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\*CORRESPONDENCE Mwangi Wambugu wambugu.geoffrey@gmail.com

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# Many winners, few losers: stable bird populations on an Afrotropical mountain amidst climate change

Mwangi Wambugu<sup>1,2\*</sup>, Laura Martínez-Íñigo<sup>1</sup>, Bernard Amakobe<sup>1,2</sup> and Mwangi Githiru<sup>1,2</sup>

<sup>1</sup>Biodiversity and Social Monitoring Department, Wildlife Works, Voi, Kenya, <sup>2</sup>Department of Zoology, National Museums of Kenya, Nairobi, Kenya

Organisms in mountainous areas are frequently exposed to climatic extremes and are among the most vulnerable to climate change. Long-term studies on birds along elevational gradients, which are vital in understanding species dynamics, are rare in tropical mountains, which limits the ability to understand their population trends in the face of climate change. We modelled local abundances of understorey bird species (N=18) over a 13-year period (2011–2023) in Mt. Kasigau, Kenya, using mist netting data collected along an elevational gradient. Our models show relatively stable bird abundances in the study period. However, we found two distinct population crashes that affected most species in 2015 and 2022, suggesting that changes in local dynamics may lead to heavy declines of bird populations in mountainous regions. Most species had stable local abundances in the study period, but parametric bootstrapping revealed a declining trend for a few species, including an endemic, threatened species. We highlight the importance of mountainous regions in maintaining relatively stable populations in the face of global environmental transformation such as posed by climate change, and the dynamism of bird species populations across relatively small spatial-temporal variations. While mountain ecosystems are viewed as potential refugia for biodiversity in the face of a warming climate, further studies are needed to understand the drivers of short and long-term declines in bird populations at higher elevations, especially in tropical Africa.

#### KEYWORDS

elevational gradient, Afrotropical, understorey birds, climate change, Mount Kasigau, refugia

# Introduction

Biodiversity declines in the Anthropocene continue to increase compared to the presumed prehuman background rate, with profound effects on ecosystem functioning and services (Loss et al., 2015; Rosenberg et al., 2019). Tropical ecosystems are important biodiversity reservoirs compared to other biomes, but their integrity continues to be

threatened by existential anthropogenic threats such as habitat loss, climate change, unregulated harvest, and other forms of humancaused mortality (Barlow et al., 2018a; Ceballos et al., 2015; Gardner et al., 2009; Pollock et al., 2022; Rosenberg et al., 2019). Increasing temperatures coupled with changing rainfall patterns in the tropics are expected to impact species' distribution patterns and population dynamics (Freeman et al., 2018; Freeman and Class Freeman, 2014; Magurran et al., 2010; Toms et al., 2012), in addition to driving upslope range shifts of lowland tropical species across taxa (Freeman et al., 2018; Freeman and Class Freeman, 2014). There is strong theoretical and empirical evidence indicating that tropical biotas are more strongly affected by anthropogenic ecosystem changes than their temperate counterparts (Colwell et al., 2008; Sekercioglu et al., 2008). Due to the global importance of tropical forests as carbon sinks and biodiversity, mitigating anthropogenic impacts on ecosystems and conserving tropical biodiversity has become an increasingly urgent research priority (Barlow et al., 2018b; Pollock et al., 2022). Despite general consensus that loss of montane forest habitat can lead to a decline of these small and isolated populations that are already elevationally constrained (Guo et al., 2013; Lomolino, 2001; McCain, 2009), few studies exist along elevational gradients especially in tropical Africa (Kittelberger et al., 2021). Furthermore, few elevational studies in Africa have focused on species trends despite the continent having steep elevation gradients many of which are unprotected (Elsen et al., 2018; La Sorte et al., 2014; Sheldon, 2019).

Baseline data are urgently needed to document how tropical species along elevational gradients have responded and will respond

to rising temperatures, deforestation, and other anthropogenic threats (Freeman and Beehler, 2018b). However, there is a scarcity of baseline data in the tropics on species' distributions (Collen et al., 2008; van der Hoek et al., 2020). There are few published elevational baselines of raw data that include the number of individuals of each species detected (Freeman et al., 2018a; Freeman and Beehler, 2018b; Pagaduan and Afuang, 2012). Here, we used a 13-year (2011 to 2023) population study of understory birds along an elevation gradient of a tropical montane forest - the longest study of its kind in the Eastern Arc Mountains - to evaluate long-term population trends from an isolated but intact forest reserve in southern Kenya. We used the number of unique individuals captured as an index of abundance (Pollock et al., 2022) and modelled the populations of 18 out of the 56 resident bird species, with the goal of determining how their abundances had changed over the 13-year sampling period.

## Methods

#### Study area

We conducted our study along an elevational gradient of Mt. Kasigau (Figure 1), the northeastern most mountain of the Eastern Arc and coastal forests biodiversity hotspot (Myers et al., 2000). These ancient crystalline mountains are characterized by high species richness and the higher concentration of endemic species richness compared to other hotspot locations, but face among the highest



FIGURE 1

Location of Mt. Kasigau in Taita Taveta County, Southern Kenya. We conducted our study along a transect traversing the mountain's elevation gradient with four ringing stations. The mist net configuration is also shown.

degrees of habitat fragmentation and loss (Newmark, 1998). The climate in the surrounding lowlands is semiarid, with average annual rainfall in the 300-500 mm range that is largely irregular and prone to fail. However, the mountain itself receives relatively higher rainfall owing to its higher elevation and forest cover, which captures cloud precipitation brought in by southeast trade winds originating from the Indian Ocean (Aerts et al., 2011). There are typically two rainy seasons, in November and April, known as the grass rains and the long rains, respectively. The rainfall pattern is bimodal alternated with a long (June-September) and a short (January-March) dry period (Aerts et al., 2011). The mountain slopes are fairly steep, rising from 600 to 1641 m within 6km. Floristically, two distinct vegetation types characterize the mountain. The lower elevations are characterized by the Vachellia-Commiphora Dryland Savannah, which transitions into patches of grassland and open shrubs in mid-elevations. Dominant species include Vachellia tortilis, V. nilotica, V. busseio, Commiphora africana, C. campestris, and C. confusa. A few emergent hardwoods include Terminalia spinosa, Melia volkensii, and Boscia coriacea, with the occasional V.

*zanzibarica*. The higher elevations are characterized by cloud montane forest, with characteristic trees including *Cola greenwayi*, *Newtonia buchananii*, *Sysygium* sp. and *Diospyros* sp. (Birdlife International, 2025).

## Data collection

We established mist net lines at four sites, each approximately 230m in elevational difference, along a 3.5km long transect on Mt. Kasigau. We set the transect on the northern side of the mountain which is relatively uniform in gradient and is more accessible and practical for ringing owing to fewer cliffs and rock faces (Figure 1). We designated the sites numbers I–IV from the lowest to the highest, with the basic vegetation type, composition and net line characteristics as described below (Amakobe, 2020).

- Site I (858m asl) is characterized by bushland vegetation type, with numerous dryland species. Dominant trees include *Vachellia hockii, Euphorbia quinquecostata* and *Commiphora baluensis*, while dominant shrubs include *Grewia bicolor* and *Catunaregam nilotica*. There is evidence of human disturbance, albeit minimal, through firewood collection, livestock grazing and isolated incidences of logging on this site. There are three net lines on this site (96m, 84m and 120m).
- Site II (1104m asl) is characterized by woodland vegetation type, with tall trees up to 20m in height and an open canopy cover of above 20%. Bushes and shrubs dominate the ground layer. Dominant trees include *Dombeya kirkii*, *Olea africana* and *Manilkara sp* with *Croton pseudopuchellus*, *Combretum exalatum* and *Searsia natalensis*. There are five net lines on this site (48m, 48m, 60m, 36m and 108m).
- Site III (1321m asl) is characteristic of evergreen forest vegetation type, largely consisting of tall, broad-leaved trees, shrubs and climbers. Trees and shrubs in this site are largely

evenly distributed. Typical trees include *Rawsonia lucida*, *Sorindeia madagascariensis*, *Tabernaemontana stapfiana*, *Dracaena steudneri*, *Garcinia volkensii* among others. There are two main shrub species at this site, *Piper capense* and *Diospyros natalensis*. There are three net lines on this site (96m, 72m and 132m).

• Site IV (1547m asl) consists of montane cloud forest of trees, shrubs and climbers with several species endemic to the area (including the larger Taita Hills Forests). Dominant trees are mainly *Myrica salicifolia* and *Psychotria lauracea*, with several other trees present in lower frequencies, including *Newtonia buchananii*, *Turraea holstii*, *Xymalos monospora*, *Sorindeia madagascariensis*, *Tabernaemontana stapfiana* among others. The main shrubs on this site are Dracaena steudneri, Diospyros natalensis and Piper capense. There are four net lines on this site (60m, 60m, 84m and 96m).

We ringed birds using standard mist netting procedures (Karr, 1981), using permanent mist net lines (positions) established at the four elevations (Figure 1). We undertook 1 to 4 sampling sessions a year, making as much effort as possible to sample birds in the one dry (January-February or July) and one wet (April-May or September-October) season annually. Sampling was suspended in 2016, 2017 and 2018 due to funding constraints, resuming again in 2019. During a sampling session, we undertook ringing at all 4 sites along the transect, each for two days, making a sampling session 8 days in total. Net lines were evenly spaced on each site, and a daily trapping effort of a total of 300 meters of mist nets per site operated for 6 hours (6:00 am to 12:00pm) maintained constant in all the 4 sites. We checked mist nets at 1-hour intervals to ensure prompt removal, processing, and release of captured birds. We restricted our assessment of species richness to understorey bird communities, i.e., 0-4m above the forest floor (Derlindati and Caziani, 2005) as these are the most reliably caught by mist nets (Karr, 1981). During periods of inclement weather, especially heavy rains, we temporarily closed the nets to pause sampling, resuming after weather conditions improved. We marked all individual birds with uniquely numbered aluminum rings and identified them to the species level using Birds of Kenya and Northern Tanzania (Zimmerman et al., 1999) field guide and expert knowledge.

#### Data analyses

We performed all analyses in R 4.4.0 (R Core Team, 2024) loaded into RStudio 2024.04.1 Build 748 for Windows. Our analysis aimed to determine the long-term trends of bird species abundance between 2011 and 2023. Despite evidence of idiosyncratic variations in bird abundances over long timescales in this population (see Amakobe, 2020; Wambugu et al., 2024), the focus of this study was to estimate long-term trends for individual bird species. We modelled the local abundance for all the species from which we captured at least 20 individuals (N=18 species). We used the number of unique individuals captured from the same species in

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each sampling session and site as a proxy for their local abundance (e.g. Blake and Loiselle, 2015a; Pollock et al., 2022). We chose this index because our sampling protocol is designed to minimize behavioral avoidance of mist nets by sampling at each site for only two days per session, and this index is expected to be reliable with this type of dataset (Remsen and Good, 1996). When we contrasted the number of captures obtained on the first and second day of each sampling session per site, the paired Wilcoxon signedrank test indicated a statistically significant difference (W = 1998, p =  $9.74 \times 10^{-6}$ ) in the number of samples collected on the first sampling day of each session at each site (median = 14) compared to the second day (median = 10). Specifically, the number of samples collected on the second day was significantly lower than the first day (Supplementary Figure S1), which indicates a slight but consistent net avoidance within sessions. Nevertheless, we did not observe systematic declines in captures between sessions (Supplementary Figure S1) or consistent increases in captures after prolonged periods without sampling, suggesting that the number of unique individuals captured was a reliable index of abundance in the long-term.

We completed our local abundance dataset post-fieldwork by including absences whenever a given species was not recorded in a season-site combination in which it was detected at some point during the study period. We modelled local abundance as a function of the year and included site and season as covariates to account for their potential influence. We did not include net hours as an offset to account for differing sampling efforts, since they remained fairly stable across the study, with 6h per day and 2 sampling days per session at each site. There was a maximum of one session per season each year of study.

We first fitted a generalized linear model using Poisson distribution for all 18 species, using the function glmmTMB from the homonymous R package, v. 1.1.9 (Brooks et al., 2017). We verified the overdispersion of the models with the function overdisp.test included in the script diagnostic\_fcns.r (Fischer et al., 2024). For those species whose models showed evidence of overdispersion (i.e., the variance is greater than the mean as indicated by the dispersion parameter being significantly greater than 1) (N=16), we fitted 3 additional models: Poisson distribution corrected for zero-inflation, negative binomial type 1 and negative binomial type 2. Negative binomial type 1, also known as quasi-Poisson, has a linear parameterization and is particularly useful when the variability of the data grows proportionally to the mean. Type 2 presents quadratic parameterization, and thus, it is more suitable when the variability increases exponentially (Ver Hoef and Boveng, 2007). We used Akaike's Information Criterion (AIC) to select the best-fitting model for each species. If the model with the lowest AIC presented overdispersion, then the model with the second lowest AIC was selected for the species. We verified the deviance and Pearson residuals of the selected, as well as the simulated residuals derived with the function simulateResiduals of the package DHARMa v.0.4.6 (Hartig and Lohse, 2022), to ensure the absence of systematic deviances of the assumptions.

Since the impact of losing a certain number of individuals depends on the initial population size, we aimed to account for this to ensure meaningful comparisons across species. Following Pollock et al. (2022), we computed two metrics derived from the slopes associated with the year ( $\beta_{year}$ ), which is the rate of change in the predicted number of unique individuals captured each year (see Supplementary Table S1 in the Supplementary material for raw  $\beta_{vear}$  estimates). The first metric was the annualized proportional change in abundance (APC) (i.e.,  $e^{\beta-1}$ ), which informs about the expected yearly change in the local abundance and, as such, conveys the speed of the change, with greater absolute values representing quicker changes in the abundance. The second metric was the total proportional change (TPC) (i.e.  $e^{\beta t-1}$ ), which represents the total local abundance variation over the full study period of 13 years. For both metrics, we calculated 95% confidence intervals by substituting  $\beta_{vear}$ with its corresponding confidence interval values. We categorized the local abundance trends as "increasing" if the 95% confidence interval only contained positive values, "decreasing" if the interval was negative and "stable" if the interval contained zero. We calculated an additional measurement of the total local abundance change by subtracting the predicted number of individuals at the end of the study (2023) according to the best-fitted model from those predicted at the beginning (2011) ( $\Delta n$ ). In order to obtain a confidence interval of the predicted local abundance increment, we performed parametric bootstrapping. This consisted of repeating 100 times the process of simulating data for each species based on their best-fitting model, refitting the model with the new sample and using it to calculate the corresponding increment. This measure captures the number of individuals expected to have been gained or lost in the local abundance over the study period.

#### Results

The trends in the number of species captured at each site over time in Mt. Kasigau elevational transect are shown in Figure 2. We registered a total of 2149 bird captures constituting 1755 unique individuals from 61 species in 30 families over the 19 sampling sessions that took place in 9 years, i.e. 2011–2015, 2019 and 2021– 2023 (Figure 2; Supplementary Table S1). The total sampling time amounted to approximately 912 net hours within the 13-year period. Out of the 61 species registered in the study period, 18 species had at least 20 individual captures and were used in our models (Figure 3).

Overall, the models indicated that 15 of the 18 species analyzed (83.33%) had stable local abundances between 2011 and 2023 (Figure 4; Supplementary Table S1). The exceptions were the Green twinspot (*Mandingoa nitidula*, APC= -0.16, APC<sub>95%CI</sub> = [-0.23, -0.09]; TPC= -0.90, TPC<sub>95%CI</sub>= [-0.97, -0.69]), and the Taita White-eye (*Zosterops silvanus*, APC=-0.11, APC<sub>95%CI</sub>= [-0.18, -0.04]; TPC=-0.78, TPC<sub>95%CI</sub>= [-0.92, -0.40]), whose declines were statistically significant, and the Eastern Nicator (*Nicator gularis*, APC= 0.07, APC<sub>95%CI</sub>= [0.02, 0.14]; TPC=1.54, TPC<sub>95%CI</sub>=[0.23, 4.23]) whose increase was statistically significant.

When we compared the estimated increments in local abundance obtained through parametric bootstrapping ( $\Delta$ n) between 2011 and 2023 (Figure 5; Supplementary Table S2), our results differed slightly. In this case, besides the Green twinspot ( $\Delta$ n= -12.31;  $\Delta$ n<sub>95%CI</sub>= [-19.81, -7.65]) and the Taita White-eye ( $\Delta$ n=-2.89;  $\Delta$ n<sub>95%CI</sub>= [-7.53, 0.4]), the Red-throated Twinspot



(*Hypargos niveoguttatus*) also showed a decreasing trend in this analysis ( $\Delta n = -9.61$ ;  $\Delta n_{95\%CI} = [-2268.93, -1.74]$ . According to theparametric bootstrap on the local abundance increment, four species showed a local abundance increase. As in the previous analysis, Eastern Nicator (*Nicator gularis*,  $\Delta n = 4.77$ ;  $\Delta n_{95\%CI} = [0.92. 8.1]$ ) was one of them. The other three were White-starred Robin (*Pogonocichla stellata*,  $\Delta n = 3.26$ ;  $\Delta n_{95\%CI} = [1.31, 5.04]$ ), Bleating Camaroptera (*Camaroptera brachyura*,  $\Delta n = 3.26$ ;  $\Delta n_{95\%CI} = [1.19, 5.13]$ ), and Bearded Scrub-robin (*Cercotrichas quadrivirgata*,  $\Delta n = 2.54$ ;  $\Delta n_{95\%CI} = [0.27, 4.79]$ ).

# Discussion

Our results show a stable population trend for most studied bird species in Mt. Kasigau, despite inter-seasonal and inter-year fluctuations (Figure 5). These results are in line with those in Manu National Park (Peru), where bird populations and rainfall were found to remain reasonably stable in a 40-year period (Martínez et al., 2023). However, our models are in contrast with those of other recent studies on montane bird population trends in tropical and Paleartic region that report generalized declines over



graphs as "other" to simplify the graph.



the last decades (Blake and Loiselle, 2024; Brown et al., 2019; Lehikoinen et al., 2014; Neate-Clegg et al., 2021; Pollock et al., 2022; Riegert et al., 2021; Zamora and Barea-Azcón, 2015). Many tropical mountains have experienced changes in their climatic conditions and vegetation structure, implying changes in species niches that are likely to be driving the population fluctuations (de la Fuente et al., 2023; Dulle et al., 2016; Riegert et al., 2021). In contrast, the vegetation cover in Mt. Kasigau has remained largely stable over the study period, as have the temperatures at the sampling sites and the rainfall at the county level (Nyambariga et al., 2023). This general intactness of the montane forest habitat in Mt. Kasigau, which is largely devoid of human activities besides small scale firewood collection in the lower altitudes, livestock grazing in dry conditions and ecotourism, may explain the largely stable bird populations. Further, tropical climates are assumed to have constant environmental conditions which lead to constancy of resources and, hence, more stable populations especially in areas

unaffected by significant human activities (Blake and Loiselle, 2015a; Sigel et al., 2006).

Despite this apparent stability, the declining trend for a globally threatened endemic species Taita white-eye, *Zosterops silvanus*, alongside Green twinspot *Mandingoa nitidula* (Figures 4, 5) may be indicative of changing habitat parameters or species-specific life history factors that do not favour these species. These declines are not likely to be caused by habitat changes as there has been minimal human disturbance in our study area during the course of the study. Besides natural tree-falls and isolated cases of selective removal of high-quality timber trees, small scale firewood collection and ecotourism are unlikely to have caused these declines. An increase in ecotourism may lead to negative impacts on birds due to behavioural changes caused by noise (Canaday, 1996), but there has not been a substantial increase in this activity during the study to affect bird populations. This suggests that other factors besides habitat changes may be driving these declines and may include but



are not limited to disease and/or climate change. There have been earlier sentiments regarding the declining Taita White-eye when the species was suspected to have experienced a population crash in Mt. Kasigau (BirdLife International, 2022). The decrease in the Taita White-eye's abundance is particularly concerning since Mt. Kasigau was identified as the species' stronghold in the late 1990s, estimated to harbour 78% of the world's population of this threatened species (Mulwa et al., 2007). A potential cause contributing to the Taita White-eye's abundance declines could be inbreeding, which can cost lifetime fitness in birds (Harrisson et al., 2019). Supporting this hypothesis is that the gene flow between Mt. Kasigau and Taita Hills populations is scarce owing to isolation of the former, and the percentage of heterozygosity is relatively low (Habel et al., 2014). Inbreeding has been shown to have a lifetime fitness cost in birds (Harrisson et al., 2019). Restricted dispersal and frequent inbreeding within "sky island" systems, such as Mt. Kasigau for the Taita White-eye, can occur even in highly mobile bird species (Ceresa et al., 2024). In contrast, the Eastern Nicator showed remarkable increases in its abundance in the same period. Further studies are needed to understand the underlying causes of these population changes despite relatively stable rainfall and temperature conditions across the study period. Moreover, other species in the same diet guilds similar to these species have not experienced similar population changes.

Despite overall stability in bird populations, our analyses show short term dips and peaks in bird population trends. These dips may be attributable to the number of sampling sessions undertaken: there was only one sampling session undertaken in 2011, 2015 and 2019 while there were 2-4 sessions in all other years. However, periodic dips and peaks in bird abundances have been observed in other studies and have been hypothesised to be the effect of large-scale climatic cycles, such as El Niño-Southern Oscillation (ENSO) which can affect bird populations in different ways across geographical regions (Ballard et al., 2003; Blake and Loiselle, 2015a; LaManna et al., 2012). These ENSO events may not only influence the breeding success on birds both positively and negatively but could also affect their foraging behaviour and diet. In our study area, periodic changes in weather parameters were suggested as driving these periodic declines in an earlier study (see Wambugu et al., 2024). Data from the Kenya Meteorological Department (Kenya Meteorological Department, n.d) reveals that both 2011 and 2015 corresponded to La Niña and El Niño extreme weather periods, respectively, which may partly explain these dips in bird population trends in our study. It is however worth noting that many of the species in our study were only captured in one or two years at each site. Thus, our dataset only provides an indication of the general trend in bird community over time but it's unclear regarding the turnover between species.

Several species were consistently present in the first half of the study (2011–2015) but absent in the second half (notably Common bulbul and Lesser Honeyguide in Site I; Spotted Flycatcher in Site II; and African Pygmy Kingfisher and African Goshawk in Site III). Likewise, other species appeared in the second half such as the Red-throated Twinspot and the Variable Sunbird in Site I. Other studies have termed similar observations as winner–loser species replacements, which may be triggered by changes in habitat parameters (Lees and Peres, 2006; Tabarelli et al., 2012). Winner–loser patterns are clearer in human–modified landscapes due to widespread habitat changes (e.g. Filgueiras et al., 2021) but less so in more intact habitats. In our study, these changes appear to have occurred immediately after population collapse, thought to be due to changes in resource availability as a result of unconfirmed events (Figure 2).

# Conclusion

Our study shows that most bird species populations in Mt. Kasigau remained stable despite reported declines in similar locations elsewhere in the tropics. This stability indicates the role of montane areas as refugia for birds in the face of a warming climate, along with other anthropogenic pressures. Our study further emphasizes that relatively small mountain regions can play an important role in maintaining stable bird populations as global environmental transformation continues to escalate. However, future studies should focus on species-specific life history aspects to better understand population trends of Afromontane birds, especially those that appear to be undergoing declines.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

## Ethics statement

The animal study was approved by National Commission for Science, Technology and Innovation (NACOSTI, Kenya) and the East African Bird Ringing Scheme. The study was conducted in accordance with the local legislation and institutional requirements.

## Author contributions

MW: Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. LM: Data curation, Formal analysis, Methodology, Resources, Software, Visualization, Validation, Writing – original draft, Writing – review & editing. BA: Data curation, Investigation, Project administration, Resources, Supervision, Writing – review & editing. MG: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## **Generative AI statement**

The author(s) declare that Generative AI was used in the creation of this manuscript. Technical support for R code writing was obtained from ChatGPT (GPT-4, OpenAI, https://openai.comb, October 2023), Gemini (Large language model, Google AI, https://gemini.google.com/, 2023) and Microsoft Copilot (GPT-4 Conversational AI Model. Microsoft, https://copilot.cloud.microsoft/, 2024).

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# Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2025.1520857/ full#supplementary-material

Number of unique individuals captured each year in each site for each species. Site I: 858m asl, Site II: 1104m asl, Site III: 1321m asl, Site IV: 1547m asl.

SUPPLEMENTARY TABLE 2

Summary of Results for Modelled species (n=18) along the Mt. Kasigau Elevational transect.

SUPPLEMENTARY FIGURE 1

Number of captures in days 1 and 2 of each sampling session and site

SUPPLEMENTARY TABLE 1

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