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Habitat selection by an extraordinary savannah raptor: environmental factors driving abundance of the Secretarybird *Sagittarius serpentarius* in the Serengeti National Park (Tanzania)

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ABSTRACT

Capsule: We estimated the population size of the Secretarybird in the Serengeti National Park and identified ecological factors characterizing the high-density areas, which should be established as high-priority conservation zones.

Aims: To estimate the abundance and density of Secretarybird within the Serengeti National Park (SNP) and investigate environmental variables driving its abundance.

Methods: In 2023, Secretarybirds were counted along 52 transects (average length = 15.3 ± 1.8 km), replicated at least three times outside of the breeding season. Twelve transects with the most observations were repeated up to eight times. Abundance and density were estimated through multiple-covariate distance sampling, while habitat selection was assessed using generalized additive mixed models and generalized linear models.

Results: We estimated an average density of 1.3 Secretarybirds/10 km^2 and an abundance of 1,513.3 individuals. Areas of highest density averaged 2.3 Secretarybirds/10 km^2 and 622.5 individuals. The greatest abundances occurred in transition zones between extensive grassland with high vegetation cover and habitats characterized by open woodlands or treed shrublands. Secretarybirds preferred flat environments with relatively more seasonal rivers and an annual precipitation of < 900 mm. Abundance decreased in grasslands with low vegetation cover and where open grassed woodland coverage was >20%. The probability of spotting single individuals versus pairs was higher in the western and central SNP and in more heterogeneous habitats with greater coverage of open grassed woodland and dense treed grassland. Closed treed shrublands were preferred by pairs. Secretarybird abundance was lower where the proportion of habitat burned for prescribed fires exceeded 60%.

Conclusion: These results for the Secretarybird's demography and ecology in the Serengeti ecosystem are essential for a long-term monitoring programme and conservation actions in Tanzania.

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Establishing the population estimate for a threatened species is important for updating its current conservation status (Stroud *et al.* 2006, Woodward *et al.* 2020, IUCN 2022, Morales & Bretagnolle 2022), and also to identify areas with the highest densities of individuals for rigorous protection, which could ultimately constitute source sites for future translocations (Griffith *et al.* 1989, Seddon *et al.* 2012). Furthermore, long-term monitoring based on the collection of demographic parameters enables robust predictions of population viability (Boyce 1992, DeSante *et al.* 2005, Aresu *et al.* 2021, Dimitriou *et al.* 2021, Oppel *et al.* 2021, Fay *et al.* 2023).

Another crucial reason for establishing and/or reviewing a species' conservation status is to plan a sampling design that accounts for detectability and spatial variation (Yoccoz *et al.* 2001); indeed, a major problem in conservation biology is the ignoring of imperfect detection that can lead to underestimation of the number of individuals, and biased results for the population size of target species (Yoccoz *et al.* 2001, Williams *et al.* 2002, Andersen 2007, Martin *et al.* 2007, Berthiaume *et al.* 2009, Sanz-Pérez *et al.* 2020). Adjusted estimates for the probability of detection are essential to control for the influence of environmental and behavioural factors that may

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negatively affect the detection of individuals (Banks-Leite *et al.* 2014). Moreover, an advantage of models that consider detectability, such as those built with distance sampling, is that they can provide a measure of uncertainty for abundance and density estimates in the sampled area (Buckland *et al.* 2015).

Knowing the number of individuals and the key vital rates within a population is often not enough to understand the reasons for higher/lower abundance and survival of individuals in specific areas. The distribution of a species and its density within an ecosystem are the result of complex relationships involving biotic and abiotic factors (including human pressures), and mobility (Soberón & Peterson 2005, Soberón 2007, 2010). For this reason, an understanding of the ecological variables that drive the distribution and the abundance of a species within an ecosystem is a key aspect of conservation biology (Morris *et al.* 2008, Costa *et al.* 2010, Zhu *et al.* 2013, Fryxell *et al.* 2014). In the last decades, several attempts have been made to model species distribution for management purposes (Wilson *et al.* 2011, Guisan *et al.* 2013, Carroll *et al.* 2024). Since a species distribution model (Guisan & Zimmermann 2000) or an ecological niche model (Peterson 2006) mainly focus on modelling the global distribution of a species or, in any case, its distribution on a wide scale (Elith & Leathwick 2009, Kramer-Schadt *et al.* 2013), they are often not appropriate when seeking to provide reliable guidelines to stakeholders trying to manage the species on the local scale. This is because sampling effort is not often equal across the range of the target species, leading a model to be limited by the coarser resolution of the less sampled areas (Kramer-Schadt *et al.* 2013). Instead, a uniform and independent sampling design for the survey area allows the collection of more representative data on the presence or abundance of the target species, avoiding bias in the results of ecological studies (Barabesi & Fattorini 2013). Another potential problem is that many models are fed only by occurrences retrieved from the Global Biodiversity Information Facility (GBIF). The spatial bias often found in this database may have negative effects on the model's predictive ability (Beck *et al.* 2014, De Araujo *et al.* 2022, García-Roselló *et al.* 2023). Even if large-scale species distribution models provide a useful overview of where a species is likely found, a habitat selection model at finer scale, built with data collected using a representative sampling design of the entire study area, is more adequate when immediate conservation effort is required locally (Whittingham *et al.* 2007, McAlpine *et al.* 2008, Mateo-Tomás & Olea 2009). Thus, a sampling design that considers the detection probability and environmental variability is necessary to avoid biased results on demography and ecology, especially if the target species is threatened and knowledge of its biology is scarce, as in the case of the Secretarybird *Sagittarius serpentarius* in East Africa. The information acquired in this way provides a solid basis for future studies and for implementing effective conservation actions.

The Secretarybird is a diurnal raptor that is widespread in grasslands and savannas in sub-Saharan Africa, is classified as Endangered in the IUCN Red List of Threatened Species (BirdLife International 2024), and is the sole extant member of the Sagittariidae family (Mindell *et al.* 2018). Secretarybirds are mainly terrestrial, spending most of the day hunting on the ground (often in pairs), and are territorial and monogamous (Kemp 1994, 1995). Observed single individuals are mostly dispersing immatures or partners alternating in incubation or parental care. Well-known threats to Secretarybirds are habitat loss due to urbanization, bush encroachment or transformation for agriculture (Hofmeyr *et al.* 2014, Shaw *et al.* 2024), collisions with energy infrastructure (Whitecross *et al.* 2019), road kills (Herholdt & Anderson 2006, Lyamuya *et al.* 2021, Ramella Levis *et al.* 2023) and direct persecution for cultural beliefs or traditional medicine (Kioko *et al.* 2015, Ramella Levis *et al.* 2023). Indirect poisoning, excessive burning of grasslands, and diseases are other potential threats (Baker *et al.* 2010, Amakobe *et al.* 2019, Romani *et al.* 2024).

The Secretarybird is declining globally (BirdLife International 2024). In Botswana and Kenya, the encounter rate during raptor road counts has significantly decreased (Garbett *et al.* 2018, Shaw *et al.* 2024). In South Africa, Lesotho and Eswatini, however, a recent study based on citizen science data indicated the Secretarybird population had not declined alarmingly since 2007 (Brink *et al.* 2024). The current estimate of mature individuals in the whole range is still very imprecise, perhaps ranging between 6,700 and 67,000 birds (BirdLife International 2024).

Most of the studies of the Secretarybird's ecology have been conducted in South Africa (Kemp 1995, Herholdt & Anderson 2006, Hofmeyr *et al.* 2014, Whitecross *et al.* 2019, Brink *et al.* 2024), but these may overlook any adaptations to different latitudes, environments or pressures, resulting from specific phenotypic expressions (Hamilton 1961, Botero *et al.* 2014, Thompson *et al.* 2022). In East Africa, protection work for the Secretarybird is still poor, even though the species requires immediate action,

mainly due to limited information on demography, ecology and behaviour that is essential for an effective future action plan. In Tanzania, the Secretarybird is mainly distributed in the north of the country (Baker *et al.* 2010) and, aside from its general distribution, fundamental data regarding its biology are currently lacking.

This study aimed to increase the understanding of the ecology and demography of the Secretarybird in the Serengeti National Park (SNP) in northern Tanzania. Given its large area, the availability of sufficient trophic resources and potentially suitable environmental conditions, this Protected Area could represent one of the last strongholds in East Africa that still supports a source population of Secretarybirds. Specifically, we addressed the following questions: (i) how large is the Secretarybird population in the SNP? (ii) Is there significant spatial variation in density? (iii) At what time of day are the birds more detectable? (iv) Which environmental factors affect the species' abundance? (v) Are there spatial differences in habitat selection between pairs and single individuals?

To answer these questions, we conducted road counts according to a sampling design that covered the entire study area and was representative of all habitats present. Using distance sampling, we adjusted density and abundance estimates for imperfect detection by taking into account environmental, behavioural and temporal variables that could have affected the observation of individuals. Abundances detected in uniformly and independently distributed sampling units throughout the surveyed area were used to model the Secretarybirds' habitat selection in the SNP, thereby identifying ecological factors characterizing the areas of highest density. Finally, we discuss the potential implications of our findings for the future management of Secretarybirds in East Africa.

Methods

Study area

The SNP (14,763 km^2) is part of the Protected Areas (PAs) network within the Serengeti – Mara ecosystem (*c.* 30,000 km^2) and is under the management of the Tanzania National Parks Authority. The wider Serengeti – Mara ecosystem encompasses the Tanzania – Kenya border, between latitudes 1–3° S, and longitudes 34–36° E. In this dynamic ecosystem, a wet and a dry season occurs cyclically; the wet season is bimodal, with a short rainy period between November and December, and a long rainy period between March and May (Norton-Griffiths *et al.* 1975). The wet season can fluctuate annually, with the short rains sometimes not occurring in the south-east of the ecosystem, or the absence of a break between the short and long rains.

Grasslands, woodlands and forests are the main vegetation types, and their distribution follows the gradient of the mean annual precipitation (between ~500 mm/year in the south-east and ~1,100 mm/year in the north-west), and also the rainfall seasonality, varying soil characteristics, topography and the Blue Wildebeest *Connochaetes taurinus* migration (Sinclair *et al.* 2019). This results in a greater concentration of extensive grassland in the central-eastern and central-southern belts of the SNP, and more woodlands and forests in the western and northern belts, which are characterized by more heterogeneous environments. Grasslands and woodlands are especially influenced by fires that, together with grazers and precipitation, are the major driving forces of this ecosystem (Sinclair & Norton-Griffiths 1979, Anderson *et al.* 2007).

The SNP can be considered the core area of the Serengeti – Mara ecosystem, with an elevation between 920 and 1,850 m a.s.l., with the lowest region near the Speke Gulf of Lake Victoria and the highest in the Gol Mountains. As well as the environmental characteristics that are potentially suitable for Secretarybirds, the SNP study area (Figure 1) was chosen for also recording the largest number of Secretarybird observations in Tanzania (Baker *et al.* 2010, GBIF 2023) and – being an extensive protected area buffered by the other PAs of the larger Serengeti-Mara ecosystem – the SNP should be subject to relatively low human pressure from land-use change, community settlements and poaching. Moreover, the SNP management policy bans all hunting. Thus, the SNP could be considered a controlled environment to assess the ecological requirements of the Secretarybird in Tanzania.

Sampling design

The multiple-covariate distance sampling (MCDS) method (Marques & Buckland 2003) was used to answer the first three research questions. The tessellation stratified sampling (TSS, Stevens 1997) was chosen as the sampling design because it performs better than uniform random sampling in obtaining unbiased density estimates when distance sampling is used (Barabesi & Fattorini 2013). TSS requires that transects are independently and uniformly planned

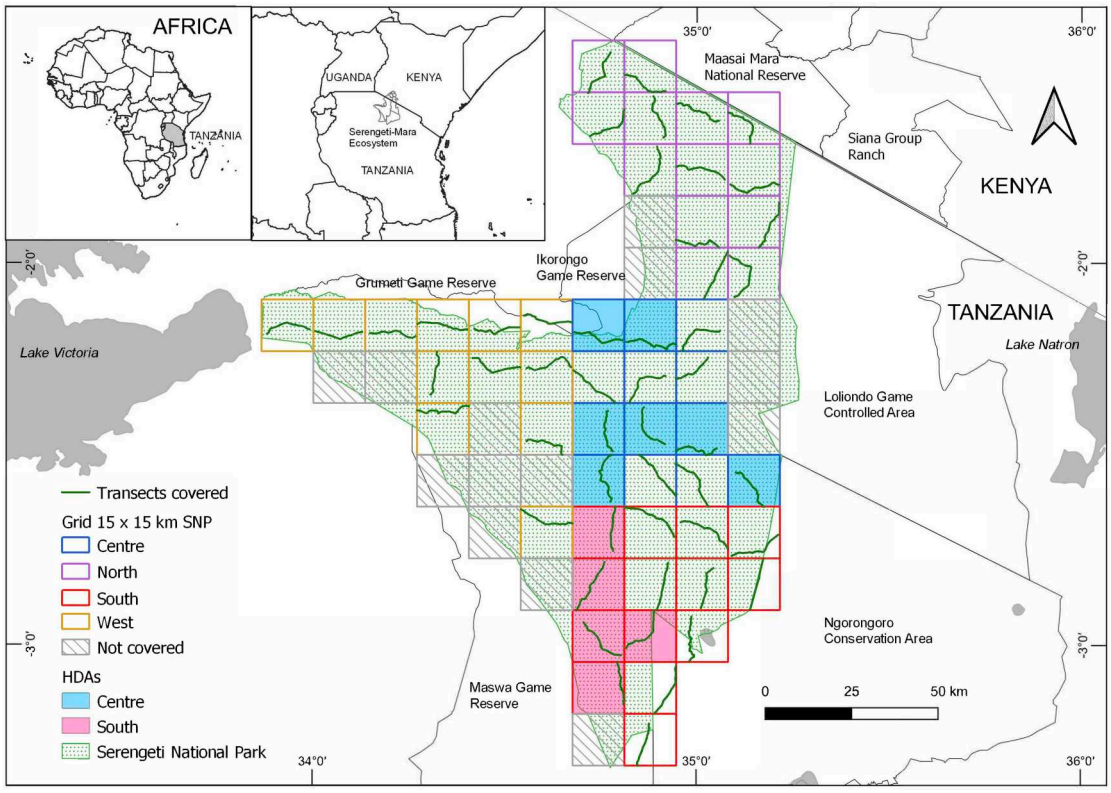

Figure 1. Study area and transects covered to investigate the population size and habitat selection of the Secretarybird in the Serengeti National Park (SNP) in 2023. The different colours of the grid represent the four *strata* (SNP sectors: Centre, North, South, West). Dashed lines indicate the cells are not covered. Filled cells indicate the Highest Density Areas (HDAs).

within adjacent polygons, which means that there must be just one randomly drawn transect per polygon (Barabesi & Franceschi 2011, Barabesi *et al.* 2012, Barabesi & Fattorini 2013). In fact, an assumption of distance sampling is that transects are placed irrespective of the distribution of the target species (Burnham *et al.* 1985, Buckland *et al.* 2001, Buckland *et al.* 2015). Moreover, according to distance sampling, at least 10–20 replicated transects should be planned to sample an area, and the survey should allow the collection of at least 30–40 observations, and ideally 60–80 (Burnham *et al.* 1985, Buckland *et al.* 2001, Buckland *et al.* 2015). To meet these assumptions, a grid of 66 square cells (15 × 15 km) was superimposed onto the SNP (Figure 1), resulting in 66 transects with an average length of ~15 km. Too large cells with longer transects would not have given a good representation of all habitats.

The sampling design was developed on QGIS v. 3.16 (QGIS Development Team 2022). Inside each cell, the transect was drawn by tracing two random points 15 km apart, and choosing the road closest and most aligned with the line between the two points. For the latter, Google Earth (© Google LLC, https://earth.google.com/web) and OpenStreetMap (© OpenStreetMap, https://www.openstreetmap.org) were used as base-map layers, as they show most of the main and secondary roads of SNP. When the focal road deviated sharply from the alignment of the drawn line, we tried to terminate the transect off-road to keep it as linear as possible and avoid pseudo-replicates (Burnham *et al.* 1985, Buckland *et al.* 2001, Buckland *et al.* 2015), where this was allowed by the lack of woodlands, swamps, permanent rivers and excessive slope. The transects falling in cells with no roads, in very remote areas, or in Black Rhinoceros *Diceros bicornis* Intensive Protection Zones (IPZs) were discarded. In this way, 52 out of the 66 planned transects (78.8%) were travelled (length: $\bar{x} = 15.3 \pm 1.8$ km) and, given that there was just one transect per cell, ~80% of the park was actually sampled (Figure 1).

Since one of the objectives of this study was to identify spatial differences in the Secretarybird's densities across the park, we stratified density and abundance into four main sectors: north (N; 13 cells), centre (C; 13 cells), west (W; 12 cells) and south (S; 14 cells) (Figure 1). Finally, in order to identify the core area for the Secretarybird in the SNP, we estimated density and abundance specifically in the subsample of cells that recorded the highest number of observations

during the first transect replicates, subsequently named Highest Density Areas, HDAs (see the section below headed 'Secretarybird abundance and density – MCDS models'; Figure 1).

A problem encountered in some studies using road transects to count raptors is human disturbance due to the presence of roads (traffic, infrastructure, telephone lines), which affects detectability (Olson *et al.* 2015). However, we assumed this is not an issue in the SNP given that animals, even the most elusive, are usually seen by tourists, and large raptors, including the Secretarybird, often nest just a few metres from the roads, camps and lodges (Eurafrica Conservation Projects unpublished data).

Road counts

Transects were replicated at least three times outside the breeding season to increase detectability, since in this ecosystem brooding Secretarybirds are mostly hidden in the canopy (Ramella Levis *et al.* 2023). Due to limited information for the breeding period of Secretarybirds in Tanzania prior to Ramella Levis *et al.* (2023), the survey was scheduled based on the previous years' active nests observed by park or lodge personnel and safari companies. Two replicates were performed for 52 transects between 15 January and 17 February 2023, since most nest observations in previous years were in April and May. The third replicate occurred between 28 June and 14 July 2023, given that in 2023 the nesting period started with the long rainy season and finished with the dry season's onset, with most breeding attempts detected in March–April (Romani *et al.* 2024).

The 12 pre-breeding transects within the cells with the highest number of observations (Figure 1) were replicated four to eight times (median = 8) until 12 August 2023 to have a sample large enough for reliable density estimates for this subsample (HDAs). Transects were travelled at speeds of 15–30 km/hour by a driver and two observers who remained the same throughout the sampling period. An open-roofed vehicle enhanced visibility. Sighting distances and angles were measured using a Kahles HELIA 42 RF binocular (accuracy ±1 m), a Nikon Prostaff 1000i rangefinder (accuracy ±0.9 m) and a digital compass (accuracy ±3 degrees). Locations were recorded with a handheld Garmin eTrex 10 (accuracy ±2 m) and the Terra Map app. Flying individuals sighted during replicates ($n = 4$; 1.1%) were excluded from counts, because we could not calculate exact distances from the transect. Censuses occurred from 6:00 to 18:00 hours. Finally, observations of pairs and single individuals beyond the start/end of the transects and before the breeding season were recorded and added to transect data to identify spatial differences in habitat selection between Secretarybird pairs and single individuals, which was our final research question.

Environmental and time variables

Raptor activity and detectability can vary during the day (Bunn *et al.* 1995, Vergara 2010, Oliveira *et al.* 2018, Tiwari *et al.* 2023). To test for differences, daily observations were grouped into four daily phases (P1, 06:01–09:00 hours; P2, 09:01–12:00; P3, 12:01–15:00; P4, 15:01–18:00). Together with perpendicular distance, coordinates, date and time, we recorded the number of individuals in a cluster (i.e. two or more Secretarybirds <300 m apart) and whether individuals were on the ground or trees. Three methodologies were employed to extract ecological variables:

- To estimate the density/abundance of individuals in the SNP and HDAs, a 0.7 km radius buffer was constructed for each transect observation, centred on the transect point from where distance was measured. The buffer was divided into two parts by the transect, and the covariates used to improve the detection function were extracted from the hemisphere facing/containing the observation. A radius of 0.7 km corresponded to the truncation distance (see below: 'Secretarybird density - MCDS models'), beyond which transect data were not considered for density estimates (Buckland *et al.* 2015).
- To determine which environmental factors affected abundance in the SNP, a 1.5 km radius buffer (linear buffer) was applied to both sides of the 52 travelled transects, from which covariates were extracted. This methodology was applied in previous studies determining environmental characteristics associated with species abundance (Ingold 2010, Pandolrno *et al.* 2011, Lara-Romero *et al.* 2012, Jankowiak *et al.* 2015, Chiatante & Panuccio 2021). A 1.5 km radius reflected the Secretarybird's average density estimate for the study area (see Results: 'Detectability, abundance and density in SNP').
- To determine spatial differences in habitat selection between individuals or pairs, covariates were extracted from a 2.0 km radius buffer around each observation of pairs or singles (ring buffer), including observations beyond the start/end of

transects. This radius reflected the expected territory size of a pair derived from density estimates (see Results: 'Detectability, abundance and density in SNP').

Environmental variables of topography included mean and median elevation and slope, computed within each buffer using the Copernicus GLO-30 Digital Elevation Model (European Space Agency 2024), a digital surface model of 30 m resolution. We also counted the number of hills within the 52 linear buffers and measured the distance from the closest hill to each ring buffer. A water courses vector layer for the Serengeti-Mara ecosystem was used to calculate the total length (km) of permanent and non-permanent rivers within buffers.

Using a 30 m resolution raster (Reed *et al.* 2009), we extracted the percentage of 20 vegetation types within the linear and ring buffers, following Grunblatt's *et al.* (1989) nomenclature (summarized in Supplementary Table S1). Using the vegetation layer we calculated Shannon's diversity index (SHDI) as a habitat heterogeneity metric (Uuemaa *et al.* 2009, Malinowska & Szumacher 2013).

We extracted data for precipitation and prescribed fires, a common management practice on the Tanzanian side of the Serengeti – Mara ecosystem to control wildfires and bush encroachment, improve foraging for grazers and facilitate tourists spotting large mammals (Green *et al.* 2015, Manyonyi *et al.* 2020). To calculate the percentage of non-burned area within the buffers, we used 500 m resolution rasters of SNP's annual burnt areas from 2001 to 2016 (Veldhuis *et al.* 2019). For each buffer, we calculated the mean of the 16 annual percentages.

Secretarybirds seem to be influenced by the amount of precipitation at nesting sites and breeding periods (Romani *et al.* 2024), so bioclimatic variables (1 km resolution) were chosen to test for a relationship between the observed abundance and precipitation, including the mean of the 16-year annual rainfall (Veldhuis *et al.* 2019), and also total annual precipitation and precipitation of the wettest month, driest month, wettest quarter, driest quarter, warmest quarter and coldest quarter (data available at WorldClim, https://www.worldclim.org; Fick & Hijmans 2017). See Supplemental Tables S2 and S3 for descriptive statistics for the environmental variables used in analyses. Data for hills, watercourses, vegetation, mean annual precipitation and non-burned areas are available from: https://serengetidata.weebly.com. Spatial data were processed with QGIS.

Secretarybird abundance and density – MCDS models

All statistical analyses were performed with R v. 4.2.0 (R Core Team 2023). MCDS improves bird density estimates compared to conventional distance sampling, even when birds are not detected (Marques *et al.* 2007). This method also avoids the need to define separate detection functions within each spatial subsample of the study area (*stratum*), increasing the estimate's precision, especially with small sample sizes (Marques *et al.* 2007, Buckland *et al.* 2015). For model building we used four covariates: (i) position (birds observed on the ground or a tree), which accounted for differing detectability, as Secretarybirds on trees are more easily seen, especially over longer distances; (ii) daily phase of the observation, to account for differing activity during the day; (iii) average slope, as steep gradients may influence detection and (iv) cluster size of observations, included in all models as a covariate to compensate for the positive bias of the cluster size within the sample (Buckland *et al.* 2015).

To test for differences in abundance and density between the four SNP sectors (*strata*), and between the whole surveyed area and the HDAs, 14 models for the Serengeti National Park (Table S4) and 14 models for HDAs (Table S5) were built using the Distance package (Miller *et al.* 2019). The 28 models were run using the covariate cluster size, all the different combinations of the other three covariates and the key functions Hazard-Rate and Half-Normal (Miller *et al.* 2019). We did not add adjustment terms (cosine, simple polynomial, hermite polynomial) to the key functions since the models that include covariates and adjustments could behave in a non-monotonic way for some covariate combinations (Miller & Thomas 2015, Miller *et al.* 2019). The best models were chosen using Akaike's Information Criterion (AIC) score, a ΔAIC value <2 and consequently the highest values of AIC weight (w_i) (Burnham & Anderson 2002).

A Q-Q plot comparing the cumulative distribution of the detection function (CDF) to the empirical distribution of the data (EDF) was used to verify the goodness of fit of the detection function (Burnham *et al.* 2004, Miller *et al.* 2019). Because the plot can be interpreted in a subjective way, we also performed the Cramér-von Mises test to check whether the values of the EDF and CDF followed the same distribution (Burnham *et al.* 2004, Miller *et al.* 2019). In addition, for the selected model a bootstrap version (1,000 iterations) of the Kolmogorov–Smirnov (KS) goodness of fit test was performed (Miller *et al.* 2019). As suggested by Buckland *et al.* (2001, 2015) and Thomas

et al. (2010) for line transects, we truncated 5% of the farthest detections, obtaining a truncation distance (w) of 700 m in the models for the whole sampled area, and of 650 m for the HDAs. Finally, using w and the average detection probability ($\hat{p}$) we calculated the effective strip-half width (μ) (Buckland *et al.* 2015).

Secretarybird habitat selection

Generalized additive mixed models (GAMMs; Zuur *et al.* 2009) were built with the mgcv package (Wood 2017) to identify the environmental factors associated with a greater abundance of Secretarybirds within the study area, and the hours in which they were seen most frequently. GAMMs can accommodate nonlinear relationships between the covariates and the response variable (Zuur *et al.* 2007, Wood 2017), which in our models was the number of Secretarybirds in each of the 52 replicated transects. Since our response variable contained positive integers and zeros, generating a skewed positive distribution, we built GAMMs with a negative binomial distribution (White & Bennetts 1996, Lindén & Mäntyniemi 2011, Stoklosa *et al.* 2022).

The covariates extracted from the linear buffers were normalized to have a mean of zero and variance of one (Quinn & Keough 2002, Zuur *et al.* 2007). The models were built: (i) by using the transect identity as a random intercept (bs = '*re*'), as each transect was repeated at least three times; (ii) by adding the categorical variable 'Time Intervals' as a linear term, since smoothing of categorical covariates is not supported in the mgcv package; (iii) setting $k = 20$ as maximum degrees of freedom for the smoothing terms, in order to have a sufficiently adequate basis dimension to realistically represent the non-linear effect of the covariates on the response variable; (iv) by setting the natural logarithm of transect length as *offset* term, because transect length varied. The natural logarithm was used to generate the link function. In addition, the thin plate regression splines with shrinkage were implemented for the smooth terms to avoid overfitting (Wood 2003, 2017). Finally, the smoothness selection of the models was made using maximum likelihood (ML).

Conventions differ for model selection and goodness of fit tests for MCDS, GAMMs and generalized linear models (GLMs, see below); we chose our approaches accordingly. Through a backward stepwise approach and using AICc for model selection, we selected the four most parsimonious models with the highest number of significant covariates (Tanaka *et al.* 2017, Tanaka *et al.* 2019). We ranked the models through the lowest AICc and the highest Akaike weight (w_i) score (Burnham & Anderson 2002). Since the models had the same random structure but different fixed effects, we also used the minimum ML score for model selection (Zuur *et al.* 2009, Faraway 2016). We tested for multicollinearity among variables for the best models by using as the threshold a concurvity value $\geq$0.8 between each covariate pair (Darby *et al.* 2021, Lempidakis *et al.* 2022, Leonardi *et al.* 2022). Concurvity represents the non-linear extension of multicollinearity (Kovács 2024). For the best models, diagnostics were performed with the *gam.check* function of the mgcv package. As suggested by Wood (2017), we verified that the model reached full convergence and ensured P values of ≥ 0.05 for the adequacy test of the basis dimension for each smooth, which may happen with small k values if the effective degrees of freedom are closer to k'. Residuals are not uniformly distributed for significant tests. Diagnostics were also conducted with the DHARMa package (Hartig 2022). Models not meeting the assumptions were discarded.

Models built with response variables containing many zeros do not necessarily mean a zero inflation (Warton 2005). Zero-inflated models are commonly used to analyse count data and are appropriate when covariates cannot explain the zeros (Wood *et al.* 2016). To verify the absence of zero inflation in the model we applied a test to compare the distribution of the observed zeros with that of the expected ones, through the DHARMa package. Finally, the proportion of deviance was used to measure how well the best model explained the observed variability (Zuur *et al.* 2007, Wood 2017).

Spatial differences in habitat selection between Secretarybird pairs and singles

To understand spatial differences in habitat selection between pairs and singles we used GLMs with binomial distribution (logit link function), where the response variable was the probability of pairs compared to single individuals (pairs = 1, singles = 0). Only pre-breeding season observations were considered to involve birds not alternating during brooding or parental care. To make the effect sizes more comparable, the covariates extracted from the ring buffers were normalized to have a mean of zero and variance of one (Quinn & Keough 2002, Zuur *et al.* 2007). Through the stepwise backward analysis, we removed covariates from a full model to obtain the eight most parsimonious models with the greatest number of significant variables (Tanaka *et al.* 2017, Tanaka *et al.* 2019). Models were then ranked

according to their AICc and w_i (Burnham & Anderson 2002). Models of Δ AICc < 2 were assessed for their fit using the DHARMa package. Models not meeting the assumptions were discarded.

To test for multicollinearity between variables, a correlation coefficient with absolute value ≥0.7 and a generalized variance inflation factors (GVIF; Fox & Monette 1992) of ≥ 10 were chosen as thresholds (Dormann *et al.* 2013), using the car package (Fox & Weisberg 2019). In the GLMs, VIF is replaced by GVIF, especially when dealing with categorical variables, because the degrees of freedom of such covariates are >1. For the best model, the relative importance of the covariates (w) was measured by summing the Akaike weights of the models in which each covariate occurred (Burnham & Anderson 2002). Finally, the performance was assessed through the area under the curve (AUC) value of the receiver operating characteristic (ROC) curve (Fawcett 2006). To generate the mean AUC value with related 95% confidence intervals, we made 1,000 bootstrap replicates using the pROC package (Robin *et al.* 2011) and randomly divided the entire dataset into training data (80%) for model calibration, and test data (20%). The best model was fitted to the training data and used to predict the test data.

Results

Secretarybird detectability, abundance and density in SNP

Excluding the truncated data (observations beyond 700 m), 222 Secretarybird observations (average cluster size $n = 1.6$, SE 0.04) were made in the whole sampled area, for a total of 364 individuals. The average number of Secretarybirds counted per transect was 1.78 (SE = 0.13, range 0–10). The best model included the Hazard-Rate key function and covariates of the cluster size, the position of birds and the time intervals: birds' position on trees, more Secretarybirds in a cluster and the time interval 3 (12:01–15:00) increased detectability as a function of distance. In contrast, detectability was lower in time intervals 2 (09:01–12:00) and 4 (15:01–18:00) (Tables 1 and S4; Figure 2). The estimated average probability of detection within the truncation distance was 53.9% (SE 4.8%) and the effective strip-half width was 377.3 m. The Cramér-von Mises and KS tests for the goodness of fit were not significant, so the fit was adequate (Table 1).

In the whole sampled area (~80% of the SNP), the estimated number of Secretarybirds was 1,513.3 (CI 95% = 1,138.9–2010.7; CV = 14%), with a density of 1.3 birds/10 km^2 (CI 95% = 0.9–1.7; CV = 14%) (Table 1). The highest densities were recorded in the central (1.7/10 km^2, CI 95% = 1.0–2.9) and southern SNP (2.0/10 km^2, CI 95% = 1.3–2.9), compared to northern (0.7/10 km^2, CI 95% = 0.4–1.2) and western SNP (0.7/10 km^2, CI 95% = 0.4–1.4) (Table 1). The estimated encounter rates of individuals per 10 km were 1.4 (SE 0.31) in the central SNP and 1.6 (SE 0.25) in the southern SNP (Table 1), while in the north and west, the encounter rates were 0.5 individuals. Summary statistics are shown in Table 1.

Secretarybird detectability, abundance and density in HDAs

The HDAs represented 23% of the surveyed area, located in central and southern SNP. Excluding the truncated data (observations beyond 650 m), 152 observations for a total of 257 Secretarybirds were collected in the HDAs (average cluster size $n = 1.7$; SE 0.04). The average number of Secretarybirds counted per transect was 3.03 (SE 0.21; range 0–10).

The best model for the HDAs included the Half-Normal key function with covariates of cluster size, the position of the birds and the average slope, with the position on trees increasing detectability as a function of distance. A greater slope determined decreased detectability, while more Secretarybirds in a cluster resulted in a negligible decrease (Tables 2 and S5; Figure 2). The average probability of detection within the truncation distance was estimated as 62.8% (SE 5.1%) and the effective strip-half width was 408.2 m. The Cramér-von Mises and KS tests for the goodness of fit were not significant, suggesting an appropriate model fit (Table 4).

In the HDAs, we estimated an average abundance of 622.5 Secretarybirds (CI 95% = 423.8–914.4; CV = 18%) and an average density of 2.3 individuals per 10 km^2, with 2.1 birds/10 km^2 (CI 95% = 1.0–4.2) in central SNP and 2.6 birds/10 km^2 (CI 95% = 2.1–3.2) in southern SNP (Table 2). In the HDAs, the average encounter rate increased (1.9/10 km; SE 0.24) compared to the whole sampled area (1.1/10 km; SE 0.16), especially in the south (2.2/10 km; SE 0.11) (Table 2). Summary statistics of the transects, sampling effort and HDAs are shown in Table 2. A map of the predicted densities is shown in Figure 3.

Secretarybird habitat selection

During the census, 372 Secretarybirds (median per transect = 2; range 0–10) were counted in the 52 replicated transects ($n = 209$). Of the four most

Table 1. Summary of the best MCDS model for the whole surveyed area, including details of data, results and model specification, as the type and number of covariates (Formula), AIC score, *P* values of Cramér-von Mises (C-vM) and Kolmogorov-Smirnov (KS) tests, the average detectability ($\hat{P}_a$) and its standard error (SE). Parameters of the detection function are presented on a natural log scale. In the summary of the survey for individuals, 'Region' represents the *strata* (C = Centre, N = North, S = South, W = West), *n* is the number of individuals detected, k is the number of transects travelled and ER is the encounter rate. In the bottom two sections of the table, estimates of density and abundance are also provided for each *stratum* (CV = coefficient of variation; CI 95% = 95% confidence intervals; df = degree of freedom).

Best model Serengeti National Park									
Key-function	Formula	AIC	C-vM *P*	KS *P*	$\widehat{P_a}$	SE ($\widehat{P_a}$)	ΔAIC		
Hazard-Rate	~size + timeInterval + Position	2,839.72	0.429	0.082	0.539	0.048	0.000		
Detection function parameters									
		Scale coefficient(s)		Estimate			SE		
		Intercept		5.039			0.410		
		size		0.319			0.206		
		Position (T)		0.753			0.326		
		timeInterval2		−0.250			0.275		
		timeInterval3		0.571			0.388		
		timeInterval4		−0.138			0.291		
Summary statistics of survey for individuals									
Region	Area (km^2)	Covered area (km^2)	Effort (km)	*n*	k	ER/km	SE	Mean size cluster	SE
C	2,925	1,489.05	1,063.61	146	13	0.14	0.031	1.6	0.06
N	2,925	829.33	592.38	29	13	0.05	0.012	1.7	0.11
S	3,150	1,428.91	1,020.65	159	14	0.16	0.025	1.7	0.05
W	2,700	783.26	559.47	30	12	0.05	0.016	1.5	0.14
Total	11 700	4,530.55	3,236.11	364	52	0.11	0.016	1.6	0.04
Abundance									
Region	Estimate	SE		CV		CI 95%		df	
C	496.5	125.3		0.25		292.6–842.7		15.2	
N	192.4	53.3		0.28		107.9–343.0		15.4	
S	623.0	116.4		0.18		424.3–914.8		22.1	
W	201.4	60.3		0.29		107.5–377.3		14.1	
Total	1,513.3	217.3		0.14		1,138.9–2,010.7		81.7	
Density: n/10 km^2									
Region	Estimate	SE		CV		CI 95%		df	
C	1.7	0.43		0.25		1.0–2.9		15.2	
N	0.7	0.18		0.28		0.4–1.2		15.4	
S	2.0	0.37		0.18		1.3–2.9		22.1	
W	0.7	0.22		0.29		0.4–1.4		14.1	
Total	1.3	0.19		0.14		0.9–1.7		81.7	

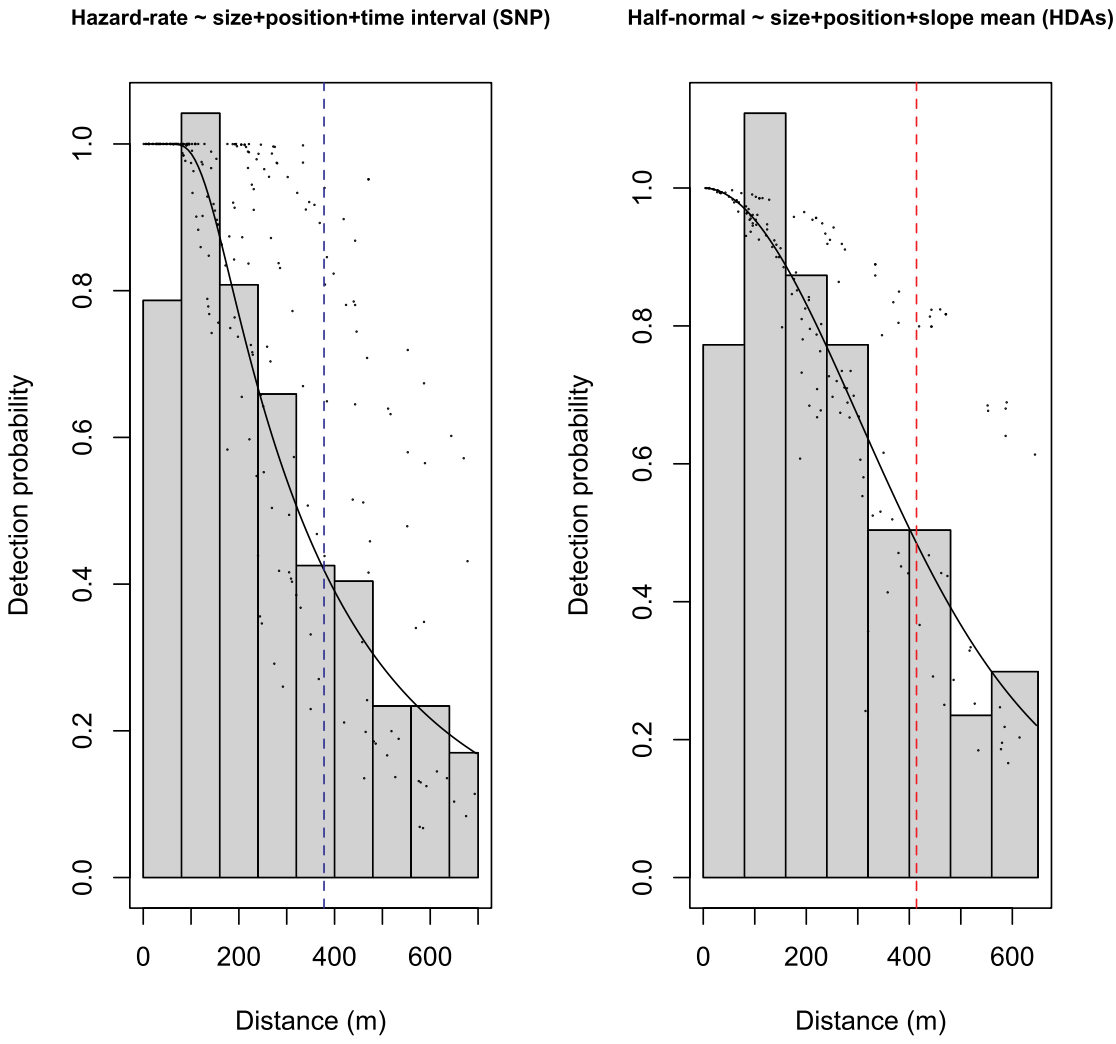

Figure 2. Fitted detection functions of the best MCDS models for the whole surveyed area (SNP, left) and the Highest Density Areas (HDAs, right). Lines represent the detection functions averaged over covariates, while points indicate the detectability for a given observation according to the covariate values of that observation. The dashed lines identify the strip-half width.

parsimonious models, two showed a ΔAICc < 2 (Table 3). Considering the small difference between models in their ML values and the greater difference between models in their AICc values, weight and relative log-likelihood, the model with the lowest AICc value was chosen as best (Table 3). Diagnostics tests using the DHARMa package did not show significant results (Quantile Test $P = 0.367$; Outliers test $P = 1$; KS uniformity test D = 0.054, $P = 0.570$; Dispersion test = 0.875, $P = 0.416$; Levene's test F = 0.965, df = 3, $P = 0.410$), suggesting an adequate model fit. The number of observed zeros was slightly higher than expected (ratio = 1.11), but the difference between observed and expected zeros was not significant ($P = 0.224$), thus zero inflation was excluded. Additionally, the model reached full convergence, actual df were not close to *k'* and no *P* values from the basis dimension test for the smooth terms were significant (Table 4). Multicollinearity among variables was excluded since pairwise comparison reported no concurvity values ≥0.8.

The model explained more than 50% of the observed variability ($D^2 = 0.513$). All environmental variables (smooth terms) were highly significant, especially the percentages of unburned areas, closed grasslands and average slope (Table 4). More Secretarybirds were found in habitats characterized by a percentage of unburned areas averaging 40–80%, closed grassland coverage of 30–70% and an average slope < 3 degrees. Open grassed woodland coverage of > 20% and open grassland of >6% was associated with fewer observed Secretarybirds, and closed treed grassland was unsuitable (Figure 4). Secretarybirds were more abundant in habitats with a mean annual precipitation of 600–900 mm and more seasonal rivers (Figure 4). Most birds were observed during the time intervals of

Table 2. Summary of the best MCDS model for the Highest Density Areas (HDAs), including data, results and model specification, as the type and number of covariates (Formula), AIC score, *P* values of Cramér-von Mises (C-vM) and Kolmogorov-Smirnov (KS) tests, average detectability ($\hat{P}_a$) and its standard error (SE). Parameters of the detection function are presented on a natural log scale. In the summary of the survey for individuals, 'Region' represents the *strata* (C = Centre, S = South), *n* is the number of individuals detected, k is the number of transects travelled and ER is the encounter rate. In the bottom two sections, estimates of density and abundance are also provided for each *stratum* (CV = coefficient of variation; CI 95% = 95% confidence interval; df = degree of freedom).

Best model highest density areas							
Key-function	Formula	AIC	C-vM *P*	KS *P*	$\widehat{P_a}$	SE	ΔAIC
Half-normal	~size + Position + Slope	1,941.49	0.945	0.903	0.628	0.051	0.000

Detection function parameters		
Scale coefficient(s)	Estimate	SE
Intercept	5.855	0.367
Size	−0.072	0.201
Position (T)	0.724	0.591
Slope	−0.155	0.119

Summary statistics of survey for individuals									
Region	Area (km^2)	Covered area (km^2)	Effort (km)	*N*	k	ER/km	SE	Mean size cluster	SE
C	1,575	1,020.50	785.00	125	7	0.16	0.040	1.6	0.06
S	1,125	774.18	595.52	132	5	0.22	0.011	1.7	0.05
Total	2,700	1,794.68	1,380.52	257	12	0.19	0.024	1.7	0.04

Abundance					
Region	Estimate	SE	CV	CI95%	df
C	327.8	100.3	0.31	163.6–659.7	7.7
S	294.7	29.1	0.10	240.7–360.8	25.4
Total	622.5	109.3	0.18	423.8–914.4	10.8

Density: *n*/10 km^2					
Region	Estimate	SE	CV	CI95%	df
C	2.1	0.63	0.31	1.0–4.2	7.7
S	2.6	0.26	0.10	2.1–3.2	25.4
Total	2.3	0.41	0.18	1.6–3.4	10.8

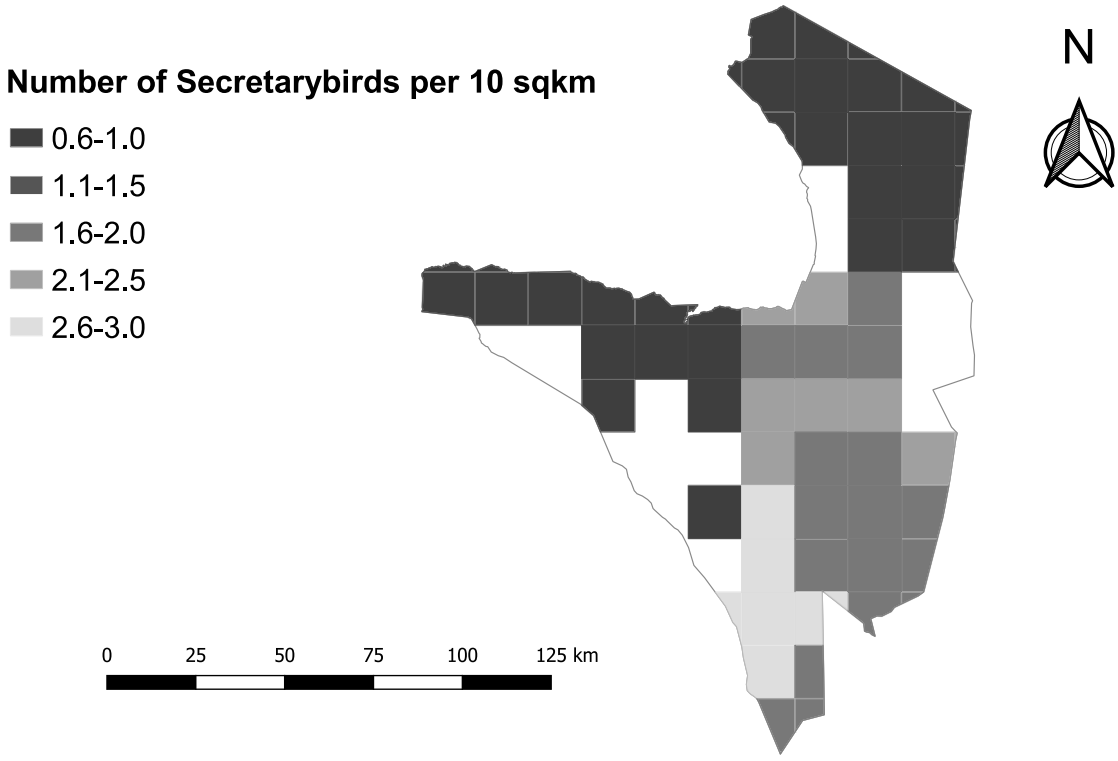

Figure 3. Average density estimates of Secretarybirds throughout the Serengeti National Park in 2023.

06:01–09:00 and 15:01–18:00, with significant differences between the first-morning phase (06:01–09:00) and the second and third phases (09:01–15:00) (Figure 4; Table 4).

Spatial differences in habitat selection between pairs and singles

During the pre-breeding season, 81 single Secretarybirds and 86 pairs were detected. Of the eight most parsimonious models, five showed a ΔAICc < 2, with the best model's AICc being $\leq$ 0.96 than others (Table 5). All diagnostics highlighted the absence of under- and over-dispersion and correlation between the residuals and fitted values (quantile test $P = 0.3411$; Outliers test $P = 1$; KS uniformity test $D = 0.055$, $P = 0.693$; Dispersion test = 0.976, $P = 0.8$; Levene's test (Position) $F = 0.016$, $df = 1$, $P = 0.899$; Levene's test (Time Interval) $F = 1.075$, $df = 3$, $P = 0.361$).

In southern SNP the probability of observing pairs versus singles was significantly lower than in the northern sector but was non-significantly higher than central and western sectors (Table 6; Figure 5). The lowest differences were between areas containing more individuals (central and southern SNP) (Figure 5). Pairs were more likely than singles to be observed from 12:01 to 15:00, while no significant difference was found between intervals 1, 2 and 4 (Table 6; Figure 5). There was some positive (non-significant) tendency to observe pairs versus singles on trees and at lower altitudes (Table 6).

The percentage of closed treed shrubland was the most significant and apparently suitable habitat for pairs, which were less likely to occupy habitats with a higher environmental heterogeneity and percentage of dense treed grassland, open grassed woodland and open grassland (Table 6; Figure 5). Correlation coefficients among continuous variables and GVIF values showed no collinearity (Table 6). Finally, the ROC curve analysis had good model predictiveness, i.e. the capability of correctly discriminate the presence of pairs or singles (mean AUC = 0.857, CI 95% = 0.691–0.981).

Discussion

Secretarybird abundance, density and detectability

This study provides the first abundance estimate for the Secretarybird in East Africa, where we estimated ~1,500 individuals within ~80% of the SNP (11,700 km^2). In South Africa, Lesotho and Eswatini (1,268,756 km^2), Brink *et al.* (2024) estimated ~8,000 individuals, while Tarboton & Allan (1984) estimated 1,100 breeding pairs in the Transvaal (286,000 km^2).

Table 3. Most parsimonious GAMMs ($n = 4$) fitted to the transect counts data of Secretarybirds in 2023. For each model: (ML = maximum–likelihood; w_i = AICc weight; *Cum* w_i = cumulative weight; *rel-Lik* = relative–likelihood; cG = closed grassland; oGW = open grassed woodland; oG = open grassland; cTG = closed treed grassland; cTS = closed treed shrubland; dTG = dense treed grassland; dTS = dense treed shrubland). Models are ranked according to their lowest AICc and ML scores.

GAMMs selection based on ML and AICc						
Formula	*ML*	*AICc*	*Δ AICc*	w_i	*Cum* w_i	*rel–Lik*
~ s(cG) + s(Unburned areas) + s(oGW) + s(oG) + s(cTG) + s(Non-permanent rivers) +s(Mean annual rainfall) + s(Slope mean) + s(ID transect, bs = 're') + Time interval + *offset* (log(transect length))	313.91	644.294	0.00	0.489	0.489	1.000
~ s(cG) + s(Unburned areas) + s(oGW) + s(oG) + s(cTG) + s(Non-permanent rivers) +s(Mean annual rainfall) + s(Slope mean) + s(ID transect, bs = 're') + s(cTS) + Time interval + *offset* (log(transect length))	313.72	644.922	0.629	0.357	0.849	0.730
~ s(cG) + s(Unburned areas) + s(oGW) + s(oG) + s(cTG) + s(Non-permanent rivers) + s(dTG) +s(Mean annual rainfall) + s(Slope mean) + s(ID transect, bs = 're') + Time interval + *offset* (log(transect length))	313.91	646.622	2.328	0.153	0.999	0.153
~ s(cG) + s(Unburned areas) + s(oGW) + s(oG) + s(dTS) + s(Non-permanent rivers) +s(Mean annual rainfall) + s(Slope mean) + s(ID transect, bs = 're') + Time interval + *offset* (log(transect length))	319.8	658.314	14.020	0.001	1.000	0.000

Table 4. Results of the best GAMM model, reported for the parametric coefficient 'Time interval' as average estimates of β_I coefficients (*Estimate*), β_I standard error (*SE*), z-values – estimated value/standard error (*Statistic*), and significance of each variable level (P1 = 06:01–09:00, P2 = 09:01–12:00, P3 = 12:01–15:00, P4 = 15:01–18:00). For the smooth terms, results are reported as estimated degrees of freedom (*edf*), maximum degrees of freedom for each term (*Ref. df*), Chi-square values (*Statistic*), significance of each covariate (*P*), maximum possible *edf* for each term (*k'*), *k–index* and significance of basis dimension test (*P-value**). Covariates: cG = closed grassland, oGW = open grassed woodland, oG = open grassland, cTG = closed treed grassland. Smooths of factor covariates (e.g. ID transect) are not supported in the mgcv package(see Methods), resulting in NA for *k-index* and *P* value of the basis dimension test.

Effect of environmental covariates on Secretarybird counts							
Parametric coefficient	*Estimate*	*SE*	*Statistic*	*P*			
(Intercept)	–2.154	0.125	–17.289	<0.001			
Time interval	*Ref. P1*						
P2	–0.590	0.148	–3.992	<0.001			
P3	–0.544	0.181	–3.014	0.003			
P4	–0.287	0.159	–1.800	0.072			
Smooth terms	*edf*	*Ref. df*	*Statistic*	*P*	*k'*	*k-index*	*P* *
s (cG)	3.029	3.753	27.167	<0.001	19	0.974	0.508
s (Unburned areas)	5.204	6.508	55.070	<0.001	19	0.948	0.383
s (oGW)	1.000	1.000	11.274	<0.001	19	1.003	0.663
s (oG)	1.000	1.000	12.046	<0.001	19	0.951	0.405
s (cTG)	1.000	1.000	13.028	<0.001	19	0.975	0.555
s (seasonal rivers)	1.000	1.000	7.647	0.006	19	0.925	0.260
s (Rainfall)	1.000	1.000	6.781	0.009	19	0.934	0.310
s (Slope, mean)	1.000	1.000	15.375	<0.001	19	0.930	0.258
s (ID transect, *bs = 're'*)	2.9e-05	43.00	0.000	0.209	52	NA	NA
Observations	209						
Deviance explained	0.513						
R^2 (adj)	0.516						

Although different methodologies and scales were used to produce these estimates, in our sampled area the density of the species was higher than reported in South Africa.

However, our estimates are not representative of the whole of northern Tanzania, given that SNP is still a huge, unfragmented, protected area with suitable environmental conditions for Secretarybirds. Outside of the park, many pressures, especially of human origin, represent barriers to the dispersion and settlement of individuals, as seen in other African countries (Hofmeyr *et al.* 2014, Whitecross *et al.* 2019, Shaw *et al.* 2024). Indeed, encounter rates decline steeply outside of the park (Eurafrica Conservation Projects, unpublished data). Nevertheless, in the SNP study area, the average Secretarybird encounter rate (1.1/10 km) was higher than in PAs of northern Botswana (0.02/10 km) and Kenya (0.11/10 km) between 2003 and 2020 (Shaw *et al.* 2024). Thus, SNP represents a key site in East Africa that deserves rigorous protection, as conservation resources are often limited and so larger populations should be preserved because of their higher evolvability (Lande & Barrowclough 1987).

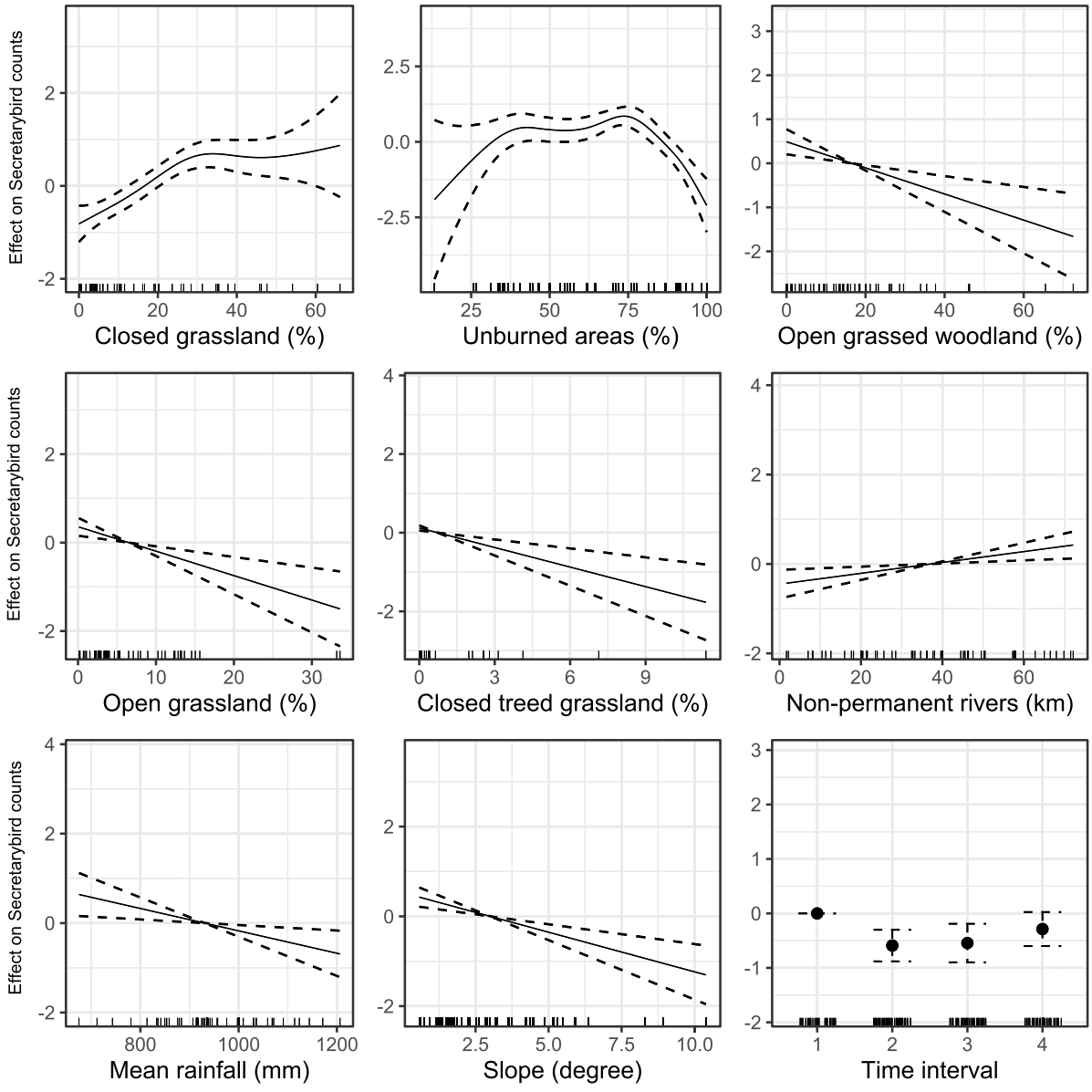

Figure 4. The response curves represent partial effects of the significant variables on the Secretarybird counts in the Serengeti National Park for the best GAMM. Dashed lines indicate the 95% confidence intervals. The small bars on the x-axis show where observations were more frequent. Parametric effects of the 'Time interval' variable on Secretarybird counts are presented in the final plot (bottom right).

Our estimate is a starting point for future management decisions. Even if it does not represent an immediate concern, the apparent slow reproductive rate, a nesting success <50% (Romani *et al.* 2024) and illegal harvesting for traditional medicine (Kioko *et al.* 2015, Nature Tanzania, unpublished data) could compromise the long-term viability of the Secretarybird population. If the population is isolated due to excessive anthropogenic pressures, environmental stochasticity (e.g. disease or catastrophic climatic events) can lead to a sudden reduction in population size (Lande 1993, Sæther *et al.* 1998, Sæther & Engen 2002). Under these conditions, the variance in vital rates increases exponentially due to demographic stochasticity (Gabriel & Bürger 1992, Legendre *et al.* 1999): the smaller the population, the greater the fluctuations of demographic parameters around the mean, and the lower chance of survival. Furthermore, in small populations genetic drift is the predominant evolutionary force shaping the gene pool, rather than natural selection, causing loss of adaptive potential and a higher probability of extinction (Lande 1988, Allendorf *et al.* 2012).

The results showed the CV for density/abundance estimates was slightly higher for the HDAs model (CV = 0.18), compared to the model for the entire

Table 5. Set of eight GLMs fitted to the occurrence data of Secretarybird pairs and singles during the pre-breeding season in 2023. For each model: (*K* = number of estimated parameters; w_i = AICc weight; *Cum* w_i = cumulative weight; *LL* = log-likelihood; H′ = Shannon diversity index; cTS = closed treed grassland; dTG = dense treed grassland; oGW = open grassed woodland; oG = open grassland; dSG = dense shrubbed grassland). Models are ranked according to their lowest AICc score.

GLMs selection based on AICc						
Formula	*K*	*AICc*	*ΔAICc*	w_i	*Cum* w_i	*LL*
~ Position + Time interval + SNP sector + H′+ cTS + dTG + oGW + oG + Altitude median	14	214.24	0.00	0.32	0.32	−91.74
~ Position + Time interval + SNP sector + H′+ cTS + dTG + oGW + oG	13	215.20	0.96	0.20	0.51	−93.41
Position + Time interval + SNP sector + H′+ cTS + dTG + oGW + oG + Altitude median + Non-permanent rivers	15	215.77	1.53	0.15	0.66	−91.29
~ Position + Time interval + SNP sector + H′+ cTS + dTG	11	215.81	1.57	0.14	0.80	−96.05
~ Position + Time interval + SNP sector + H′+ cTS + dTG + oGW	12	216.19	1.96	0.12	0.92	−95.08
~ Position + Time interval + SNP sector + H′+ cTS + dSG	11	218.38	4.14	0.04	0.96	−97.34
~ Position + Time interval + SNP sector + H′+ cTS	10	219.25	5.01	0.03	0.99	−98.92
Position + Time interval + SNP sector + H′	9	222.68	8.45	0.01	1.00	−101.77

Table 6. Results of the best GLM model reported as average estimates of β_I coefficients (*Estimate*), 95% confidence intervals (*CI 95%*), z-values — estimated value/standard error (*Statistic*), the significance of each variable, generalized variance inflation factor (*GVIF*) and the relative importance of each covariate (*w*). Coefficients: T = tree, C = Centre, N = North, S = South, W = West, cTS = closed treed grassland, dTG = dense treed grassland, oG = open grassland, oGW = open grassed woodland, H′ = Shannon Diversity Index, P1 = 6:01–9:00, P2 = 9:01–12:00, P3 = 12:01–15:00, P4 = 15:01–18:00.

Pairs – single individuals						
Coefficient	*Estimate*	*CI 95%*	*Statistic*	*P*	*GVIF*	*w*
(Intercept)	1.94	0.74–3.31	2.99	0.003	–	–
Altitude, median	−0.77	1.64–0.05	−1.79	0.073	5.86	0.47
Position	*Ref. G*	–	–	–	1.23	0.98
T	0.79	−0.18–1.79	1.57	0.115	–	–
SNP sector	*Ref. S*	–	–	–	8.79	0.98
C	−0.42	−1.44–0.59	−0.81	0.415	–	–
N	1.55	0.09–3.08	2.04	0.041	–	–
W	−1.58	−4.17–0.90	−1.23	0.218	–	–
cTS	0.78	0.31–1.32	3.05	0.002	1.88	0.97
dTG	−0.74	−1.28 – −0.25	−2.88	0.004	2.06	0.93
oG	−0.34	−0.78–0.04	−1.64	0.101	1.09	0.67
oGW	−0.54	−1.12 – −0.01	−1.92	0.052	2.27	0.79
H′	−0.66	−1.14 – −0.22	−2.83	0.005	1.54	0.98
Time interval	*Ref. P3*	–	–	–	1.85	0.98
P1	−2.60	−4.04– −1.33	−3.80	<0.001	–	–
P2	−1.84	−3.15– −0.66	−2.93	0.003	–	–
P4	−2.58	−4.03– −1.31	−3.76	<0.001	–	–
Observations	167					
AICc	214.24					

sampling area (CV = 0.14). However, estimates for the HDAs in the southern sector had a low CV (0.10) compared to those in the central sector (0.31), suggesting greater variation in the presence of individuals rather than of detectability, whose average value was quite high (0.63). The higher CV of the HDAs could be due to poorly understood ecological dynamics in the central sector. However, in both the general model and the HDAs model, the average CVs were below 0.20, indicating fairly accurate and precise estimates of the Secretarybird's abundance and density (Buckland *et al.* 2001, Buckland *et al.* 2015); this protocol can therefore be applied for future counts of Secretarybirds in the Serengeti ecosystem. The use of a distance sampling method works within this framework because: (i) the bias related to cluster size is avoided since Secretarybirds mostly occur alone or in pairs; (ii) distances can be easily measured as the birds spend most of the day walking on the ground and are very visible; (iii) assuming the territoriality of the species, the risk of pseudo-replication during each survey is low and (iv) the high density of roads generally allows a random choice of the transects, representative of all environments.

According to MacKenzie & Royle (2005) when detectability is greater than 0.5, three replicates per sampling unit (e.g. transect) can adequately sample a species. Based on our CV and probability of detection, we suggest censusing Secretarybirds with at least three replicates and during the dry season, avoiding the risk of underestimation during the breeding period and

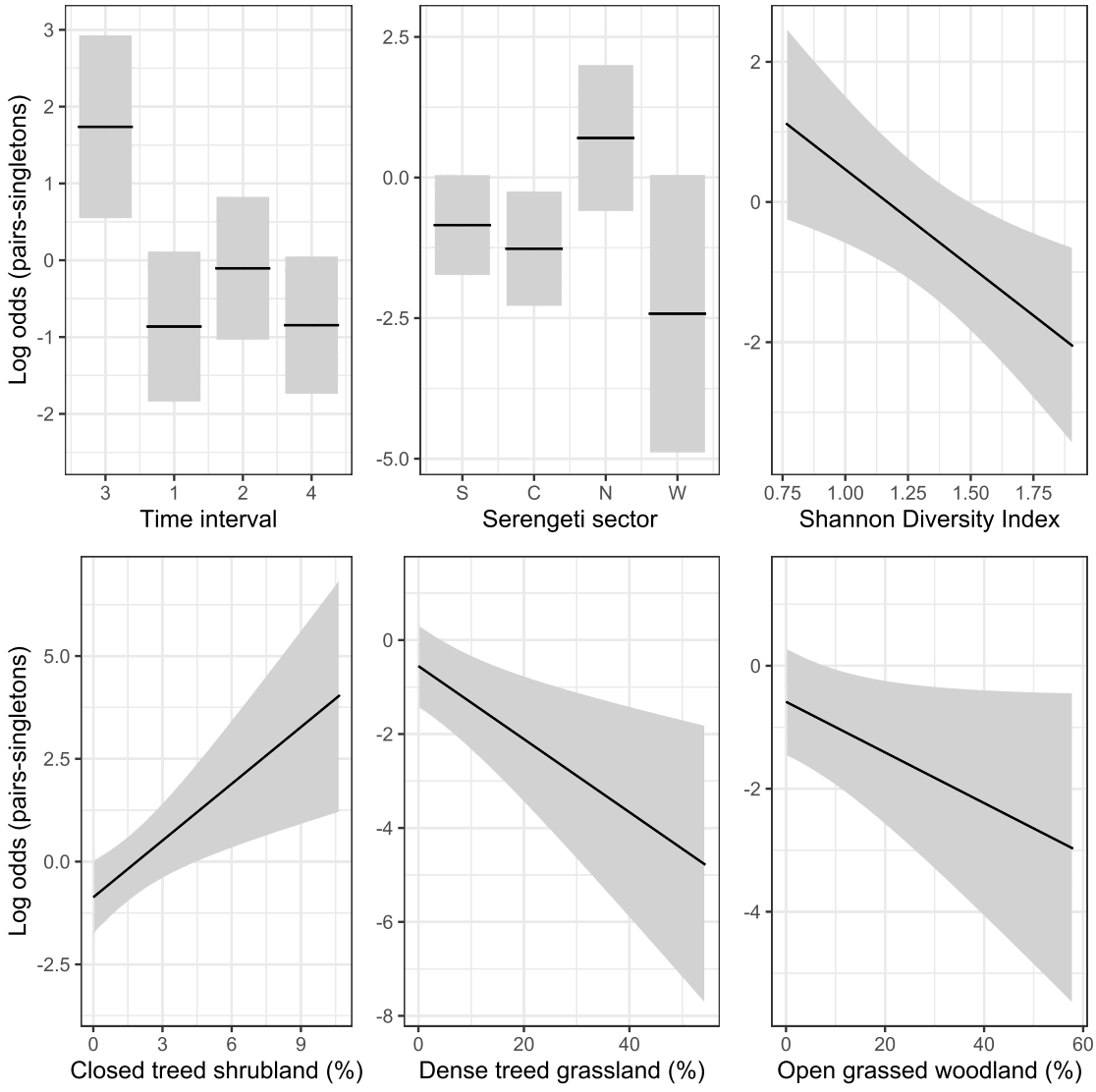

Figure 5. Estimated relationship from the best GLM between the significant covariates and the probability of Secretarybird pairs compared to single individuals. Light grey bands represent the 95% confidence intervals.

the logistical difficulties of muddy roads. In the rainy season, many White Storks *Ciconia ciconia* are also in the Serengeti ecosystem (Pennycuick 1972, Berthold *et al.* 2006, Kennedy 2014), making it more difficult to identify Secretarybirds at greater distances due to the similar colours, size and habits. An openable car roof is also highly recommended, especially for sighting individuals in tall grass.

The results from the MCDS model for the entire sampled area highlighted greater detectability with increasing distance during the first time interval (06:01–09:00) compared to the second (09:01–12:00) and fourth intervals (15:01–18:00), with smaller differences between the first and fourth intervals. Consistent with these results, the GAMM predicted more individuals counted in the first interval compared to the second or fourth, with significant differences between the first and second intervals. Furthermore, according to the MCDS model, detectability increased with distance in the third interval (12:01–15:00); however, the GAMM indicated the same time interval had a negative effect on Secretarybird counts, giving a potential contradiction between models. Ideally, in distance sampling the number of observations should be greater at distances closer to the transect and decrease gradually with distance; this is a basic requirement for building the detection function and avoiding underestimation (Buckland *et al.* 2001, Buckland *et al.* 2015). The frequency of observations as a function of distance for the entire dataset, and for time intervals 1, 2 and 4, were distributed in this way. The third interval instead showed fewer observations at closer distances and more observations at 200–500 m. During this time, the

Secretarybirds' hunting activity declines and they often fly, rest in shade or lie in the grass (Kemp 1994, Ramella Levis & Romani pers. obs.). These behaviours increase the difficulty of observing Secretarybirds. Resting birds might also avoid roads, shifting the distribution of distances and underestimating of numbers present. This phenomenon could be clarified with a study involving an equally large number of transect replicates for each time interval.

Considering the results predicted by the GAMM, and the previous considerations, transects should be ideally travelled early in the morning and late in the afternoon. This requires significant effort when sampling a huge area, so the whole day could be used to survey, but avoiding the hottest hours. These recommendations are also useful for teams wishing to assess relative abundance indices based on encounter rates (e.g. kilometric abundance index).

One final consideration is the SNP area that was not sampled (~20%, Figure 1) due to logistical (lack of roads) or access reasons (e.g. in rhinoceros IPZs). Whilst biased estimates of density and abundance are excluded by being derived from the area actually surveyed, doubts may exist over the accurate identification of HDAs. However, we are rather confident that areas of high Secretarybird density are absent in the remaining 20% of the SNP, because the unsampled cells were located in sectors with higher annual rainfall and forest/woodland coverage (northern and western SNP, Reed *et al.* 2009), which also contain numerous hills (especially the western SNP). Additionally, in excluded areas, the limited grassland is severely burned annually due to the importance of the woodlands (Veldhuis *et al.* 2019), so the probability of there being high densities of Secretarybirds appears remote.

Habitat selection

Areas of higher Secretarybird abundance were particularly located on the edge of the 'Serengeti Plains', in the transition zone between expansive grassland and more heterogeneous habitats characterized by woodlands and shrublands. These sites have features that promote abundance. Grasslands with high vegetation cover are more important than those with less, such as open grassland. A closed grassland percentage of > 30% could support Secretarybirds via a greater abundance of grasshoppers and other Orthoptera (Quinn & Walgenbach 1990, Prendini *et al.* 1996, de Visser *et al.* 2015), that form much of their diet (Kemp 1994, 1995, Davies *et al.* 2014), as well as Anurans that become abundant especially during the rainy season. In these areas we found more than 50 active nests during 2023–2024 (Romani *et al.* 2024), sometimes just a few (~2) km apart, suggesting particularly important breeding sites.

Prescribed fires covering >60% of land (unburned areas <40%) negatively affected Secretarybird abundance. We often observed Secretarybirds in areas of active fire, chasing prey escaping from the flames, but after about two days the burned areas were unused, with the birds hunting in nearby unburned grassland. The ecological requirements linked to the minimum closed grassland cover suggest at least 30% should be unaffected by fires to support a higher abundance of birds. However, Secretarybird abundance decreased when the percentage of unburned areas exceeded 80%; such areas lie in the eastern part of southern Serengeti (Veldhuis *et al.* 2019), with habitats characterized mainly by grasslands with variable, even low, vegetation cover (McNaughton 1985, Reed *et al.* 2009). Soil features and low annual rainfall make these areas drier and less productive in the dry season, leading to the absence of trees for hundreds of km^2 (McNaughton 1985, Sinclair *et al.* 2019). Since Secretarybirds require trees for nesting and roosting, and grasslands with high vegetation cover, the lower abundance of individuals could be attributed to the ecological characteristics of these sites rather than the absence of fires.

Regarding the average slope, the results suggest that Secretarybirds prefer flat environments, probably due to anatomical and physiological constraints. Indeed, the species usually takes a run-up in order to take flight, and landing is followed by a short run before closing the wings (Kemp 1994). Short runs are also made when hunting. Excessive slopes may compromise these movements and increase energy consumption, while flatter ground may help to maintain visual contact between partners and spot potential predators.

Another factor favouring Secretarybird abundance was the presence of seasonal rivers. Sites of high river density were also those where most nests were found and, since in this ecosystem the Secretarybird's breeding season coincides with the rainy season (Romani *et al.* 2024), non-permanent rivers could represent important water resources for chicks during parental care, which is known to be important (Kemp 1994, Eurafrica Conservation Projects, unpublished data).

The western and northern sectors of the Serengeti had lower densities of Secretarybirds than the central and southern sectors. The first two macro-areas have undergone a compositional change of grass species over time (Anderson 2008) and are characterized by a

higher average annual rainfall (900–1200 mm), which promotes more wooded habitats (Anderson 2008, Reed *et al.* 2009), possibly affecting the Secretarybird's prey. Because this species apparently prefers habitats with 20% or less of open grassed woodland, average annual rainfall higher than 900 mm negatively influences abundance. Furthermore, the tree species mostly chosen for nesting and roosting in this ecosystem are *Vachellia tortilis* and *Balanites aegiptyaca* (Ramella Levis *et al.* 2023), which are more abundant in the south and central Serengeti compared to the north and west where other species predominate, including *V. robusta* and *V. gerrardii* (Rugemalila *et al.* 2017). Finally, the grass height in the Serengeti ecosystem follows the rainfall gradient, being shorter in the south-east and taller in the north-west (Anderson & Talbot 1965, Sinclair & Norton-Griffiths 1979, McNaughton 1983, 1985). The HDAs are located in an intermediate range, suggesting that too short or too tall grass probably deters high abundances, as seen in South Africa for tall grass (Kemp 1994). This could be due to a greater difficulty in walking, spotting predators and maintaining contact between pairs when hunting if the grass exceeds 70–80 cm tall. Very short grass, which often occurs in areas of lower vegetation cover (Reed *et al.* 2009), may not support adequate prey.

The GAMM used as a response variable the number of individuals within each transect, but without considering imperfect detection within the model. Incorrect counting could negatively affect the reliability of the results (Banks-Leite *et al.* 2014), especially at sites where detectability decreased due to environmental factors interfering with observations. This could occur in the SNP when transects crossed habitats of extensively wooded areas and slopes. However, Secretarybirds naturally avoid excessive woodland cover, so woodlands with or without slopes should be unimportant here. Nevertheless, problems could arise in areas with suitable vegetation and rainfall that contain slopes. The large sample of transects, their independent and uniform distribution in the study area, the multiple replicates (≥3), the low speed during sampling, the openable car roof and an average detection probability greater than 0.5 minimize the issue. Consequently, we are confident that counts were representative of the individuals present and that the model is reliable.

The GAMM explained ~51% of the observed variability, although the model was built without considering interactions with other animals (Sobèron & Peterson 2005, Sobèron 2007, 2010). Parameterizing inter-specific competition, predation, prey species and their availability and disturbance caused by large mammals (Romani *et al.* 2024) requires many years of data collection. The great biodiversity, extent and dynamism of the Serengeti ecosystem (Kideghesho *et al.* 2005) also make it particularly complex to document the entire area. However, habitat selection models based on environmental covariates acquired through remote sensing (e.g. vegetation, rainfall, burned areas, topography, watercourses) reliably identify the species ecological needs (Rechsteiner *et al.* 2017, Herniman *et al.* 2020), providing indications for management.

The GLM found significant differences in habitat selection between pairs and single individuals. In the northern SNP, the probability of pairs was higher than other sectors. Since northern Secretarybird density was lower than in central and southern SNP, the most suitable areas could be occupied and actively defended by pairs with larger territories, leaving fewer opportunities for others to settle (Newton 2003, Martínez-Hesterkamp *et al.* 2018). Less difference occurred between the southern and central sectors, where HDAs and optimal habitats were located. Here, pairs could be more tolerant towards other individuals or could have smaller territories (Newton 2003), which was possibly reflected by some short distances between nests (Eurafrica Conservation Projects unpublished data).

The difference between western and other sectors could be due to more heterogeneous habitats (Anderson *et al.* 2008), with a higher probability of encountering single individuals than pairs in more heterogeneous habitats. However, the singles seen in the west could also have been pairs dividing their hunting territory in smaller grassland patches. Such small patches could alternatively be temporarily occupied by sexually immature birds during dispersal, but these hypotheses require verification by telemetry studies. The closed-treed shrublands were surprisingly preferred by pairs, but the range of this vegetation type within the buffers was small (0–10.7%). The higher probability of seeing pairs in closed-treed shrubland could reflect a high prey diversity (Cramer & Willig 2005) or larger prey, such as snakes and lagomorphs that are good food resources for chicks.

Finally, in the third daily phase (12:01–15:00) it was easier to spot pairs than singles, as hunting activity decreases and individuals often lie down in the grass or fly, increasing the probability of observing pairs rather than lone individuals. This factor should be considered when planning a Secretarybird census, since during the third time interval single individuals

may be erroneously excluded from counts. During the other time intervals, singles and pairs can be observed with a similar probability.

Conclusions

This work represents the first study aimed at deepening our knowledge of Secretarybird ecology and demography in Tanzania, so it is difficult to compare our findings. We strongly encourage neighbouring countries to conduct similar research to take better decisions for the future conservation of Secretarybirds at the international level, especially in view of a global Secretarybird Action Plan. Although our results have highlighted important relationships between Secretarybird abundance and environmental characteristics in the study area, future research is needed to clarify the precise mechanism by which some variables affect the species. Studies of nest-site selection and nestling survival in relation to abiotic and biotic factors could be informative. Nevertheless, we answered our main questions to provide the first guidelines for a management plan for Secretarybirds in the Serengeti – Mara ecosystem.

The Secretarybird abundance estimated for the SNP is a positive signal, considering the species' global decline. The SNP population could be one of the largest in Sub-Saharan Africa and an important source population for East Africa. Within the SNP there were areas of particularly high density that should be established as Secretarybird high-priority conservation zones. Here, management actions should aim to preserve their ecological characteristics and minimize negative human activities, such as excessive use of prescribed fires. Habitats within these areas could be taken as a reference for choosing sites for restocking programmes. Finally, research on Secretarybird ecology and demography should include population genetics studies, as it is unknown whether Secretarybirds in the PAs can freely disperse outside the borders or are limited by anthropogenic pressures, resulting in insufficient movement between populations. Knowledge of genetic structuring, diversity and demographic history is urgently needed to properly update the Secretarybird's national and global conservation status.

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Author contributions

F Romani and E Ramella Levis contributed equally to this manuscript. F Romani and E Ramella Levis designed the study, secured funding, analysed data and wrote the paper. EC Mmassy, F Romani and E Ramella Levis collected data. M Posillico and D Pellitteri-Rosa contributed to data analysis. EC Mmassy, D Pellitteri-Rosa and M Posillico revised the paper. All authors commented on and approved the final manuscript.

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