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Value of combining transect counts and telemetry data to determine short-term population trends in a globally threatened species

Corinne J. Kendall[1,2] | **Claire Bracebridge**[1] | **Emily C. Lynch**[1] | **Msafiri Mgumba**[3] | **Ara Monadjem**[4,5] | **Aaron Nicholas**[3] | **Adam Kane**[6]

[1]Conservation, Education and Science, North Carolina Zoo, Asheboro, North Carolina, USA

[2]Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA

[3]Wildlife Conservation Society, Ruaha-Katavi Landscape Program, Tanzania

[4]Department of Biological Sciences, University of Eswatini, Kwaluseni, Eswatini

[5]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Hatfield, Pretoria, South Africa

[6]School of Biology and Environmental Science and Earth Institute, O'Brien Science Centre West, University College Dublin Belfield, Dublin, Ireland

Correspondence
Corinne J. Kendall, Conservation, Education and Science, North Carolina Zoo, 4401 Zoo Parkway, Asheboro, NC 27205, USA. Email: Corinne.kendall@nczoo.org

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Abstract

To evaluate conservation interventions, it is necessary to obtain reliable population trends for short (<10 years) time scales. Telemetry can be used to estimate short-term survival rates and is a common tool for assessing population trends, but it has limitations and can be biased toward specific behavioral traits of tagged individuals. Encounter rates calculated from transects can be useful for assessing changes across multiple species, but they can have large confidence intervals and be affected by variations in survey conditions. The decline of African vultures has been well-documented, but understanding of recent trends is lacking. To examine population trends, we used survival estimates from telemetry data collected over 6 years (primarily for white-backed vultures [*Gyps africanus*]) and transect counts conducted over 8 years (for 7 scavenging raptors) in 3 large protected areas in Tanzania. Population trends were estimated using survival analysis combined with the Leslie Lefkovitch matrix model from the telemetry data and using Bayesian mixed effects generalized linear regression models from the transect data. Both methods showed significant declines for white-backed vultures in Ruaha and Nyerere National Parks. Only telemetry estimates suggested significant declines in Katavi National Park. Encounter rates calculated from transects also showed declines in Nyerere National Park for lappet-faced vultures (38% annual declines) and Bateleurs (18%) and in Ruaha National Park for white-headed vultures (*Trigonoceps occipitalis*) (19%). Mortality rates recorded and inferred from telemetry suggested that poisoning is prevalent. However, only 6 mortalities of the 26 presumed mortalities were confirmed to be caused by poisoning, highlighting the challenges of determining the cause of death when working across large landscapes. Despite declines, our data provide evidence that southern Tanzania has higher current encounter rates of African vultures than elsewhere in East Africa. Preventing further declines will depend greatly on mitigating poisoning. Based on our results, we suggest that the use of multiple techniques improves understanding of population trends over the short term.

KEYWORDS
cross-validation, decline, population models, survival, Tanzania, vulture

Importancia de combinar los conteos de transectos y los datos de telemetría para determinar las tendencias poblacionales a corto plazo de especies amenazadas a nivel mundial

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Resumen: Para evaluar las intervenciones de conservación es necesario obtener tendencias poblacionales confiables para escalas temporales cortas (<10 años). La telemetría puede usarse para estimar las tasas de supervivencia a corto plazo, además de que es una herramienta común para analizar las tendencias poblacionales, pero tiene limitantes y puede sesgarse con el comportamiento específico de los individuos marcados. Las tasas de encuentro calculadas a partir de transectos pueden ser útiles para analizar cambios en varias especies, aunque pueden tener intervalos grandes de confianza y verse afectadas por las variantes en las condiciones del censo. La declinación de los buitres africanos está bien documentada, pero hace falta el conocimiento sobre las tendencias recientes. Usamos las estimaciones de supervivencia tomadas de datos telemétricos recolectados durante seis años (principalmente del buitre *Gyps africanus*) y los conteos de transecto de siete especies carroñeras realizados durante ocho años en tres áreas protegidas en Tanzania. Estimamos las tendencias poblacionales con la combinación de análisis de supervivencia y el modelo de matriz Leslie Lefkovitch hecho con los datos telemétricos y usando modelos bayesianos de regresión lineal generalizada de efectos mixtos hechos con los datos de los transectos. Ambos métodos indicaron declinaciones significativas de *Gyps africanus* en los Parques Nacionales Ruaha y Nyerere. Sólo las estimaciones telemétricas sugirieron una declinación significativa en el Parque Nacional Katavi. Las tasas de encuentro calculadas a partir de los transectos también indicaron declinaciones de *Torgos tracheliotos* (38% de declinaciones anuales) y de *Terathopius ecaudutus* (18%) en el Parque Nacional Nyerere y de *Trigonoceps occipitalis* (19%) en el Parque Nacional Ruaha. Las muertes registradas e inferidas a partir de la telemetría sugieren que el envenenamiento es prevalente. Sin embargo, sólo se confirmaron seis muertes por envenenamiento de las 26 supuestas, lo que resalta los obstáculos para determinar la causa de muerte cuando se trabaja en paisajes amplios. A pesar de las declinaciones, nuestros datos proporcionan evidencia de que el sur de Tanzania tiene tasas actuales de encuentro con buitres africanos más altas que en cualquier otra parte del occidente de África. La prevención de declinaciones en el futuro dependerá principalmente de evitar el envenenamiento. Con base en nuestros resultados, sugerimos que el uso de técnicas múltiples incrementa el conocimiento sobre las tendencias poblacionales a corto plazo.

PALABRAS CLAVE
buitre, declinación, modelos poblacionales, Tanzania, supervivencia, validación cruzada

INTRODUCTION

Biodiversity loss has been well documented at a global scale, particularly since the 1970s (Díaz et al., 2019; Leclère et al., 2020; WWF, 2020). Studies assessing these declines often rely on historical data and focus on long-term trends. However, historical data (>20 years) tend to be biased in terms of the geographic and taxonomic scope for which they are available and are missing for large parts of the world. In particular, such data may be lacking in developing areas, where some of the most important remaining natural areas occur (Farooq et al., 2020). In efforts to mitigate declines, it is important to understand short-term (<10 years) population trends to assess management interventions. However, short-term population monitoring can be challenging. Telemetry is often used to examine population trends, but it can be limited by high costs (particularly of tracking devices and satellite fees), weight constraints, which may prevent use on smaller species, and technology constraints (i.e., areas without global systems for mobile communication) that limit duration of function and number of fixes (Newton et al., 2016). Line and roadside transects are also commonly used for population monitoring, but they too have limitations such as high cost, sensitivity to weather variability, variation in observers or vehicles used, lack of precision due to challenges in estimating detection probabilities, and high variability (McClure et al., 2021). Adaptive management requires robust estimation of key state variables (e.g., survival, abundance, and fecundity) and understanding population trends for endangered species, particularly over short periods.

As with many species, vulture population trends have been measured primarily over long periods (>20 years). Declines in African vulture populations have been well documented, leading to the uplisting of several species as endangered or critically endangered (Garbett et al., 2018; Ogada et al., 2016, 2022; Thiollay, 2007; Virani et al., 2011). The most significant threat to African vultures is poisoning, and vultures' tendency to aggregate while feeding makes them particularly susceptible (Ives et al., 2022; Kendall & Virani, 2012; Murn & Botha, 2017; Ogada, 2014, 2015). Indirect poisoning of vultures occurs when they eat a carcass laced with pesticides intended to kill carnivores in retaliation for human-carnivore conflict. In sentinel poisoning, poachers poison vultures directly to reduce detection. Vultures are also poisoned directly for the trade in vulture parts (Mateo-Tomás & López-Bao, 2020; Ogada, 2014; Ogada & Buij, 2011; Ogada et al., 2015, 2016). Current interventions to protect vultures include reducing human-wildlife conflict, improving antipoaching programs, and training in rapid poison response (Botha et al., 2017; Ogada et al., 2016). Due to their important role in waste removal and disease control, the loss of vultures is likely to have cascading effects; thus, it is critical to understand and mitigate the current declines (Buechley & Sekercioglu, 2016).

Efforts to assess short-term population trends in African vultures are needed to evaluate current actions, but they can be challenging. Nest counts have been used, but these provide information only about breeding individuals, and may obscure wider population trends, and are based on the assumption that individuals have not changed nesting location, which is not always the case (Benson & McClure, 2020; Hirschauer et al., 2020; Virani et al., 2012). While nest counts are more easily conducted for highly colonial cliff-nesting species, aerial surveys for tree-nesting species can be used to estimate abundance but are expensive and are based on the assumption that nests are highly visible from aircraft, which is not the case for all species in all areas (Monadjem & Garcelon, 2005; Murn et al., 2013). For example, African white-backed vulture (*Gyps africanus*) nests in palm trees and hooded vulture (*Necrosyrtes monachus*) nests tend to be difficult to spot from the air. To date, estimates of short-term population trends have relied on modeling and mark-recapture techniques based on wing tags (Monadjem et al., 2018; Murn & Botha, 2017). Such studies require high resighting rates (Monadjem et al., 2013, 2018), which are not possible in all areas (Kendall & Virani, 2012) and can be biased if tag loss is common (Cowen & Schwarz, 2006; Monadjem et al., 2013). There are also concerns about the impact of wing tags on vulture movement (Curk et al., 2021). Counts of vultures at provisioned carcasses are ineffective for estimating population trends, given the wide-ranging behavior of these species (Pomeroy et al., 2011, 2012).

Roadside transects have been widely used to assess changes in encounter rates (ERs) of large birds of prey over time, although standardized methods across studies are mostly lacking (McClure et al., 2021). Speed of the vehicle and position of observers in the vehicle have important ramifications for such methods (Murn & Holloway, 2016). Transect studies have mostly focused on habitat effects, emphasizing the importance of protected areas (PAs) (Herremans & Herremans-Tonnoeyr, 2000; Pomeroy et al., 2019; Shaw et al., 2019), rather than attempting to monitor population trends in the short term (Ogada & Keesing, 2010). When using transects to monitor vultures, an important challenge is the tendency for social species, particularly hooded, Cape, Rüppell's (*Gyps rueppellii*), and African white-backed vultures, to aggregate while foraging and feeding. Overdispersion caused by this behavior is typically addressed using negative binomial distribution (Lindén & Mäntyniemi, 2011), but this does not address the aggregation itself, which could lead to high counts when carcasses are present along a transect. We included carcass presence on the transect as a variable in a novel approach to addressing bias that may arise from this social behavior, which can lead to inconsistencies between counts on the same transect.

Distance sampling to establish density is difficult with high-flying birds, such as vultures; thus, it is often not used for these species for 2 reasons. First, estimates of the perpendicular distance from the observer typically used to estimate detection bias can be challenging to establish due to the high height and large distance from the observer at which vultures typically fly (Pomeroy et al., 2014). Second, as highly conspicuous birds in flight and when feeding, there is likely to be limited detection bias based on distance for these species, which means distance sampling does not greatly improve estimates, as it would for species that are harder to detect.

The use of telemetry for survival analysis is common in wildlife management (Kenward et al., 2000), but it has not yet been applied to detecting population trends in African vultures. Few researchers have conducted survival analyses with vultures (Newton et al., 2016). Recently, survival analysis for 2 critically endangered vulture species in Nepal was used to review a vulture safe zone, and as this technique becomes more common, it would be useful to understand how it compares with other methods.

Southern Tanzania is a key area for the conservation of vultures (Botha et al., 2017) because of its large protected area network and significant wildlife populations; yet vultures have received limited research attention in this region (Peters et al., 2022, 2023). It is recognized as a stronghold for other wide-ranging large mammal species, such as elephants and antelopes (Lindsey et al., 2017), which are a significant part of vultures' diet (Houston, 1974), further supporting the potential for it to be a stronghold for these endangered species.

We determined population trends based on 2 methods: survival estimates from telemetry data over 6 years (2015 to 2021) and transect counts conducted over 8 years (2013 to 2021) for 7 scavenging raptors in 3 large PAs in southern Tanzania. Our telemetry work targeted the critically endangered African white-backed vulture, because as a wide-ranging, social feeder, we expected this species to be more sensitive to the threat of poisoning in this landscape. We considered seasonal variation in counts and in telemetry-detected mortalities. We expected higher counts in the dry season when birds tend to be more aggregated in PAs (Kendall, 2013), but higher mortality in the wet season as measured by mortalities of tagged birds, when poisoning may be higher due to greater human-wildlife conflict and increased challenges in patrolling due to poorer road conditions (Kolowski & Holekamp, 2006). We used these two methods to explore the value and limitations of telemetry and transect methods in detecting population trends over short periods.

MATERIALS AND METHODS

Location

We focused on 2 landscapes in southern Tanzania (Figure 1). The vast Ruaha-Katavi landscape (115,000 km^2), with the key

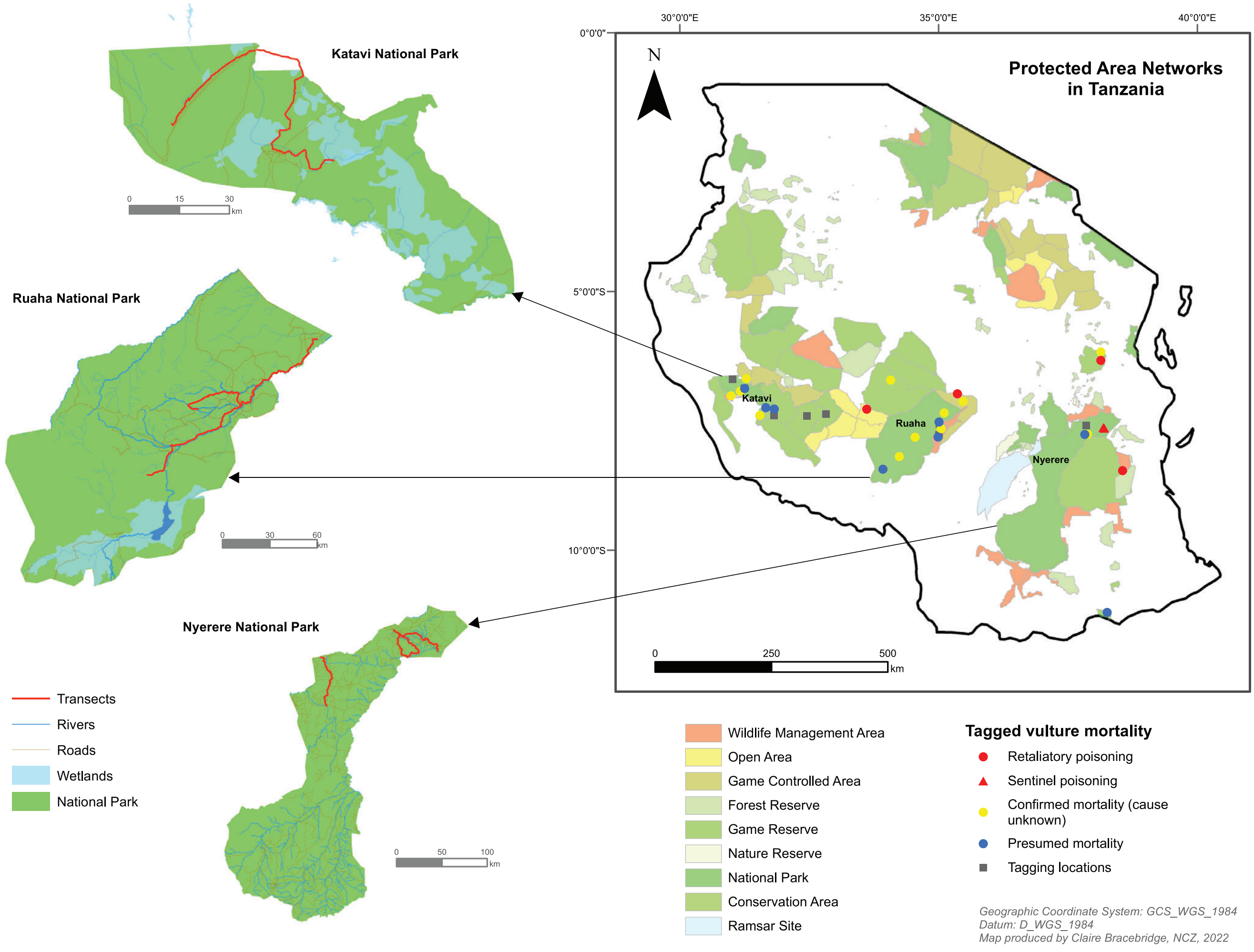

FIGURE 1 Tanzanian protected area network, locations of the 3 national parks where transect surveys of scavenging raptors took place, tagging locations in the telemetry study, and tagged bird mortality by cause of death (red lines, transect surveys).

PAs of Ruaha (20,226 km^2) and Katavi (4,471 km^2) National Parks (NPs) situated at the eastern and western sides of the landscape, approximately 250 km apart (based on Tanzanian NP and GRs websites [https://www.tanzaniaparks.go.tz/ and https://www.tawa.go.tz/]). About 200 km east of Ruaha NP is the greater Selous landscape (50,000 km^2), encompassing Selous GR, and Nyerere and Mikumi NPs. At the end of 2019, Selous GR was officially split into Selous GR (16,749 km^2) and Nyerere NP (30,893 km^2), now the biggest NP in East Africa. Based on our telemetry work, these two landscapes appear to have 2 separate vulture populations; the Eastern Arc Mountain range acts as a geographical barrier for east-west movement (Peters et al., 2023).

These NPs are connected by a network of GRs, forest reserves, game-controlled areas, open areas, and wildlife management areas (Figure 1). In Tanzania NPs, only nonconsumptive use is permitted (e.g., photographic tourism), whereas the other PA types, such as GRs, also permit consumptive use (e.g., hunting). Generally, the NPs have higher wildlife densities and, thus, were chosen as presumed areas of importance for vulture foraging and monitoring in the landscape. We focused on PAs (as for NPs) because higher rates of decline outside of PAs are already well described (Pomeroy et al., 2014; Shaw et al., 2019; Virani et al., 2011). In addition, for wide-ranging species, such as African white-backed vultures, it can be assumed that lower abundance and higher declines outside PAs than inside are partially explained by reductions in their use of these areas as they undergo habitat conversion and reductions in wildlife abundance. Thus, declines seen in PAs are likely more indicative of overall population trends and more predictive of future trends because PAs are more likely to retain wildlife, and their accompanying scavengers, over longer periods.

Land cover varied in our study areas; miombo, *Senegalia*, and *Combretum* woodland, and bushland and savanna grasslands predominated. Lakes and seasonal floodplains are present throughout Katavi, northern Nyerere, and southern Ruaha. There are 2 distinct seasons in southern Tanzania: dry season from May to October and wet season from November until April. Wildlife move away from seasonally flooded areas.

TABLE 1 Number of tagged vultures by location and species from 2015 to 2021.

	Species			
Tagging location	**African white-backed vulture**	**Hooded vulture**	**White-headed vulture**	**Total**
Ruaha-Katavi landscape ($n = 41$)				
Ruaha National Park	18	2	1	21
Rukwa Game Reserve	6	0	0	6
Katavi National Park	4	0	1	5
Lukwati-Piti Game Reserve	9	0	0	9
Nyerere-Selous landscape ($n = 21$)				
Nyerere National Park	21	0	0	21
Total	58	2	2	62

Telemetry

We tagged 62 vultures from 2015 to 2021. The majority were African white-backed vultures ($n = 58$; 44 adult birds, 13 immatures, and 1 fledgling), but we also tagged 2 hooded (both immatures) and 2 white-headed vultures (*Trigonoceps occipitalis*) (1 adult and 1 immature). Forty-one vultures were tagged in the Ruaha-Katavi landscape across 5 PAs. The majority were in Ruaha NP ($n = 21$), 6 in Rukwa GR, 5 in Katavi NP, and 9 in Lukwati-Piti GR. Twenty-one African white-backed vultures were tagged in northern Nyerere NP beginning in 2018 (Table 1 and Figure 1).

Vultures were trapped using nooses, set up as lines along carcasses, which they walked into while feeding (Watson & Watson, 1985; Kendall et al., 2014). Nooses were made of coated wire cord or monofilament 10–15 cm in diameter, and the noose line was made of parachute cord. The noose lines, consisting of 6–8 nooses, were staked into the ground with tent pegs for added stability. We used grass or carrion to help hold the nooses upright to increase the chance of capture. Once a bird was captured, its' eyes were covered to reduce stress, and the handler restrained both feet and the head. Processing took approximately 15 min per bird. Protocols for trapping work were approved by the North Carolina Zoo research committee and under a permit approved by the Tanzanian Wildlife Research Institute and Tanzania Commission for Science and Technology.

Solar-powered ARGOS/GPS PTT tags (Microwave Telemetry, Columbia, Maryland) (units) (70 g for larger species and 45 g for Hooded vultures) were attached as backpacks with 11-mm teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania). The backpacks are designed to fall off within a few years because recapture of tagged individuals is generally infeasible. Units were set to take GPS waypoints every hour from 0600 to 1900 and at 2400 each day (15 points per day) and to transmit data every day via ARGOS satellites. The transmitters provided information on velocity, altitude, and location (GPS coordinates) and had an internal activity sensor that detected movement. When a mortality event was identified based on transmitter metrics (lack of movement, limited activity based on the sensor, and changes in battery life, which could occur if the bird dies on its back), follow-up was made as rapidly as logistically possible to determine the cause of death.

Survival analyses

All statistical analyses were conducted in R 3.4.4 (Team RC, 2020). We report the maximum and minimum estimated hazard ratios (calculated as the exponential of the model coefficient) and the upper and lower 95% confidence intervals. Presumed mortalities were situations in which a unit stopped transmitting, activity sensor of the unit indicated the bird was inactive prior to end of transmission, and the area was searched, but we were unable to find the remains of the vulture (in most cases the unit was also missing, suggesting the bird and unit may have been moved or destroyed). The minimum treated presumed deaths as mortality events, whereas the maximum right-censored these individuals. In this way, we were able to establish an estimated range of survival probabilities for each covariate (Kenward et al., 2000).

We used the Kaplan–Meier survival estimate (Kaplan & Meier, 1958) to estimate survival for all vultures ($n = 62$) with the surv_fit () function in the survival package (Therneau & Lumley, 2015). For the following survival analysis, we removed 1 vulture that flew out of the study area as an outlier. To better understand survival probabilities across locations, we calculated survival probabilities from initial tagging to 2 years, generated by Kaplan–Meier analysis, for each NP. We then exponentiated this value to the 0.5 power to estimate annual survival probability across the 2 years. This estimate was later used in our population models to set survival of immatures and adults.

We used Cox proportional hazard (Cox PH) regression models (Cox, 1972), in coxph () function (R package survival [Therneau & Lumley, 2015]), to consider predicted survival probabilities as a function of time since tagging across different locations. Cox PH models allow for an examination of right-censored survival data, while including continuous and discrete covariates as a regression model. As a covariate in our model, we included the term *location*, which represented either the location of the mortality event or, for those censored, location of tagging (location:

Ruaha, *n* = 20; Katavi, *n* = 20; Selous, *n* = 21). Movement data for these 3 tagging sites show that Ruaha-Katavi and Nyerere NPs represent completely separate populations, with no overlap in movements between the 2 sites recorded to date (Peters et al., 2022). Although vultures do move between Ruaha and Katavi NPs, movements are highly suggestive of a subpopulation structure, which is likely to lead to variation in mortality rates between the sites (Monadjem et al., 2018). We were unable to include age as a covariate in any of our models due to unequal sample sizes (adults, *n* = 45; immatures, n = 17). Maximum estimates considered only individuals that were confirmed dead (*n* = 18) as a mortality event, whereas minimum estimates included presumed deaths (*n* = 8) as a mortality event. For both, individuals with active units as of December 2021 (*n* = 23) or individuals with failed units (*n* = 12) were right-censored.

Finally, we explored the variation in mortality rate between years of study in 2 ways. First, we created a time-to-event data set to explore whether and how the hazard for mortality may change over time. Each row in the data set represented 30 days of survival time for each vulture (*n* = 1,023). We used the survdiff() function (R package survival [Therneau & Lumley, 2015]) to implement a log-rank test to assess differences between observed mortalities and expected mortalities (Bland & Altman, 2004) for each year in the time-event data set (2016, *n* = 37; 2017, *n* = 107; 2018, *n* = 153; 2019, *n* = 213; 2020, *n* = 257; 2021, *n* = 256). This method tests the observed mortalities against the null hypothesis (or expected mortalities) without assuming a distribution. Second, we used the surv_adjustedcurves() function (R package survminer [Kassambara et al., 2017]) to build a univariate Cox PH model, which produced survival probabilities for each year, given days of survival since tagging. This method enabled a comparison of risk of death between the years, revealing which years, if any, exhibited significantly higher risk of death. Maximum and minimum estimates were considered for both methods. The year 2015 was excluded from these analyses due to the small sample size (only 2 birds were tagged that year).

Population growth estimates

We estimated the population projection for tagged vultures with a Leslie Lefkovitch matrix model (Monadjem et al., 2018). For this analysis, we categorized our birds into 6 age classes: 0–1, 1–2, 2–3, 3–4, 4–5 years old, and adults (>5 years old) because this species reaches sexual maturity after 5 years (Mundy et al., 1992). The fecundity of all age classes <5 years old was set to zero; for adults, it was set to 0.3. Fecundity was set to 0.3 (average fledging success of 0.60 divided by 2 [for females only]) (Monadjem et al., 2018).

We used an annual estimate of survival based on the estimated survival for the first 2 years from our Kaplan–Meier analysis in our population model to set survival for all age classes in each park, except the 0–1 age class. The survival value was assumed to be the same for all other age classes, given our low sample rate for immatures from telemetry study. The 0–1 age class (fledglings) survival rate was based on survival rates for fledgling Cape vultures (Piper et al., 1999). We created a prebreeding census matrix with 5 columns. The off diagonals corresponded to immature survival rates, the bottom right-hand corner was adult survival rate, and the top right-hand value represented the product of fledgling survival over their first year multiplied by the adult fecundity. In prebreeding census models, the 0–1 age class did not get its own column because numbers were generated from the survival multiplied by fecundity of the adult birds. We used the R package popbio to extract lambda, the population growth rate at the stable age distribution for 6 matrices. Lambda represented the upper and lower ranges of survival estimates for each of the 3 NPs.

For these models, we used estimates for fecundity and age of first reproduction, drawn from other studies and locations, and made several assumptions. We assumed a stable age structure that the survival rates of adults and of immatures older than 1 year are equal; and that reproduction takes place every year. This latter point results in an overestimate of fecundity because not all adults breed each year (Mundy et al., 1992). Hence, true fecundity is likely lower than estimated, but the proportion of breeding adults to nonbreeding adults in any given breeding season is not known, so a correction factor cannot be calculated. By setting fecundity at the higher end, we ensured that predicted declines in the vulture population would not be due to unnaturally low fecundity estimates. All models are available at https://github.com/kanead/trends/blob/main/code/Matrix_pop_model.R.

Transects

Vulture (hooded vulture, lappet-faced vulture [*Torgos tracheliotos*], Rüppell's vulture, African white-backed vulture, and white-headed vulture) and scavenging raptor (bateleur [*Terathopius ecaudatus*] and tawny eagle [*Aquila rapax*]) counts were performed along roadside transects. Flying and perched birds were counted by observers along both sides of the road. When it was necessary to stop to identify birds, additional birds sighted through binoculars only were not counted. Transects were treated as lines, and the distances measured with the vehicle odometer and time to complete the transect were recorded based on the start and end times of each transect. Transects were driven along main roads and other paths; the average pace was 30 km/h. Data were collected in CyberTracker on Nexus tablets. Transects were chosen to represent a large diversity of habitats and to maximize coverage across each park. Transects were also chosen along roads that were likely to be useable during wet and dry seasons, which often limited useable road networks for the surveys. All transects were completed on days of good weather (i.e., no rain) from 0900 to 1700, which is the peak activity period for most scavenging raptors, especially vultures (Mundy et al., 1992). All transects had at least 2 observers in addition to the driver; the number of observers was recorded as was the vehicle type.

For each bird sighted, we recorded distance along the transect, GPS location, species, flock size, activity (flying, perching, nesting, feeding), flight height (<10, 11–50, 51–200, >201 m), and distance from the road (0–100, 101–500, >500 m). Presence of all fresh carcasses >50 kg visible along the transects was also noted.

The effort was made to conduct transects at least once per year, but the frequency of replicates varied from year to year. Beginning in 2013, 4 transects in Ruaha, totaling 220 km, and 2 transects in Katavi, totaling 113 km, were surveyed 1–4 times per year during the wet and dry seasons up to 2021. Beginning in 2018, 3 transects in Nyerere NP (in what was previously the Selous GR), totaling 246 km, were conducted once or twice per year during the wet and dry seasons up to 2021.

Transect analyses

To assess population trends in scavengers across the 3 NPs, we ran mixed-effects generalized linear models with a negative binomial error structure. In these models, the total count by species for each time a transect was surveyed was used as the response variable. There were too few Rüppell's vultures to include them in any analysis. A negative binomial structure was deemed appropriate given that the data were counts and tended to be overdispersed (Lindén & Mäntyniemi, 2011). We fitted the model within a Bayesian framework with the brms package in R 4.0.3 (Bürkner, 2018). We modeled the counts as a function of time (in months, starting in August 2013) spent interacting with park. Additive effects were the presence of carrion, the season (wet or dry), and a random effect of the transect nested within the park. We also included the log length of the transect as an offset to account for unequal sampling effort. The priors on all slope terms were flat, but we also ran models with informative priors to assess their effect on the trends. This was done to curtail biologically unrealistic values for the population at the start of the survey (August 2013) for Nyerere, which was surveyed from 2018. We ran the models with 4 chains, 2000 iterations per chain, a warmup of 1000 iterations, and a thinning rate of 1. We modified the sampler (setting adapt_delta = 0.999, max_treedepth = 15) to deal with divergent transitions. We assessed model convergence by visually inspecting the chains, ensuring Rhats <1.1, and model fit by running a posterior predictive check.

Median monthly and yearly rates of change were estimated, as was the proportion of posterior distribution that was negative in the Bayesian regression models (Table 2). Katavi was the baseline estimate; hence, the other 2 parks were added to this value to provide their coefficient estimates rather than deviations from the baseline. Because the models provided estimates on the log scale, we converted them back into percent change with $[\exp(x)-1]*100$. Similarly, to get the annual percent change, we used $[\exp(x*12)-1]*100$. To get a measure of confidence in the sign (i.e., how probable were the negative trends) of the estimates, we measured the proportion of the posterior distribution that was less than 0.

We calculated recent ER as birds per 100 km from the last 3 years of study (2019–2021) for comparison with other work. ERs for the 3 southern Tanzania NPs were compared with other savannah ecosystems in East Africa based on recent counts from across Kenya (Ogada et al., 2022) and Uganda (Shaw et al., 2019).

RESULTS

Cause of death for tagged vultures

Of the 62 vultures tagged in southern Tanzania, we had 18 confirmed and 8 presumed mortalities (Table 3 and Figure 1, main inset). Most mortalities occurred in Ruaha NP and surrounding areas, 8 of which were confirmed and 3 presumed. Six confirmed and 2 presumed mortalities were recorded in Nyerere NP and surrounding areas, and there were 4 confirmed and 3 presumed mortalities in and around Katavi NP (Table 3).

Six mortalities were the direct result of confirmed poisoning events, all of which were on the edges or around Nyerere NP (4 mortalities) and Ruaha NP (2 mortalities) (Table 3, Figure 1, inset). Four poisoning events were linked to carnivore-livestock conflict on the periphery of Ruaha and Nyerere NPs, where livestock and wildlife use the same resources (water and grazing). Two sentinel poisoning events were recorded in Nyerere NP.

Survival analysis based on telemetry

A total of 62 vultures tagged in southern Tanzania provided 29,944 cumulative days of data. There were 13,609 days of data for vultures in Ruaha NP, 9,222 for vultures in Nyerere NP, and 6,565 for vultures in Katavi NP. The average length of tracking was 483 days per individual. Of these, 71.5–77% of the vultures (the majority of which were African white-backed vultures) survived 1 full year (365 days) after tagging (Figure 2). Overall median time for survival of tagged birds was 951–1,702 days (Figure 2) (survival estimates over time in Table 4). Our log-rank test was significantly different from the null hypothesis ($p < 0.001$). Both our log-rank test and Cox PH model confirmed that mortality was higher than expected in 2018 (average max–min: 2.1 times higher) ($p < 0.001$, SE: 1.1) (Table 5). There were 0 mortalities in 2017, despite having 10 tagged birds that year. Annual survival rates for each NP across 2 years after tagging were 89.4% (SE: 0.09) for Ruaha NP (no presumed mortalities across two years after tagging), 61.6–83.7% (SE: 0.1) for Katavi NP, and 80–85.4% (SE: 0.1) for Nyerere NP. These estimates were used in the population models. The effect of location on survival probability was not significant (maximum estimate: Wald = 0.2, df = 2, $p = 0.9$; minimum estimate: Wald = 2.32, df = 2, $p = 0.3$).

Population models based on survival estimates from telemetry data

Katavi had the lowest estimated population growth (0.69–0.92), followed by Nyerere (0.89–0.94). Ruaha had the highest estimated population growth (0.98). All were less than 1, suggesting a decline at the stable age distribution.

TABLE 2 Summary of mean estimates[a] of monthly and annual rates of change of scavenging raptor counts in 3 Tanzanian parks for all species from regression models related to transect data including confidence in demonstrated decline (based on proportion of posterior in negative).

Species	Park	Estimate	Monthly percent change	Annual percent change	Proportion of posterior in negative
White-backed vulture	Katavi	−0.003	−0.317	−3.734	0.719
White-backed vulture[b]	Ruaha	−0.016	−1.632	−17.923	1
White-backed vulture[b]	Nyerere	−0.026	−2.529	−26.462	0.982
Hooded vulture	Katavi	0.015	1.463	19.043	0.082
Hooded vulture	Ruaha	−0.003	−0.262	−3.094	0.645
Hooded vulture	Nyerere	0.011	1.125	14.371	0.309
Lappet-faced vulture	Katavi	−0.004	−0.44	−5.154	0.695
Lappet-faced vulture	Ruaha	−0.004	−0.439	−5.148	0.737
Lappet-faced vulture[b]	Nyerere	−0.04	−3.945	−38.308	0.975
White-headed vulture	Katavi	−0.007	−0.662	−7.657	0.751
White-headed vulture[b]	Ruaha	−0.018	−1.752	−19.113	0.989
White-headed vulture	Nyerere	−0.003	−0.279	−3.295	0.55
Bateleur	Katavi	0.001	0.055	0.665	0.435
Bateleur	Ruaha	−0.001	−0.144	−1.71	0.684
Bateleur[b]	Nyerere	−0.016	−1.616	−17.756	0.972
Tawny eagle	Katavi	0.001	0.11	1.323	0.452
Tawny eagle	Ruaha	−0.008	−0.789	−9.065	0.921
Tawny eagle	Nyerere	−0.04	−3.922	−38.13	0.9

[a] Estimates are changes when all other variables in the model are held constant.

[b] Estimates for which the proportion of the posterior distribution in the negative space was > 95% (i.e., probability that the estimate is negative and population is declining is very high).

TABLE 3 Types of mortality of tagged African white-backed vultures by location and across years ($n = 26$).

Mortality type	Location*	2015	2016	2017	2018	2019	2020	2021	Total
Retaliatory poisoning	Nyerere	–	–	–	1	–	1	–	2
	Ruaha	–	–	–	–	–	–	2	2
Sentinel poisoning	Nyerere	–	–	–	1	1	–	–	2
Confirmed mortality, cause unknown	Katavi	–	–	–	3	–	1	–	4
	Nyerere	–	–	–	–	2	–	–	2
	Ruaha	2	1	–	2	–	1	–	6
Presumed mortality	Katavi	–	–	–	–	1	–	2	3
	Nyerere	–	–	–	1	1	–	–	2
	Ruaha	–	–	–	–	–	3	–	3
Total mortalities		2	1	0	8	5	6	4	26
Total active tags		2	11	10	26	29	28	31	

*The location includes the park and the surrounding area.

Population trends based on transects

Population declines were found in Ruaha and Nyerere NPs (95% of posterior distribution of the date coefficient negative), but populations appeared stable in Katavi NP (Table 2). For African white-backed vultures, rates of decline ranged from 3.7% in Katavi to 17.9% in Ruaha to 26.5% for Nyerere NP (annual percentage change in Table 2). The estimates were taken from the regression models for the coefficients over time (Supporting Information Table S1). In particular, African white-backed and white-headed vultures had a high probability of being in decline in Ruaha NP, and African white-backed, lappet-faced vultures, and bateleurs had a high probability of decline in Nyerere NP, but all were much less likely to be declining in Katavi NP. For all other species, probability of declines was less than 0.95 (Table 2). All estimates of the population trend

TABLE 4 Survival estimates (minimum, maximum) from Kaplan–Meier analysis for tagged vultures.

Time (days since tagged)	N. Risk[a]	N. Event[b]	Survival Prob	Lower CI	Upper CI
1	62, 62	0, 0	1.00, 1.00	1.00, 1.00	1.00, 1.00
30	60, 60	2, 2	0.97, 0.97	0.92, 0.92	1.00, 1.00
60	53, 53	3, 3	0.92, 0.92	0.85, 0.85	0.99, 9.90
180	35, 35	11, 8	0.72, 0.77	0.61, 0.67	0.84, 0.89
360	31, 31	0, 0	0.72, 0.77	0.61, 0.67	0.84, 0.89
540	22, 22	2, 1	0.66, 0.74	0.54, 0.64	0.81, 0.87
720	17, 17	2, 0	0.63, 0.74	0.50, 0.64	0.76, 0.87
900	9, 9	2, 2	0.54, 0.64	0.40, 0.49	0.74, 0.83
1080	6, 6	3, 1	0.36, 0.55	0.21, 0.37	0.63, 0.82
1260	6, 6	0, 0	0.36, 0.55	0.21, 0.37	0.63, 0.82
1440	4, 4	1, 0	0.30, 0.55	0.16, 0.37	0.58, 0.82
1620	4, 4	0, 0	0.30, 0.55	0.16, 0.37	0.58, 0.82
1800	2, 2	1, 1	0.23, 0.41	0.10, 0.21	0.54, 0.83

[a] Number of tagged African white-backed vultures within the time interval.

[b] Number of mortalities within the time interval.

TABLE 5 Results from the log-rank test comparing observed deaths per year with expected deaths (presented as maximum, minimum) of tagged vultures.

		Maximum estimate				Minimum estimate			
Year[a]	n[b]	Observed deaths	Expected deaths	p[c]	χ^2	Observed deaths	Expected deaths	p[c]	χ^2
2016	37	1	0.2	0.7	3	1	0.2	0.77	2.5
2017	107	0	1.3	0.9	1.3	0	1.7	0.88	1.7
2018*	153	7	1.7	0.005	16.6	8	2.4	0.02	13.3
2019	213	3	3.2	1	0	5	4.7	1	0
2020	257	3	4.4	0.99	0.4	6	7	0.99	0.2
2021	256	2	5.2	0.8	2	4	8	0.84	2

[a] Asterisk: suggested notable deviations from the observed mortality rate.

[b] Number of rows in the time-event data set for each year.

[c] Calculated at a significance level of 0.05.

had uncertainty (95% CIs in Supporting Information Table S1), so we use these credible intervals to measure confidence that there was a decline. These trends held when the models were tested with more informative priors (e.g., African white-backed vultures in Supporting Information Appendix S1).

Carcass presence along the transect increased counts for African white-backed vultures and hooded vultures (estimate for African white-backed vultures was 0.629, 95% CI 0.141–1.172, corresponding to an 88% increase), but did not likely affect the other species (Supporting Information Table S1). Full details on average ERs by year, season, and NP are in Supporting Information Table S2.

Comparison with other sites

Other than hooded vultures and tawny eagles, southern Tanzania had the highest recent ERs for 4 of the 6 scavenging raptors considered followed by Kenya and Uganda (Table 6).

DISCUSSION

Vulture declines and possible causes in southern Tanzania

Overall, our study shows declining population trends of endangered vultures and other scavenging raptors in southern Tanzania. For white-backed vultures, telemetry and transects suggested significant declines in Ruaha and Nyerere NP. However, annual rates of decline estimated using population models with survival estimates based on telemetry, were higher for Katavi NP (8–31%) than those estimated by transects (3.7%), which suggested a nonsignificant probability of decline (72%). Transect data also suggested declines for other species in Ruaha and Nyerere NPs, including lappet-faced and white-headed vultures and bateleurs.

Our detected rates of annual mortality in southern Tanzania of 23–28%, based on telemetry, are similar to those found in the Mara-Serengeti ecosystem (~25%), an area with high rates

TABLE 6 Comparison of average encounter rates (number per 100 km) of scavenging raptors from the last 3 years of this study (2019-2021) (Tanzania) with recent counts for protected areas (PAs) in Kenya and Uganda.

	Tanzania[a]			**Kenya**[b]	**Uganda**[c]
	Ruaha	**Katavi**	**Nyerere**	**several protected areas**	**several protected areas**
African white-backed Vulture	26.6	52.0	42.9	18.2	9.1
White-headed vulture	1.4	2.6	1.9	NA	0.5
Lappet-faced vulture	4.9	2.4	3.3	2.2	0.9
Hooded vulture	3.7	2.9	4.1	4.0	0.5
Bateleur	21.8	15.8	12.7	8.2	7.7
Tawny eagle	3.8	1.2	0.2	5.8	2.5

[a] This study.
[b] Ogada et al. (2022).
[c] Shaw et al. (2019).

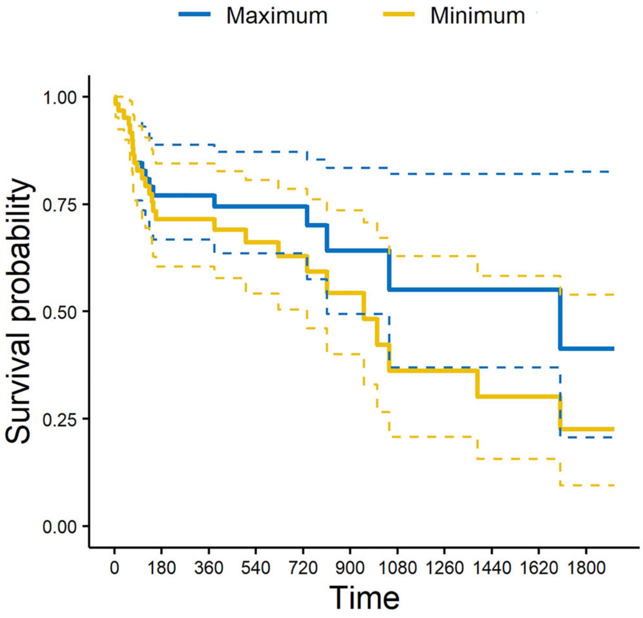

FIGURE 2 Kaplan–Meier survival curve for African white-backed vultures for time since tagged in days, reflecting maximum and minimum estimates (dashed lines, 95% CI).

of poisoning. However, methods of estimating declines differed between southern Tanzania and the Mara-Serengeti ecosystem (Kendall & Virani, 2012). In sites with less human influence, survival for vultures tends to be considerably higher (Arrondo et al., 2020; Monadjem et al., 2013, 2014;). Monadjem et al. (2013) found the annual survival rate of adult African White-backed vultures to be 99.9% in South Africa after the age of 2 based on a mark-recapture study with wing tags. Other studies suggest similarly high survival rates for adult *Gyps* vultures: 96.8% for vultures in areas with less human influence (Arrondo et al., 2020) and 91.3% (±6.3%) for Cape vultures (Monadjem et al., 2014).

Telemetry studies are one of the best ways to detect poisoning and can provide important insights into poisoning hotspots, causes, and frequency (Kendall & Virani, 2012). We found that poisoning in southern Tanzania is sometimes motivated by retaliatory poisoning of carnivores, sentinel poisoning related to bushmeat snaring, and trade in vulture parts. Retaliatory poisoning was detected across the PA networks in our study and primarily occurred in areas surrounding the NPs, where the presence of pastoralism and vulture foraging likely overlap (Peters et al., 2023). Challenges to the mitigation of retaliatory poisoning are the growth of pastoral populations, particularly around the northeast edge of Nyerere NP, and the nomadic nature of pastoralism in southern Tanzania (Beattie et al., 2020; Kuiper et al., 2015).

Although we found only 6 confirmed poisoning events, most of which killed fewer than 100 individuals over an 8 year period (C.K. and C.B., personal observation), modeling studies show that even infrequent poisoning can have devastating effects for vultures. For Asian vulture declines, Green et al. (2004) estimated that very low poisoning rates (0.13% of carcasses) can lead to high levels of decline (22–50% annually), and Murn & Botha (2017) suggest vulture population extinction in southern Africa could occur with as little as 1 poisoned elephant carcass every 2 years. While our number of confirmed large poisonings is small, many of the presumed mortalities ($n = 8$) or those with unconfirmed cause ($n = 12$) were suggestive of smaller poisoning events, based on tags having been removed or the location of death being near park boundaries. This is particularly concerning given recent findings by Rigas et al. (2021) that even small, but frequent, poisoning events can have devastating consequences.

In addition, our telemetry survival estimates suggest that there was variation between years in mortality rates, where the highest mortality occurred in 2018. The lack of mortalities detected in 2017 (when 10 tags were active) and lower rate of mortality in 2016, followed by consistently higher mortality rates across 2018–2021, suggest that poisoning may be on the rise. Transect analyses did not detect differences in decline between years, although a previous exploratory investigation of data with generalized additive models suggested that declines began around 2018, which is consistent with increasing mortalities from telemetry data seen starting in 2018. While poisoning incidents may be highly variable between years, increases in poisoning incidents in the last few years, possibly due to limitations on funding and resources for antipoaching efforts—as a result of COVID-19 pandemic—could be driving an increased rate of decline.

Comparison of the two methods

Identification of declines, even where their exact magnitude may be hard to determine, in the short term (<10 years) is critical for evaluating conservation interventions. We found that even with a relatively small sample size telemetry and transects can be used to assess short-term population trends. However, the magnitude of decline varied between methods for the 3 sites considered. Telemetry studies may have small or uneven sample sizes because of cost limitations and are not suitable for all species due to body-size requirements for tagging. For instance, the lower duration of tags on birds in Katavi (caused by 5 birds in Katavi being tagged toward the end of our study, despite having the same total number of individuals tagged) relative to other sites contributed to the larger range in the decline estimates from telemetry and perhaps to the higher rates of decline estimated for this site, as compared with the transect estimates. It has been suggested that the trappability of animals, particularly with passive traps like what we used, may lead to a biased sample of individuals with systematic differences in personality or life-history characteristics (Biro 2013; Garamszegi et al. 2009, Stuber et al. 2013). It is possible that vultures trapped and tagged could be bolder or more exploratory than the rest of the population, which could lead to higher estimates than actual mortality rates based on telemetry studies. However, rates of decline from telemetry were not consistently higher than those calculated from transects.

For telemetry, survival estimates can be difficult to extrapolate to population trends. For the population models, we used estimates for fecundity, age of first reproduction, and population size pulled from other areas, and made several assumptions. We assumed that the survival of immatures and adults were equal, partially because we lacked specific data on immatures, but also following the reasoning explained herein. Adults were expected to have higher survival rates than immatures in the absence of threats (Monadjem et al., 2018; Piper et al., 1999). However, if mortality from poisoning is compensatory for immatures, which normally suffer higher mortality rates than adults due to starvation, as is likely in this system, then we might expect adults and immatures to have similar mortality rates. In addition, sensitivity and elasticity testing for African white-backed vulture population models show that adult survival is the main factor affecting population trends, as would be expected for a *K*-selected species (Monadjem et al., 2018). Thus, population growth estimates extrapolated from adult survival estimates from telemetry still provide useful insight into site-specific trends.

Our data suggest that poisoning is more common in Nyerere NP, based on the detection of 4 poisoning events in 4 years, which also killed a larger number of vultures, as compared to 1 in Ruaha NP and 1 in between Ruaha and Katavi NP in 7 years (Kendall and Bracebridge, personal observation). Despite this, neither our survival nor transect results showed differences by location. Other studies have demonstrated that variation in poisoning rates between 2 sites that were 200 km apart (which is a similar distance between Nyerere NP and Ruaha NP) led to different survival rates in subpopulations (Monadjem et al., 2018). A limitation of our study is that we had fewer years and less data overall for Nyerere NP than for the Ruaha-Katavi landscape, which may have prevented us from detecting a difference between sites. Future studies are needed to explore the subpopulation structure of vultures in southern Tanzania to inform conservation efforts.

Despite on-going population declines, we found that southern Tanzania is an important stronghold for African vultures and has some of the highest ERs for African white-backed vultures, lappet-faced vultures, and white-headed vultures in East Africa. As had been predicted previously due to their mixed woodland savannah habitat, these large PAs in southern Tanzania had some of the highest ERs for the critically endangered white-headed vultures in the continent (Murn et al., 2016); hence, this region is crucial for their preservation. African white-backed vulture ERs in southern Tanzania were more than double those in Kenya in some parks (Virani et al., 2011). Although we considered only PAs, we expect even higher rates of decline outside these parks, as shown elsewhere in Africa (Pomeroy et al., 2014; Shaw et al., 2019; Virani et al., 2011). Our results demonstrate both significant declines and the importance of southern Tanzania for the conservation of African vultures, where greater efforts will be needed to mitigate the threat of poisoning.

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ORCID

Corinne J. Kendall https://orcid.org/0000-0003-4429-4496

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SUPPORTING INFORMATION

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

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