture movement ecology in southern Africa' studies.

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Received 25 April 2019;
revision accepted 18 March 2020.
Associate Editor: Wouter Vansteelant.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Information for each of the 30 Hooded Vultures included in this study.

Table S2. Monthly home-range size (km^2, mean ± sd) for both birds ('Chicken' and 'Franco's Ten') combined (n = 12 months), when calculated using two different duty cycles, where 'h' = a fix taken every 30 s if moving (as determined by an accelerometer), or a fix hourly if not, continually, day and night, and 'g' = a fix taken hourly, precisely on the hour, continually, day and night.

Table S3. Complete list of all eight candidate models used in our analyses.

Table S4. Breeding seasons (known or assumed) of Hooded Vultures in the six countries in which our study birds were tagged. Observations of laying dates in eastern Africa (Van Someren 1956), western Africa (Elgood *et al.* 1994; Dowsett-Lemaire & Dowsett 2014) and southern Africa (Steyn 1982; Tarboton & Allan 1984; Thompson *et al.* 2017) suggest that Hooded Vultures generally start breeding (i.e. lay eggs) early in the dry season.

Table S5. Ranking of models predicting monthly home-range size estimates (95% KDE, 50% KDE and 100% MCP, km^2) of Hooded Vultures *Necrosyrtes monachus*.

Table S6. Estimated sizes (coefficients) of fixed effects contained in the best approximating model (as determined by multimodel inference) fitted by restricted maximum-likelihood estimation (REML) for monthly 95% KDE, 50% KDE and 100% MCP (km^2). Fixed effects are ranked according to their estimate sizes.

Fig. S1. Monthly home-range size estimates (km^2) of Hooded Vultures *Necrosyrtes monachus* calculated with the same data (all originally in duty cycle 'g'), which was then subsampled to conform to the other six duty cycles ('a' to 'f'). A description of the various duty cycles is given in Table S1. Thick black lines represent medians, and the tops and bottoms of boxes depict the 1st and 3rd quartiles.