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The conservation consequences of taxonomic uncertainty: Integrative evidence supports species status for the Zanzibar tree hyrax (*Dendrohyrax neumanni*)

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Cryptic mammalian diversity is increasingly recognised, yet undescribed taxa may face extinction before receiving formal protection. We compared the Zanzibar tree hyrax *Dendrohyrax validus neumanni* with *D. v. validus* from Mt. Kilimanjaro, Tanzania, using external appearance, cranial morphometrics, vocalisations and habitat. The taxa differed in cranial morphology, pelage and loud calls, while their environments also differed markedly. Individuals from both populations produced complex songs, reported here for the first time for both populations. The populations have been geographically isolated at least since the end of the Pleistocene. Based on this integrative evidence, we propose that the Zanzibar tree hyrax represents a distinct species, *Dendrohyrax neumanni*, although molecular analyses are needed to further assess its taxonomic status. The species is likely endemic to the Zanzibar Archipelago, where the small remaining population depends on scarce cave systems for shelter. Its restricted distribution, small population and ongoing threats require urgent targeted conservation measures.

Introduction

IUCN assessments are particularly important for species that are threatened by extinction because they provide internationally recognised and standardised evaluations of extinction risk. These evaluations inform conservation action, funding priorities, legal protection and species recovery planning (Rodrigues *et al.* 2006, Mace *et al*. 2008). IUCN Red List assessments depend on recognised taxonomic units, meaning that unresolved or undescribed diversity may not be adequately represented in extinction-risk assessments (IUCN Standards and Petitions Committee 2024, Garnett *et al.* 2026). Scientifically undescribed taxa lack official conservation status. Formal species descriptions, including the elevation of subspecies to full species rank, often require the integration of multiple lines of evidence, including morphological, ecological, behavioural and genomic data, a process that may take years or even decades to complete (Mace 2004, Bickford *et al.* 2007). Liu *et al.* (2022) examined extinction risk in recently described vertebrate species and found that the proportion of threatened species increased from 11.9% among species described in 1758–1767 to 30.0% among those described in 2011–2020. Their analysis projected that this proportion could increase to 47.1% by 2050, leading them to conclude that undescribed species have higher extinction risk. Here we present a case study of a mammalian taxon with an unresolved taxonomy, the Zanzibar tree hyrax, which is already on the brink of extinction.

Biodiversity hotspots, such as the Eastern Afromontane and the Coastal Forests of East Africa hotspots, harbour exceptionally high levels of endemism and ecological specialisation. Yet even many groups of mammals within these hotspots remain taxonomically unresolved due to subtly similar or convergent morphology (Bickford *et al.* 2007). Cryptic species are particularly common among nocturnal taxa or taxa living in forests, where limited visibility and conservative phenotypes obscure diversity (Hending 2025, Zhang & Wiens 2026). Failure to recognise cryptic taxa may underestimate extinction risk by masking true distribution ranges and population sizes (Vogel Ely *et al.* 2017, McDonald *et al.* 2022). The analysis of vocalisations can serve as a powerful tool for uncovering cryptic diversity among nocturnal arboreal mammals, as it targets their primary mode of communication, which is subject to strong selective pressures (Snowdon 1989).

Eastern Africa has experienced several drastic climatic oscillations and tectonic uplifts during the Miocene–Pleistocene period. The Eastern Arc Mountains and the coastal forests of the Zanzibar Archipelago have acted as important refugia for plants and animals (Lovett 1998, Burgess *et al.* 2007). A land connection between the African mainland and the Zanzibar Archipelago (hereafter Zanzibar) existed intermittently during the Neogene Period, allowing the dispersal of terrestrial species to Zanzibar. This land connection was finally severed in the late Pleistocene or early Holocene (Prendergast *et al.* 2016). However, many taxa remain shared between the Eastern Arc Mountains and Zanzibar (Kingdon 1990). Within these refugia, isolated populations of forest-dependent species survived environmental change, which gave rise to extensively shifting biogeographical barriers, and allopatric speciation may have led to high rates of endemism (Burgess *et al.* 1998). In such systems, behavioural traits such as acoustic signals often diverge more rapidly than external morphology and can therefore provide strong indicators of lineage differentiation (Wilkins *et al.* 2013, Pozzi *et al.* 2019). Numerous studies have shown that acoustic divergence is a reliable indicator of speciation in many groups of organisms (Wilkins *et al.* 2013, Pozzi *et al.* 2019, Parmentier *et al.* 2022), with subtle differences between populations reflecting genetic distance, isolation duration and habitat-specific adaptations (Sebastián-González & Pérez-Granados 2025).

Tree hyraxes (genus *Dendrohyrax*) are nocturnal, arboreal mammals whose species-level taxonomy is not fully resolved (Roberts *et al.* 2013). The IUCN Red List assessment for the eastern tree hyrax, *D. validus*, classifies the species as Near Threatened (NT) (Hoeck *et al.* 2015). *Dendrohyrax validus* has traditionally (e.g. Hahn 1934, Swynnerton & Hayman 1950) been divided into four subspecies. The nominate subspecies *D. v. validus* True, 1890 lives

on Mt. Kilimanjaro and Mt. Meru, *D. v. terricola* in the Taita Hills and the Pare and Usambara Mountains, *D. v. schusteri* in the Uluguru Mountains, and possibly also the Udzungwa and Rubeho Mountains, and *D. v. neumanni* in Zanzibar, Pemba and Tumbatu Islands. *Dendrohyrax validus neumanni* was named by Matschie in 1893 based on four specimens collected from Zanzibar (Matschie 1893).

Interpretation of cranial and dental variation in hyraxes requires consideration of both ecological and biological sources of morphological differentiation. Cranial dimensions have been linked to feeding-related adaptations and masticatory function in different hyrax lineages (Moyano *et al.* 2019). A recent study demonstrated sexual dimorphism in the upper incisors of the rock hyrax (*Procavia capensis;* Hara 2025). In this species, the upper incisors show age-related sexual dimorphism: in females they become hypsodontic and eventually cease growing with age, whereas in males they remain hypselodontic and continue growing throughout life (Hara 2025).

Eastern tree hyraxes are acoustically highly active, with loud and diverse vocalisations, including songs (Rosti 2023, Rosti *et al.* 2023b). Previous studies have suggested strong acoustic differentiation, with distinct call zones, among these four populations (Roberts 2001, Roberts *et al.* 2013). It is not known whether these are dialects or whether they represent taxonomic differences.

Despite the acoustic evidence and the geographical isolation imposed by the oceanic channel separating Zanzibar from the mainland, no study has integrated general appearance, cranial morphology, vocal communication and habitat information to evaluate the extent of differentiation between the Zanzibar tree hyrax and its mainland relatives. Tree hyraxes are known to have poor dispersal ability (Lawes *et al.* 2000), to rely heavily on stable forest refuges for shelter and to be currently largely restricted to habitats that have undergone extensive fragmentation due to deforestation. If the Zanzibar population is indeed a separate species, its extremely limited range and small population size would warrant a reassessment of its conservation status. Accordingly, this study aims to address the issue by examining the general appearance, cranial shape, acoustic characteristics and ecological setting of the Zanzibar tree hyrax in an integrative framework and comparing it with the nominate subspecies, *D. v. validus*. The expectation is that if the Zanzibar tree hyrax represents a distinct species, the previously noted patterns of divergence in its vocal behaviour should be accompanied by corresponding differences in morphology and habitat use. Together, these data lay a foundation for further evaluating taxonomic diversity within *D. validus*, with direct implications for the conservation of these taxa.

Methods

Study areas

Fieldwork was conducted in Tanzania, in Zanzibar in 2025 and on the southern slopes of Mt. Kilimanjaro in 2023. In Zanzibar, the study sites were on the main island Unguja (–6.259, 39.403), mostly in Jozani National Park (hereafter Jozani; Fig. 1), and on Pemba Island, where the study sites were around Ngezi Forest Reserve (–4.913, 39.706). On Mt. Kilimanjaro, the study sites were in Kilimanjaro National Park (KINAPA; between –3.139, 37.233 and –3.195, 37.519).

The total land area of Zanzibar is 2462 km^2. The human population of the Zanzibar Archipelago was approximately 1.9 million in 2022 (Tanzania National Bureau of Statistics 2022), with an average population density of 768 people/km^2. Unguja Island (1666 km^2) was covered by coastal forest before humans arrived (Kukkonen & Käyhkö 2014). Since then, almost all natural forests have been cleared and replaced by exotic plantations or agricultural land. The most important exotic plantation tree species on Unguja are beach casuarina (*Casuarina equisetifolia*), ear-pod wattle (*Acacia auriculiformis*) and Caribbean pine (*Pinus caribaea*). Zanzibar is one of the Reducing Emissions from Deforestation and Forest Degradation (REDDb) pilot areas aiming to find solutions for hazards following climate change (Caplow *et al*. 2014). Sea level rise, a consequence of climate change, is currently 3.2 mm per year (National Oceanic and Atmos-

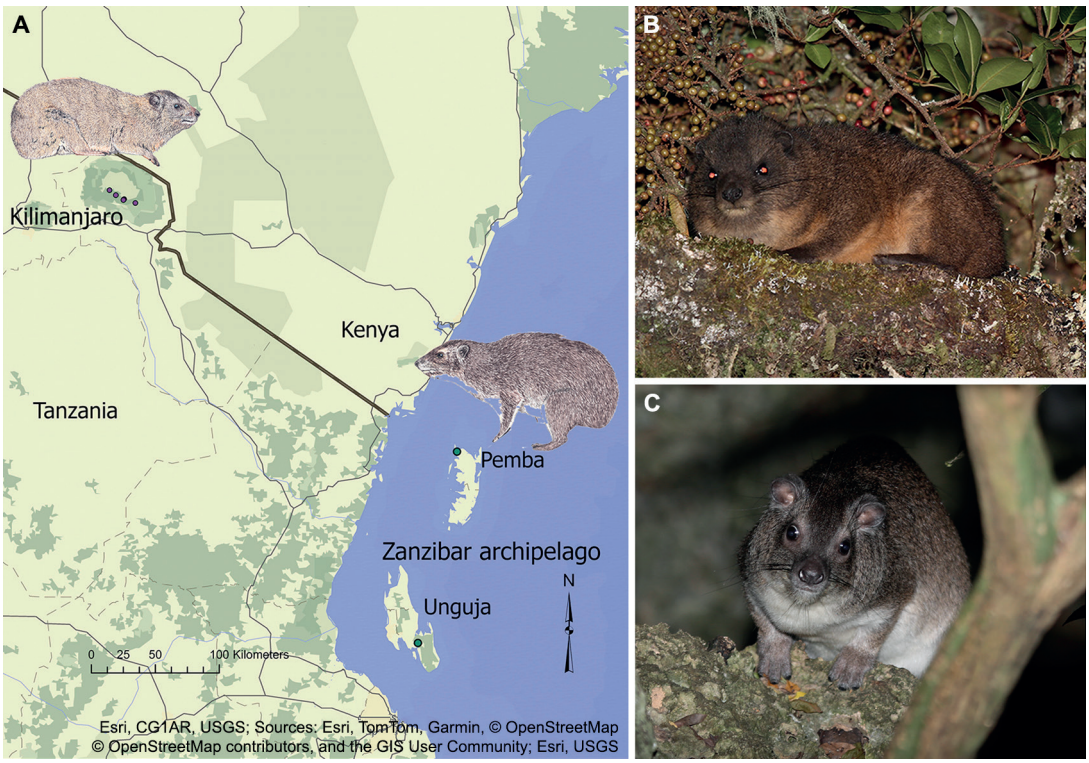

Fig. 1. The study area and studied taxa. — **A**: Study sites (dots) on Mt. Kilimanjaro and in the Zanzibar Archipelago. — **B**: Kilimanjaro tree hyrax photographed near Mandala Hut, Mt. Kilimanjaro. — **C**: Zanzibar tree hyrax photographed in the Jozani Forest, Zanzibar. Basemap: sources and copyright attribution provided within the figure. Basemap material is excluded from the licence applicable to the article and may be subject to separate terms of use.

pheric Administration 2024). Temperatures are high throughout the year. The hottest month is February, with an average temperature of 28 °C, and the coolest month is August, with an average temperature of 24.8 °C. Due to climate change, temperatures are rising with more extremely hot days and nights (Abdalla *et al.* 2023).

Jozani (50 km^2) is mostly secondary forest, with small open clearings that have regrown naturally, and patches of exotic trees. The predominant soil type is "Maweni", a dark red, black or brown laterite with high organic content (Alders 2023). The soil layer is on top of coralline limestone and is so shallow that the roots of sizable trees commonly extend partially above the soil surface. In some locations, the limestone basement has numerous caves and cavities of varying sizes. During spring high water tides, sea water seeps into the ground in Jozani, especially at the northern end of the forest (Said 2017). In Jozani, black plum (*Vitex doniana*) is the main tree species, accompanied by tamanu (*Calophyllum inophyllum*) and oil palm (*Elaeis guineensis*) (Leskinen *et al.* 1997).

The forests of Jozani on Unguja belong to the Zanzibar–Inhambane coastal forest mosaic and occur on coral rag and alluvial substrates. Vegetation is heterogeneous, comprising coral rag thicket and groundwater forest. Coral rag areas support low-stature, structurally dense vegetation (generally 5–15 m), with species such as *Diospyros* spp., *Combretum* spp. and *Erythrina* spp., reflecting shallow soils and seasonal water limitation. Groundwater forest patches, associated with higher fresh- and saltwater availability, reach greater heights (up to ca. 20 m) and include *Syzygium cumini*, *Ficus* spp. and *Rauvolfia caffra*. Overall, the forest shows limited vertical stratification and comparatively low epiphyte abundance (Burgess & Clarke 2000).

The Ngezi Forest on Pemba represents a structurally highly developed coastal forest system on coral-derived substrates. In contrast to many coastal forests of the region, canopy height can be very high, with emergent trees reaching up to 60 m**,** indicating the presence of large, old-growth individuals and favourable local growth conditions. The forest exhibits a multi-layered structure with a relatively continuous canopy and well-developed vertical stratification. Dominant taxa include *Milicia excelsa*, *Afzelia quanzensis*, *Pterocarpus* spp. and *Terminalia* spp., alongside a diverse assemblage of coastal forest species. The vegetation can be classified as semi-evergreen, with some seasonal leaf dynamics, but overall high biomass and canopy closure. Structural variability persists due to differences in soil depth and coral substrate exposure, yet the forest clearly exceeds typical coral rag systems in height and complexity (Rodgers *et al.* 1986, A. Hemp unpubl. data).

Mt. Kilimanjaro is the highest mountain in Africa and located in the East African Rift System (Ebinger *et al.* 1997). The mountain is a relatively young dormant volcano; its volcanic activity began 2.5 Ma ago, eventually forming three peaks. The highest peak, Kibo at 5895 m a.s.l., is the result of volcanic activity between 274 and 170 ka ago (Nonnotte *et al.* 2008). The slopes of the mountain encompass the 1688 km^2 Kilimanjaro National Park, with a continuous natural forest belt between 1900–3100 m. The Mt. Kilimanjaro forest belt forms part of the Afromontane evergreen forest biome, extending approximately from 1800 to 3000 m a.s.l. Vegetation is structured along a clear elevational gradient. Lower montane forests are dominated by species such as *Ocotea usambarensis, Albizia gummifera* and *Macaranga kilimandscharica*, forming a tall, multilayered canopy typically reaching 25–40 m. Higher up (2200–2500 m a.s.l.), the forests are dominated by *O. usambarensis* and have a high epiphytic biomass (mosses, lichens, ferns), receiving the highest annual rainfall. In the upper montane zone above 2700–2800 m a.s.l., *Podocarpus latifolius* gradually replaces *O. usambarensis* and becomes the prevailing species (Hemp 2006a, b). At higher elevations, the forest transitions into cloud forest with *Erica excelsa*, *Hagenia abyssinica* and *Rapanea melanophloeos*, characterised by reduced canopy height but increased epiphyte load and persistent atmospheric moisture. The system is defined by strong vertical stratification and evergreen vegetation (Hemp 2001, 2006a, b).

In Kilimanjaro National Park, tree hyraxes are found in old-growth forests at elevations of 2400–3100 m a.s.l. (Kundaeli 1976, H. Rosti unpubl. data). At these elevations, the mean annual temperature is 10–15 °C (Appelhans *et al.* 2016). The tree hyrax populations in the national park are mainly threatened by forest fires near the upper forest line (Hemp 2005).

Morphology

We studied, photographed and measured 32 tree hyrax skulls in the collections of the Swedish Museum of Natural History, Stockholm, Museum für Naturkunde, Berlin, and the Natural History Museum, London. We also examined several skins of tree hyraxes in these collections.

Skull morphometrics

We used the skull measurement protocols applied by Oates *et al.* (2022) for *Dendrohyrax dorsalis* and *D. interfluvialis* (Fig. 2, Table 1). We measured 12 skulls from Zanzibar (four males, five females and three of undetermined sex) and 20 skulls from Mt. Kilimanjaro (five males, five females and ten of undetermined sex). We only included specimens determined to be adults based on their dentition. Measurements were taken by HP, HR, DCK and TG directly from the specimens using digital callipers, recorded in millimetres to two decimal places. We did not replace missing values with means or use other transformations. Four specimens for which some measurements were missing were excluded from the final analysis.

Analysis for skull morphology

Morphological variation was assessed using cranial and mandibular measurements from museum specimens representing the Mt. Kili-

manjaro and Zanzibar populations. Only specimens with complete data for the measurements included in each analysis were used.

Potential sexual dimorphism in individual cranial measurements was examined before the multivariate analyses using Type III analysis of variance (ANOVA), including population, sex and their interaction as explanatory variables. Only specimens with unambiguous sex assignments were included in the analyses. Measurements showing a significant effect of sex (GWR) were excluded from subsequent analyses of cranial morphology.

Overall skull size was calculated for each specimen as the geometric mean of the 10 remaining cranial measurements CBL, MTL, PPL, LIB, PBPL, LCH, GMH, MCW, LTL and PWC. Differences in overall skull size between populations were tested using a linear model with population as the explanatory variable. To assess whether the population difference in skull size was influenced by sex, a second linear model was fitted to specimens of known sex, with population, sex and their interaction as explanatory variables. The effects of population, sex and their interaction were evaluated using ANOVA.

Overall differences in cranial morphology between the Mt. Kilimanjaro and Zanzibar populations were tested using permutational multivariate analysis of variance (PERMANOVA) with the adonis2 function in the R package vegan (Oksanen *et al.* 2025). The 10 retained measurements were standardised, and Euclidean distances were calculated from the standardised measurements. No size correction was performed because overall skull size was considered an integral component of cranial morphology and a potentially informative character for population differentiation. The effect of population was tested using 9999 permutations. Homogeneity of multivariate dispersion between populations was assessed using distances to group centroids with betadisper and a permutation test with 9999 permutations.

Principal component analysis (PCA) was used to summarise the major patterns of cranial morphological variation and to identify the measurements contributing most strongly to morphological differentiation. The 10 retained measurements were standardised prior to PCA. PCA was performed using FactoMineR (Lê *et al.* 2008) on the correlation matrix. Eigenvalues and the proportion of total variance explained were

Table 1. Abbreviations used for cranial and mandibular measurements, modified from Oates *et al.* (2022).

	Description
CBL	Condylobasal length: distance between the anteriormost point of the premaxilla and the posteriormost margin of the occipital condyle.
GWR	Greatest width of the rostrum: greatest width across the incisor capsules on the dorsal side, measured at the point where the palate is narrowest.
LCH	Lambdoid crest height: greatest distance from the apex (or apices, if bilobate) of the lambdoid crest to the ventral apices of the occipital condyles, measured along the midline.
LIB	Least interorbital breadth: least distance between the anterodorsal corners of the orbits.
LTL	Lower cheektooth row length: greatest distance between the anteriormost surface of P1 and the posteriormost surface of M3.
GMH	Greatest mandibular height at the mandibular condyle.
MCW	Mandibular condyle width: greatest distance between the medial and lateral surfaces of the mandibular condyle.
MTL	Maxillary toothrow length: greatest distance between the anteriormost surface of P1 and the posteriormost surface of M3.
PBPL	Postorbital bar-premaxillary length: distance between the rostral surface of the premaxilla and the caudal surface of the postorbital bar where it articulates with the zygomatic arch, measured obliquely to the long axis of the cranium.
PPL	Palato-premaxillary length: greatest distance between the rostral surface of the premaxilla and the caudal surface of the choanae on one side, rather than from the midline tubercle.
PWC	Posterior width of choanae: maximum posterior width of the posterior nasal apertures.

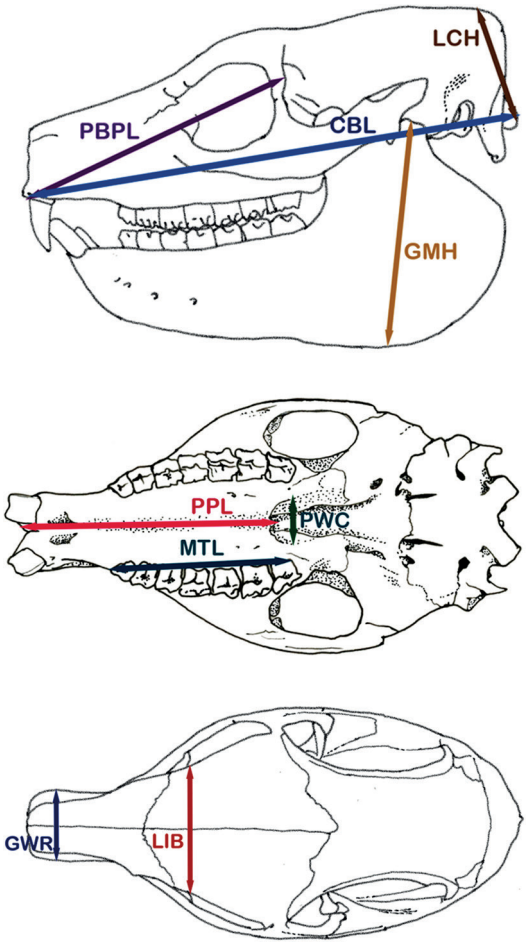

Fig. 2. Tree hyrax skull in lateral, ventral, and dorsal view showing the morphometric measurements used in this study. Abbreviations are explained in Table 1. MCW and LTL are not illustrated.

calculated for each principal component, and variable loadings were examined to determine the contributions of individual cranial measurements to the major components.

Fieldwork

In Zanzibar, in and around Jozani, resident tree hyraxes were located with the help of local knowledge provided by forest rangers, by transects on foot and by searching for existing resting sites (cave formations) in the remaining forests. Fieldwork in Zanzibar was done between 5 and 30 January 2025. Animals were monitored during the night and observed with a thermal imaging camera Pulsar Helion 2 XP50 (Yukon Advanced Optics Worldwide, Vilnius, Lithuania). Animals were also photographed. On Mt. Kilimanjaro, fieldwork was done between 10 and 28 February 2023. Recorders were placed at the long-term research sites of the Kili-SES research group. These sites were located along the Machame, Umbwe, Mweka, Maua and Marangu routes.

Recordings

On Unguja Island, at each location where the presence of Zanzibar tree hyrax had been verified either by calls or latrines, we placed AudioMoth recorders (v. 1.1.0, Open Acoustic Devices, Southampton, UK; Hill *et al.* 2018) in the habitat. We did several transect walks through Jozani and made opportunistic recordings at locations where we had not found tree hyrax faeces, as their loud calls can be recognised over long distances. On Pemba, recorders were placed at locations with tree hyrax latrines and within Ngezi Forest Reserve. The recording period was from 24 hours a day with full hour recordings. However, for the analysis only hours between 19.00 and 06.00 was analysed, as this is the active calling period for tree hyraxes. We collected 1113 hours of recordings from Unguja Island and 142 hours from Pemba Island. Recordings from Mt. Kilimanjaro totalled 1800 hours.

Call analysis

We compared loud calls used by tree hyraxes in Zanzibar and on Mt. Kilimanjaro. Loud calls were very loud, typically more than 100 dB, and were considered likely to be used for advertisement. Loud calls of tree hyraxes were classified into three main categories. 1) Single calls were continuous, i.e., did not have any silent breaks within the call. 2) Patterned sequence calls comprised a series of variable syllables interspersed with silent breaks – a pattern similar to the songs of some songbirds. These calls were given in (nearly) the same way each time and could be used to identify the species or population. Pat-

terned sequence calls consisted of a stereotyped series of syllables separated by short silent intervals, with the sequence produced in a consistent order. 3) Songs were longer and more complex vocalisations composed of several element types whose number and order varied within and among vocalisations, lasting from 20 s to several minutes. The chackle was classified as a patterned sequence call rather than a song because its syllable sequence was highly stereotyped, whereas songs were longer and showed greater variation in the number and order of vocal elements.

Loud acoustic calls (n = 160) from Zanzibar (including Unguja and Pemba) were compared with calls recorded on Mt. Kilimanjaro (n = 160). On Mt. Kilimanjaro, calls were chosen from 15 different locations at different times and in Unguja and Pemba, calls were chosen from six locations. A maximum of 10 calls were chosen from one calling sequence. Calls were isolated in Raven Pro 1.6 (v. 1.11.0 Open Acoustic Devices, Southampton, UK). The sampling rate was 48 kHz, with 16-bit encoding. Hann window was 512 samples. Only clear loud calls, without any overlapping mammal calls, were used in the call analysis; however, some acoustic interference from chorusing Orthoptera was unavoidable. Acoustical and statistical analyses were done in R (v. 4.5.1) and RStudio (v. 2025.09.2+418; R Core Team 2025). Acoustic measurements were extracted from each vocalisation using spectro_analysis in the warbleR package (Table 2; Araya-Salas & Smith-Vidaurre 2017). This function calculates spectrographic and temporal descriptors from annotated sound selections, including duration, frequency distribution, dominant frequency and entropy-based acoustic parameters. Principal component analysis (PCA) was performed using package FactoMineR (Lê *et al.* 2008) on the correlation matrix to visualise differences among calls in relation to different parameters.

Data in CSV format and sample calls as WAV files are openly available at https://zenodo.org/records/19553712.

Table 2. Acoustic parameters measured with warbleR (Araya-Salas & Smith-Vidaurre 2017).

	Description
duration	Total duration of the call (s)
meanfreq	Mean frequency of the call spectrum (Hz)
sd	Standard deviation of frequency (Hz), describing spectral spread
freqmedian	Median frequency dividing the spectrum into two equal-energy halves (Hz)
freqQ25	First quartile (25%) of the frequency distribution (Hz)
freqQ75	Third quartile (75%) of the frequency distribution (Hz)
freqIQR	Interquartile range of frequency (freqQ75 – freqQ25)
timemedian	Median time of energy distribution within the call (s)
timeQ25	First quartile (25%) of the temporal energy distribution (s)
timeQ75	Third quartile (75%) of the temporal energy distribution (s)
timeIQR	Interquartile range of temporal energy distribution (s)
skew	Skewness of the frequency spectrum, indicating asymmetry
kurt	Kurtosis of the frequency spectrum, indicating peakedness
sp.ent	Spectral entropy, measuring tonal vs. noisy structure
timeent	Temporal entropy, describing temporal energy dispersion
entropy	Overall entropy of the signal, summarising acoustic disorder
sfm	Spectral flatness measure, indicating tonality vs. noisiness
meandom	Mean dominant frequency across the call (Hz)
mindom	Minimum dominant frequency detected (Hz)
maxdom	Maximum dominant frequency detected (Hz)
dfrange	Range of dominant frequency (maxdom – mindom)
modindx	Frequency modulation index, describing modulation depth
startdom	Dominant frequency at the beginning of the call (Hz)
enddom	Dominant frequency at the end of the call (Hz)
meanpeakf	Mean peak frequency across time windows (Hz)



Fig. 3. Zanzibar tree hyraxes from Unguja Island, Zanzibar. — **A**: Frontal view showing details of the face; males have long and sharp upper incisors. — **B**: Lateral view showing a white belly, short feet and brownish overall appearance, with dorsal pelage with different shades of brown and with black hair tips. — **C**: Dorsal view showing the distinctive dorsal gland, with long pale hair. — **D**: Typical inhabited cave on Unguja Island, with an actively used latrine in the foreground. Photographed in 2025.

Results

General appearance

The dorsal pelage of the Zanzibar tree hyrax specimens was coarse, with a wax-like texture. Under-hair was absent. Colour was brown or greyish, with different shades, many hairs had black tips (Figs. 1C and 3A–C). The ventral pelage was white or light yellow, feet were grey. The easily visible dorsal spot (dorsal gland) was usually ochre-coloured, with the base of the hairs brown.

The dorsal pelage of the Mt. Kilimanjaro tree hyrax specimens was dense, soft and fluffy with under-hair. Colour was blackish with a reddish-brown shade. The ventral side was commonly yellowish brown, only rarely white, feet were typically black. The dorsal spot was usually ochre-coloured, and it was sometimes difficult to find.

In museum specimens, the best distinguishing pelage characters between tree hyraxes from Zanzibar and Mt. Kilimanjaro were the shorter hair, waxy pelage texture and lack of under-hair in individuals from Zanzibar. Specimens from Mt. Kilimanjaro had distinctly longer hair and appeared very furry.

Skull morphology

To determine whether sexual dimorphism could influence comparisons of cranial morphology between populations, the effects of sex were examined in specimens with unambiguous sex

assignments (n = 19, 10 females and 9 males). Of the cranial measurements examined, GWR showed a significant difference between sexes after accounting for population ($F_{1,15}$ = 7.83, P = 0.014). The population × sex interaction was not significant ($F_{1,15}$ = 0.06, P = 0.805), indicating that the sex difference in GWR did not differ significantly between populations. GWR was therefore excluded from subsequent analyses of cranial morphology.

Overall skull size differed significantly between tree hyrax specimens from Zanzibar and Mt. Kilimanjaro. Zanzibar specimens had a larger geometric mean skull size (mean ± SD = 32.6 ± 1.08, n = 12) than Mt. Kilimanjaro specimens (29.3 ± 1.26, n = 20). Population had a significant effect on overall skull size ($F_{1,30}$ = 58.10, P < 0.001), explaining 66.0% of the variation in skull size (R^2 = 0.660).

The population difference remained significant when sex was included in the analysis of specimens for which sex could be assigned ($F_{1,18}$ = 33.24, P < 0.001). Neither sex ($F_{1,18}$ = 1.89, P = 0.186) nor the population × sex interaction ($F_{1,18}$ = 0.05, P = 0.826) was significant. Thus, Zanzibar specimens had substantially larger skulls than Mt. Kilimanjaro specimens, with no evidence that the observed population difference in overall skull size was attributable to sex.

Mean values were greater in Zanzibar specimens for all 10 cranial measurements included in the multivariate analyses (Table 3, Fig. 4). The most pronounced differences included CBL (98.47 vs. 87.21 mm), LIB (26.22 vs. 22.03 mm), PBPL (58.41 vs. 51.69 mm) and PPL (52.29 vs. 46.08 mm) in Zanzibar and Mt. Kilimanjaro specimens, respectively. In contrast, PWC differed little between populations (8.36 vs. 8.10 mm).

Table 4. Loadings of the cranial measurements on the first three principal components (PC1–PC3) of the principal component analysis (PCA), with eigenvalues and proportions of variance explained. Abbreviations are explained in Table 1.

	PC1	PC2	PC3
CBL	–0.376	0.077	0.035
MTL	–0.305	0.144	0.583
PPL	–0.375	0.004	0.043
LIB	–0.343	0.204	0.081
PBPL	–0.367	–0.098	0.107
LCH	–0.244	–0.379	0.009
GMH	–0.330	–0.028	–0.447
MCW	–0.312	–0.121	–0.599
LTL	–0.302	0.409	0.085
PWC	–0.120	–0.772	0.270
Eigenvalue	6.694	1.233	0.656
Variance explained (%)	66.9	12.3	6.6
Cumulative variance (%)	66.9	79.3	85.8

Overall cranial morphology differed significantly between the Zanzibar and Mt. Kilimanjaro populations (PERMANOVA: pseudo-$F_{1,30}$ = 24.88, R^2 = 0.453, P < 0.001), with population accounting for 45.3% of the multivariate variation in skull measurements. Multivariate dispersion did not differ between populations (PERMDISP: $F_{1,30}$ = 0.01, P = 0.926), indicating that the PERMANOVA result was not attributable to differences in within-population dispersion.

Principal component analysis showed that the first three principal components accounted for 85.8% of the total variation in cranial morphology (Fig. 5, Table 4). PC1 explained 66.9% of the variation and had similarly directed load-

Table 3. Skull measurements of *Dendrohyrax v. neumanni* from Zanzibar (n = 12) and *D. v. validus* from Mt. Kilimanjaro (n = 20). Measurements are in mm. Abbreviations are explained in Table 1.

	CBL	MTL	PPL	LIB	PBPL	LCH	GMH	MCW	LTL	PWC
D. v. neumanni										
Mean	98.47	35.68	52.29	26.22	58.41	28.97	43.96	12.59	36.26	8.36
SD	3.66	1.32	2.65	1.50	2.53	2.07	2.57	1.39	1.15	0.55
Median	99.66	36.15	52.35	26.02	59.42	28.39	43.76	12.61	36.50	8.33
D. v. validus										
Mean	87.21	33.03	46.08	22.03	51.69	26.77	40.31	10.65	33.19	8.10
SD	4.10	1.42	2.54	2.35	2.33	1.44	2.85	0.72	1.64	0.78
Median	87.48	33.27	46.34	22.19	51.48	26.84	40.84	10.62	33.65	8.09

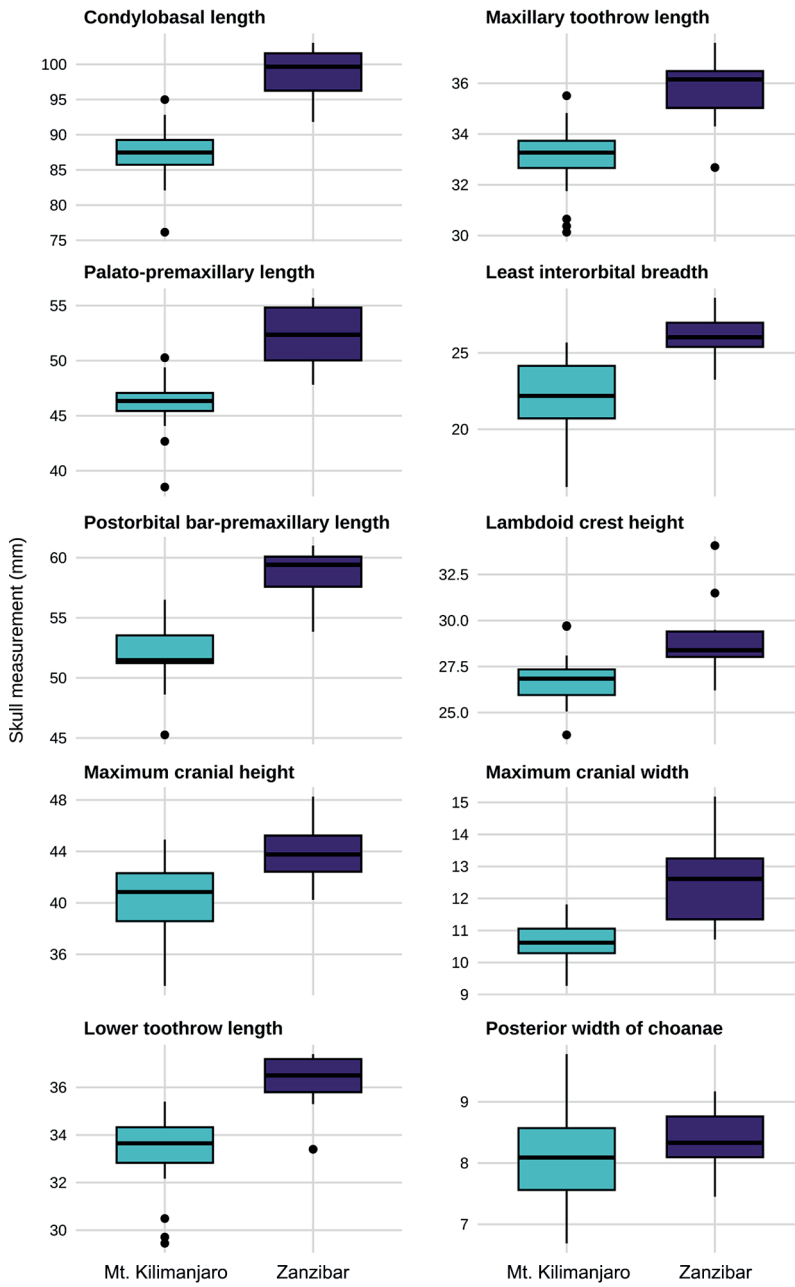

Fig. 4. Boxplots of ten cranial measurements from tree hyraxes from Mt. Kilimanjaro and Zanzibar. Boxes represent the interquartile range with the median indicated by the horizontal line, whiskers extend to observations within 1.5 times the interquartile range, and points indicate outliers. Measurements are in millimetres. Zanzibar: n = 12, Mt. Kilimanjaro: n = 20.

ings for all measurements, with the strongest contributions from CBL, PPL, PBPL and LIB, indicating that this axis primarily represented overall skull size. PC2 explained 12.3% of the variation and was dominated by PWC (loading = –0.772), with additional contributions from LTL (0.409) and LCH (–0.379), indicating variation in cranial proportions. PC3 explained a further 6.6% of the variation and was primarily associated with MCW (–0.599), MTL (0.583) and GMH (–0.447).

The type specimen of the Zanzibar tree hyrax *Dendrohyrax validus neumanni*, ZMB_Mam_21098 Type: *Dendrohyrax neumanni* (Matschie, 1893), is from Tumbatu, Zanzibar. This specimen is deposited in the Museum für

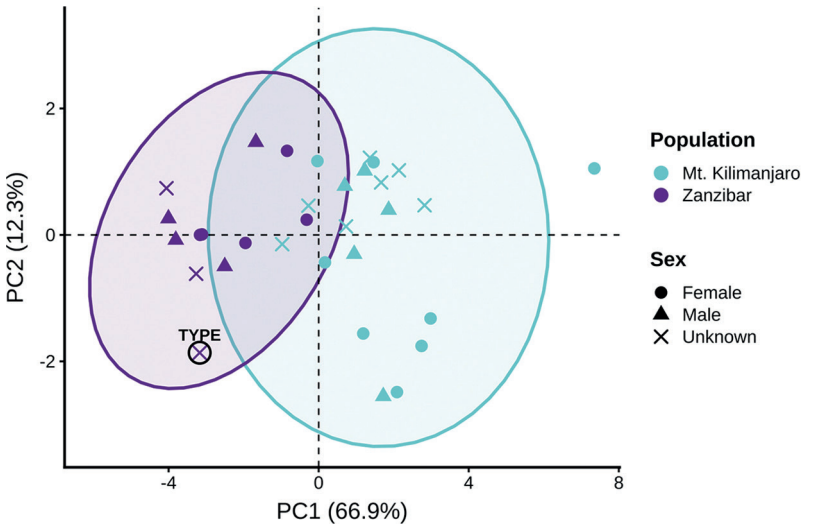

Fig. 5. Principal component analysis of 10 cranial measurements from Mt. Kilimanjaro and Zanzibar tree hyraxes. PC1, primarily representing overall skull size, explained 66.9% of total variation, while PC2, representing variation in cranial proportions, explained 12.3%. Points represent individual specimens and shaded areas represent 95% confidence regions. The type specimen of the Zanzibar tree hyrax is indicated. Zanzibar: n = 12, Mt. Kilimanjaro: n = 20.

Naturkunde, Berlin, Germany, and was included in the analysis. The lectotype specimen of *D. validus validus* True, 1890 is deposited in the National Museum of Natural History (Smithsonian Institution), Washington, D.C., USA (NMNH USNM:MAMM:18986).

Vocalisations

The loud calls in Zanzibar and on Mt. Kilimanjaro were clearly different (Fig. 6). In both populations, calling typically consisted of counter calling bouts between several individuals, followed by long silences. The Zanzibar tree hyrax used patterned sequence calls, in which a call, lasting more than two seconds, always followed the same pattern. On Mt. Kilimanjaro, the animals used single calls, i.e. short individual calls. These were combined into sequences. In these sequences, the silence between single calls was longer than the calls themselves; this distinguished these calls from songs.

We named the distinct patterned sequence loud call of the Zanzibar tree hyrax the *chackle*. It was a broadband vocalisation combining rhythmic, laughter-like elements and *hacs* (Fig. 6A and B). It had a wide frequency range (e.g., 0.1–20 kHz); however, the calls of some individuals, possibly smaller females, did not exceed 10 kHz even when recorded at close range. The *chackle* typically began with loud, short, vertical *hac*, with a frequency range of 0–22 kHz, followed by two frequency-modulated descending *haa* notes from 12 to 8 kHz. These gave the impression of strange laughter and are clearly differentiated in the waveform of the call (Fig. 6A and B). *Haa* was followed by several notes, comprising 6–9 distinct pulses of *hacs* with a frequency range of 1–20 kHz. Calling animals typically emitted sequences of 5–20 calls. The mean duration of the loud call was 3.32 s, and the maximum frequency was 4.4 kHz (n = 160). The peak frequency of the call was 1.5 kHz. Typically, several individuals vocalised in turns during a calling bout that lasted about a minute.

The tree hyraxes on Mt. Kilimanjaro used short, variable, frequency-modulated calls. The mean duration of loud single calls was 0.8 s, with a maximum frequency of 6.9 kHz (n = 160). One of the call types used has been previously named the *strangled thwack* (Roberts 2001, Rosti *et al.* 2020). The animals also used *hacs* and *wheezes* on Mt. Kilimanjaro (Fig. 6C).

The number of calls emitted at one site by tree hyraxes on Mt. Kilimanjaro surpassed 5500 per night, whereas the highest number of calls recorded in Zanzibar was only 120 calls per night. This most likely reflects both call type (*chackle* is long and thus energetically demanding), and number of calling individuals.

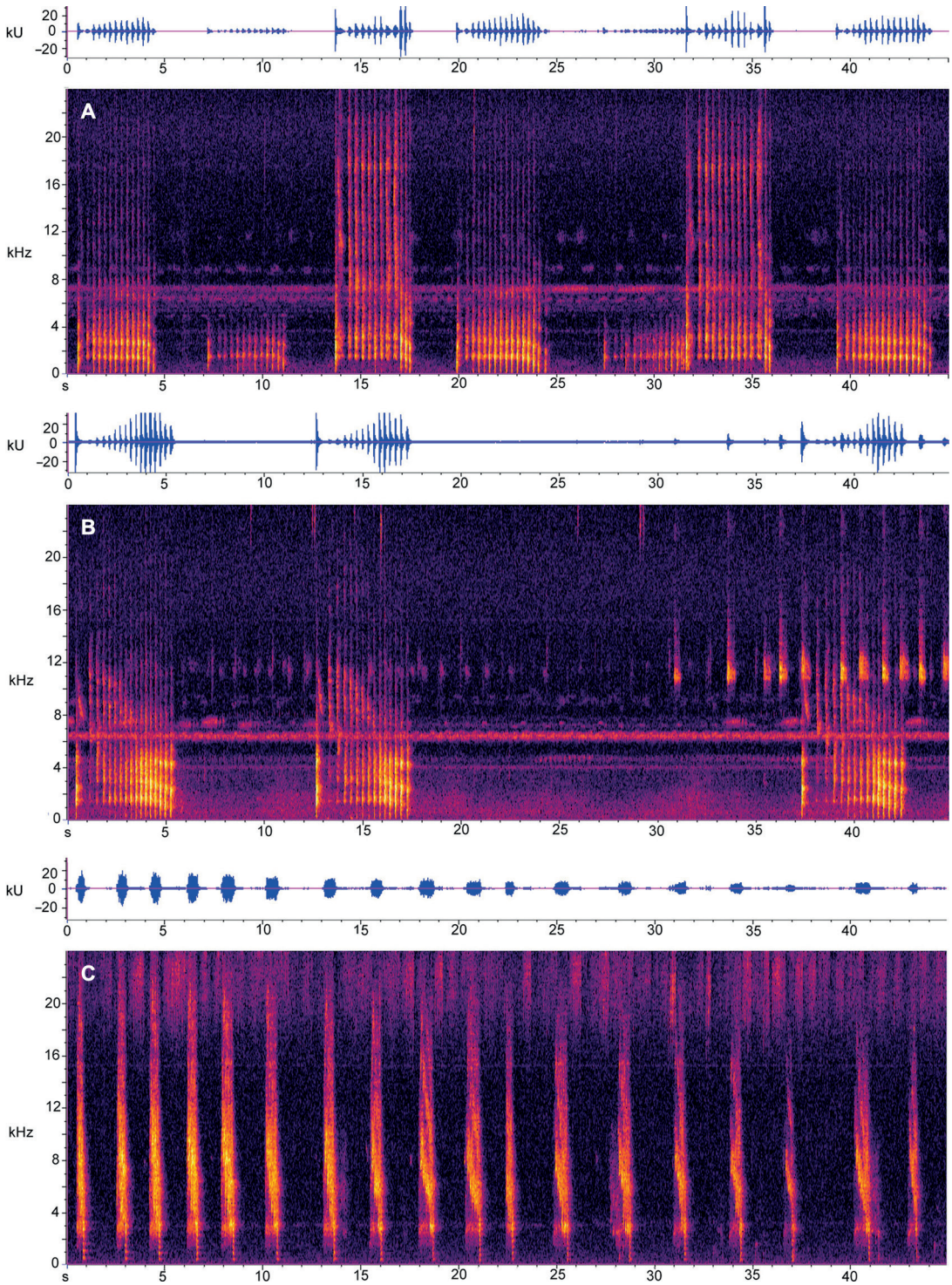

Fig. 6. Spectrograms of tree hyrax calls recorded from Zanzibar and Mt. Kilimanjaro. The oscillogram in the upper panel shows the temporal pattern, including changes in the sound amplitude of the acoustic signal. — **A**: Zanzibar tree hyrax *chackle* (patterned call) from Unguja Island, Zanzibar. — **B**: Zanzibar tree hyrax *chackle* from Pemba Island, Zanzibar. — **C**: Eastern tree hyrax sequence of single *strangled thwack* calls from Mt. Kilimanjaro. Sound samples are available on Zenodo: https://zenodo.org/records/19553712.

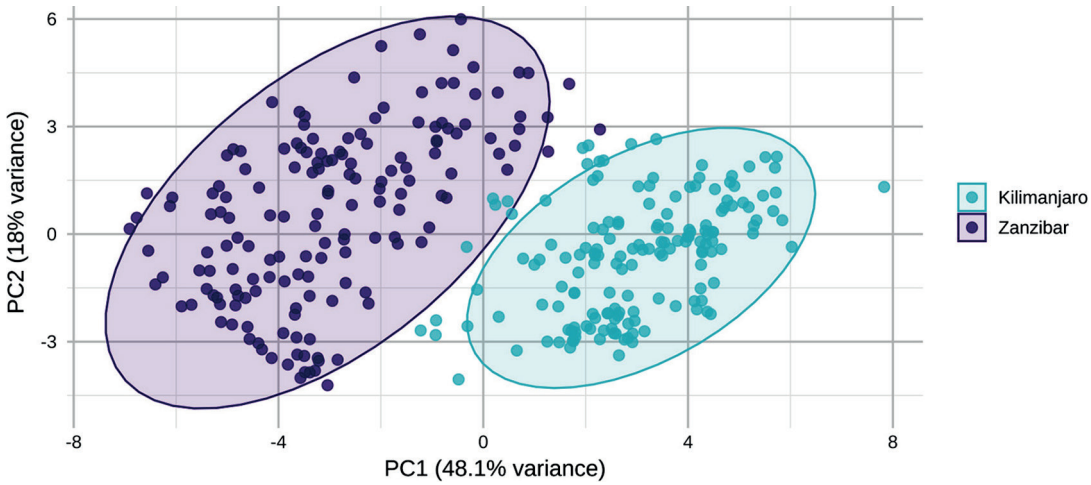

Fig. 7. Principal component analysis of 25 measurements of loud calls used by Zanzibar tree hyraxes and eastern tree hyraxes on Mt. Kilimanjaro. Together, PC1 and PC2 accounted for 66.1% of the total variance. Ellipses represent 95% confidence intervals around group centroids.

Variation in acoustic call structure was examined using PCA (Fig. 7, Table 5). The first principal component (PC1), accounting for 48.1% of the total variance, was primarily associated with mean dominant frequency, median frequency, frequency quartiles and call duration parameters. The second component (PC2) explained 18% of the variance and was driven mainly by measures of spectral dispersion and frequency range, including dominant frequency range and maximum dominant frequency. The first three principal components (PC1–PC3) accounted for 77.3% of the acoustic variation. These results indicate that both overall frequency structure and variability contributed to the differences in calls observed between tree hyraxes from Zanzibar and Mt. Kilimanjaro. Representative songs recorded from Zanzibar and Mt. Kilimanjaro are shown in Fig. 8.

Habitat, behaviour and threats

On Mt. Kilimanjaro, tree hyraxes typically lived in trees and used tree cavities for shelter. Individual animals typically had their own favourite sun-basking sites, where they were often found during the day. As observed in previous studies, tree hyraxes also lived on boulders on Mt. Kilimanjaro (Grimshaw *et al.* 1995, Kingdon 1997).

In Zanzibar, tree hyraxes were only found at locations with coral caves. The animals spent the

Table 5. Percentage contributions of the acoustic variables to the first three principal components (PC1–PC3) of the principal component analysis (PCA), with eigenvalues and proportions of variance explained. Abbreviations are explained in Table 2.

	PC1	PC2	PC3
duration	6.106	2.434	3.987
meanfreq	6.437	4.014	0.034
sd	1.125	16.799	1.989
freqmedian	6.956	1.082	0.274
freqQ25	6.753	0.008	0.054
freqQ75	6.061	5.318	0.002
freqIQR	3.204	10.830	0.010
timemedian	6.280	1.943	3.466
timeQ25	5.901	1.011	3.196
timeQ75	6.156	2.514	3.798
timeIQR	5.513	3.721	3.754
skew	3.994	2.780	7.400
kurt	2.765	3.366	6.761
sp.ent	4.938	0.340	9.524
timeent	5.560	2.712	5.212
entropy	1.605	2.164	20.795
sfm	5.269	0.078	4.691
meandom	7.163	0.001	0.027
mindom	1.364	1.707	0.465
maxdom	0.441	17.126	2.272
dfrange	0.324	17.677	2.393
modindx	0.017	0.248	19.314
startdom	1.996	0.653	0.002
enddom	0.562	0.246	0.074
meanpeakf	3.450	1.211	0.505
Eigenvalue	12.03	4.51	2.80
Variance explained (%)	48.1	18.0	11.2
Cumulative variance (%)	48.1	66.1	77.3

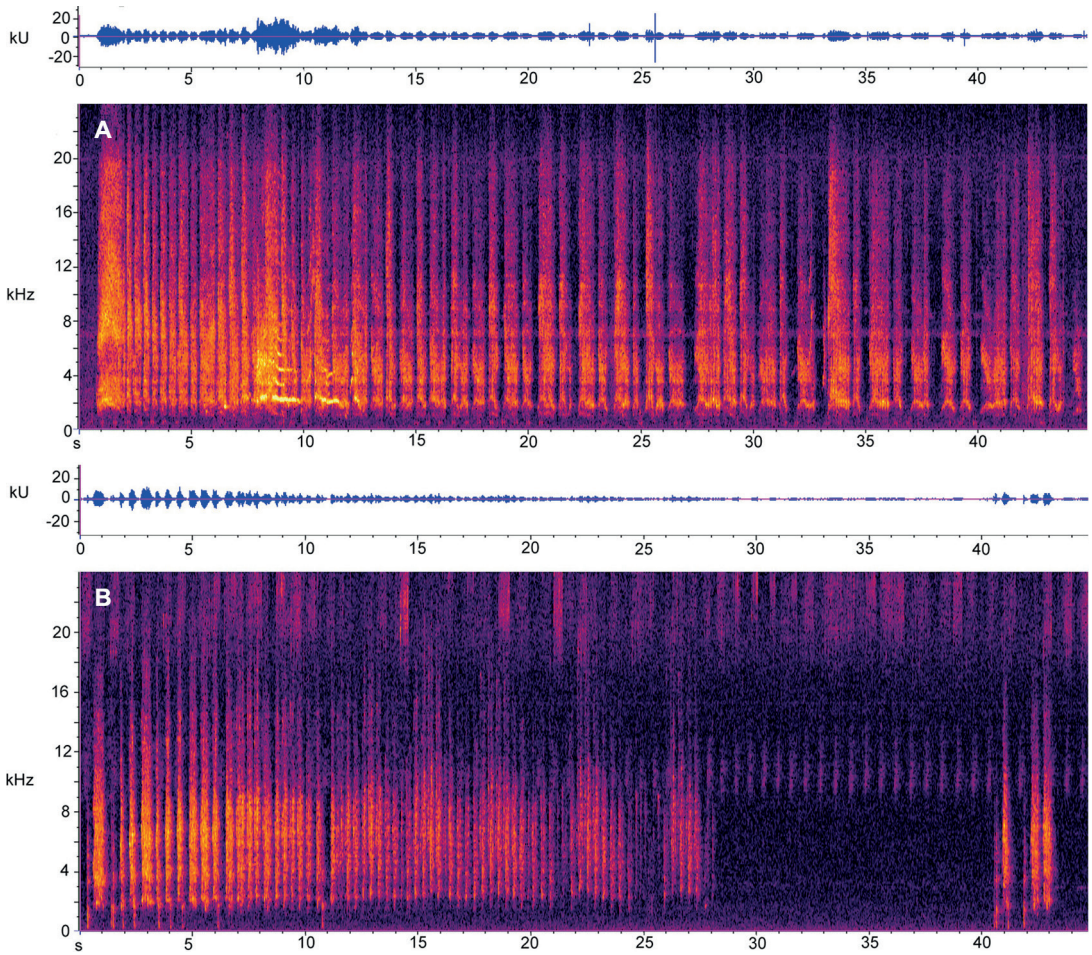

Fig. 8. Spectrograms of tree hyrax songs recorded from Zanzibar and Mt. Kilimanjaro. The oscillogram in the upper panel shows the temporal pattern, including changes in the sound amplitude of the acoustic signal. — **A**: Zanzibar tree hyrax song recorded from Unguja Island, Zanzibar. — **B**: Eastern tree hyrax song recorded from Mt. Kilimanjaro. Sound samples are available on Zenodo: https://zenodo.org/records/19553712.

day underground and fed in indigenous trees and shrubs at night.

We found caves in three different areas in and around Jozani. Given the current absence of big trees, we estimated that the total area of habitats suitable for tree hyraxes in Unguja Island was less than one km^2. Based on the number of groups found, we estimated that the tree hyrax population on the island consists of fewer than 200 individuals. We have not yet conducted a similar survey on Pemba, but our preliminary findings suggest that suitable habitats (caves) are scarce and patchily distributed, and that the population size is very small also on Pemba. In Zanzibar, illegal hunting with snares and dogs continues and poses a threat to the remaining tree hyrax populations. We found snares at one field site, with tree hyraxes being the likely target species. Large packs of up to ten large dogs are used to hunt bushpigs in Jozani, but the dogs may also kill other species, including tree hyraxes.

Discussion

In 1893, the German zoologist Paul Matschie (1861–1926) described the tree hyrax from Zanzibar as a species new to science, naming it *Procavia neumanni*. During his career, Matschie described and named a very large number of

mammal species, most of which were later shown to be invalid and sunk into synonymy (for a discussion of Matschie's taxonomic approach, see Groves 2008). However, the results of the present study suggest that, at least in this case, Matschie was correct. Thus, rather than a subspecies of the eastern tree hyrax *Dendrohyrax validus* True, 1890, the tree hyraxes from Zanzibar should be considered a full species, *Dendrohyrax neumanni* (Matschie, 1893). As its English vernacular name, we suggest 'Zanzibar tree hyrax'.

Our comparisons of the outer appearance, cranial morphology and vocalisations show a clear divergence between tree hyraxes from Zanzibar and Mt Kilimanjaro. The extent of differentiation across these three independent datasets is consistent with the long-term isolation of the two populations dating back at least to the early Holocene (Prendergast *et al.* 2016) and suggests a deeper evolutionary separation than previously recognised.

Cranial morphology provides strong quantitative support for divergence between Zanzibar tree hyraxes and eastern tree hyraxes from Mt. Kilimanjaro. However, cranial variation can arise through acclimatisation to local ecological conditions without an evolutionary change. For example, Lalis *et al.* (2009) reported significant skull shape differences between neighbouring populations of the Natal multimammate rat (*Mastomys natalensis*) that nevertheless formed a single panmictic genetic unit, attributing the morphological divergence to environmental differences and resource use. However, the much stronger cranial differentiation observed here suggests that ecological variation alone is unlikely to account for the observed pattern. The PERMANOVA demonstrated a highly significant separation between the two populations, with population accounting for 45.3% of the multivariate variation in cranial measurements ($R^2 = 0.453$). This indicates substantial morphological differentiation, particularly given that the groups are currently treated as closely related taxa, although direct comparisons among studies are complicated by differences in morphometric methods and taxonomic scales. Sexual dimorphism was unlikely to account for the morphological divergence between populations. Only GWR differed significantly between sexes, and Zanzibar specimens had significantly larger sculls even after sex was included in the analysis.

Oates *et al.* (2022) described a new tree hyrax species, *D. interfluvialis*, from West Africa, based on comparisons of acoustic, skull morphometric and genetic data. Their skull morphometric data can be compared with our dataset.

The larger skull size of the Zanzibar archipelago population could also be consistent with predictions of the island rule (Foster 1964, Lomolino 2005), which predicts insular gigantism in small-bodied species and dwarfism in large-bodied species. However, the generality of this pattern remains debated, as Meiri *et al.* (2006) found no support for the island rule in a broad analysis of mammalian body-size variation based on skull length (CBL) measurements.

Acoustic analyses revealed that the Zanzibar tree hyrax produces a unique patterned sequence call that we refer to as the *chackle*. This call has not been recorded from any mainland population in Tanzania or Kenya. In contrast, *D. validus* on Mt. Kilimanjaro produces single calls, and a similar vocalisation is also used in coastal Kenya, the Usambara Mountains and the Pare Mountains (Rosti *et al.* 2023a, 2025, Pihlström *et al.* 2025). In the Uluguru and Udzungwa Mountains (Tanzania), *D. validus shusteri* employs a different call repertoire dominated by *hac* calls that often culminate in a rapid "*ping–pong*" finale (Roberts 2001). Among the East African populations, the *chackle* call is confined in the Zanzibar Archipelago. As it is possible that this vocalisation may simply reflect geographic variation (i.e., a regional dialect) within a single species, molecular analyses are required to assess whether it corresponds to a distinct taxonomic lineage.

Songs from the Zanzibar tree hyrax and the Mt. Kilimanjaro tree hyrax are described here for the first time. The occurrence of songs in both Zanzibar and mainland populations suggests shared ancestral acoustic behaviour. However, morphological and ecological divergence, as well as the presence of a unique call type in Zanzibar, likely reflects long-lasting isolation and possibly some unique selective pressures in this region.

Ecological observations further highlight the distinctive nature of the Zanzibar tree hyrax. Although the animals forage in trees, they seek shelter in caves; this behaviour was briefly

mentioned by Hahn (1934: 263). The absence of large, cavity-bearing trees, particularly on Unguja Island, means that coral caves are essential for shelter, thermoregulation and refuge. Consequently, the number, size and distribution of caves appear to strongly limit both the distribution and total population size of the animals.

Use of rocky refuges has been documented in several *Dendrohyrax* populations across Africa, including *D. v. validus* on Mt. Kilimanjaro (Kingdon 1997), on the Kenyan coast (Seibt *et al.* 1977, Rosti *et al.* 2023a), in the Usambara Mountains (Brauer 1916) and in the Pare mountains (Rosti *et al.* 2025), as well as in Benin tree hyraxes (*D. interfluvialis*) in West Africa (Oates *et al.* 2022). However, in Zanzibar, the reliance on caves appears obligatory rather than opportunistic, most likely because the landscape is nearly devoid of large trees.

Zanzibar hyraxes use latrines, as observed in rock-dwelling populations elsewhere (Roberts *et al.* 2013, Rosti *et al.* 2023a, Rosti *et al.* 2025, Pihlström *et al.* 2025), apparently reflecting behavioural convergence with other tree hyraxes that live in rugged or open habitats. Tree hyraxes on Mt. Kilimanjaro also use latrines to some extent; Kundaeli (1976) counted latrines when he studied tree hyraxes on Mt. Kilimanjaro. However, when in trees, tree hyraxes on Mt. Kilimanjaro and other forests defecate where they are and faeces may be scattered on the ground.

Environmental differences between Zanzibar and Mt. Kilimanjaro likely shape aspects of tree hyrax physiology and behaviour. At higher elevations on Mt. Kilimanjaro, where temperatures may be as low as 10 °C during the day and may approach freezing at night, tree hyraxes often bask in the sun on exposed tree trunks near their home cavities. In Zanzibar, where daytime temperatures can reach 36–38 °C, no tree hyraxes were encountered outside caves during the day. Dependence on caves may therefore be driven by the need to avoid overheating in the islands' year-round hot conditions. Hyraxes are thermolabile and have relatively low heat tolerance, and studies of free-living rock hyraxes have shown that animals use cooler refuges when ambient temperatures exceed their thermoneutral range (Taylor & Sale 1969, Louw et al. 1972, Brown & Downs 2006).

Historically, tree hyraxes were believed to be solitary (Kundaeli 1976). However, recent studies, including observations in Zanzibar and on Mt. Kilimanjaro, contradict this view (Rosti *et al.* 2020, 2022, 2023a, b, 2025). Acoustic exchanges, shared caves and direct observations have provided strong evidence that *Dendrohyrax* species are quite social. In Zanzibar, at Pete Cave, up to ten individuals may sometimes be seen to rest in close proximity. Local rangers and other informants consistently report that the Zanzibar tree hyrax only calls at night, in contrast to the tree hyraxes on Mt. Kilimanjaro, which call mostly at night, but also quite commonly during the day. Other mainland populations, e.g., in the Taita Hills and the Pare Mountains, as well as *D. interfluvialis* in West Africa, (Oates *et al.* 2022) also show diurnal or cathemeral behaviour, suggesting that the strict nocturnality of Zanzibar hyraxes is mainly explained by the high ambient temperatures during the day.

The conservation outlook for the Zanzibar tree hyrax is troubling. With cavity-bearing trees gone, the species presently depends entirely on caves, which only occur at a limited number of sites. Habitat destruction caused by charcoal production, slash-and-burn agriculture and disturbance within key cave areas threatens the remaining populations. Sea-level rise further endangers coastal caves, which may flood during storms or high tides. Hunting pressure compounds these threats. We found snares in occupied hyrax habitats, and dogs used for illegal hunting in the Jozani Forest pose additional risks. Given the species' dependence on rare structural refuges, any further habitat loss is likely to have severe consequences. The provision of artificial refuges might offer a valid mitigation tool. In Israel, artificial boulders have successfully supported rock hyrax populations (Kershenbaum *et al.* 2011), suggesting that comparable structures could be tested in Zanzibar to enhance habitat availability and connectivity.

Based on the results of this study, the Zanzibar tree hyrax is sufficiently distinct morphologically and acoustically to warrant recognition as a separate species of high conservation priority. Pending formal taxonomic resolution, we advocate its treatment as a distinct species in conservation planning, as the loss of this population could

result in the irreversible extinction of a unique evolutionary lineage. A comprehensive genetic assessment of the Zanzibar tree hyrax to determine its taxonomic status is in progress. This should be followed by an updated IUCN assessment reflecting its restricted distribution and the multiple threats it faces. Immediate conservation actions are needed, as taxonomic assessment may take time. These include strict protection of remaining cave habitats, restoration of adjacent vegetation and the possible use of artificial cave or boulder refuges to facilitate dispersal and gene flow among isolated groups. Community-based conservation and low-impact ecotourism could further support protection efforts and raise awareness of this highly threatened population. Together, these measures are essential to reduce the risk of extinction of the Zanzibar tree hyrax.

Although species are the most commonly used unit of biodiversity, speciation is a complex and nearly always gradual process, and recognised species may contain genetically structured and historically isolated populations that represent important units for conservation (Coates *et al.* 2018). Substantial knowledge gaps remain even among mammals, with approximately one third of species receiving little or no research attention (Tam *et al.* 2022). These gaps are particularly important for cryptic and taxonomically unresolved taxa, for which substantial evolutionary divergence may remain unrecognised (Bickford *et al.* 2007, Hending 2025). Recent evidence indicates that cryptic diversity is widespread among vertebrates and that taxa that are apparently plentiful and widely distributed may contain distinct lineages facing a much greater risk of extinction (Zhang & Wiens 2026). Consequently, reliance on formally recognised taxonomic units in extinction-risk assessments can create a gap between evolutionary diversity and conservation attention, with distinct lineages potentially declining or disappearing before their taxonomic status is resolved.

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References

Abdalla A.H., Kai K.H., Khamis S.A., Kondowe A.L., Osima S.E., King'uza P.H. & Hamad A.O. 2023: The influence of climate change and variability on spatio-temporal rainfall and temperature distribution in Zanzibar. — *Atmospheric and Climate Sciences* 13: 282–313, https://doi.org/10.4236/acs.2023.132016.

Alders W. 2023: Open-access archaeological predictive modeling using zonal statistics: A case study from Zanzibar, Tanzania. — *Journal of Computer Applications in Archaeology* 6: 117–142, https://doi.org/10.5334/jcaa.107.

Appelhans T., Mwangomo E., Otte I., Detsch F., Nauss T. & Hemp A. 2016: Eco-meteorological characteristics of the southern slopes of Kilimanjaro, Tanzania. — *International Journal of Climatology* 36: 3245–3258, https://doi.org/10.1002/joc.4552.

Araya-Salas M. & Smith-Vidaurre G. 2017: warbleR: An R package to streamline analysis of animal acoustic signals. — *Methods in Ecology and Evolution* 8: 184–191, https://doi.org/10.1111/2041-210X.12624.

Bickford D., Lohman D.J., Sodhi N.S., Ng P.K.L., Meier R., Winker K., Ingram K.K. & Das I. 2007: Cryptic species as a window on diversity and conservation. — *Trends in Ecology & Evolution* 22: 148–155, https://doi.org/10.1016/j.tree.2006.11.004.

Brauer A. 1916: Die Verbreitung der Hyracoiden. — *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften* 17–19: 436–445.

Brown K.J. & Downs C.T. 2006: Seasonal patterns in body temperature of free-living rock hyrax (*Procavia capensis*). — *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 143: 42–49, https://doi.org/10.1016/j.cbpa.2005.10.020.

Burgess N.D., Clarke G.P. & Rodgers W.A. 1998: Coastal

forests of eastern Africa: Status, endemism patterns and their potential causes. — *Biological Journal of the Linnean Society* 64: 337–367, https://doi.org/10.1111/j.1095-8312.1998.tb00337.x.

Burgess N.D. & Clarke G.P. (eds.) 2000: *Coastal forests of eastern Africa*. — IUCN, Gland and Cambridge.

Burgess N.D., Butynski T.M., Cordeiro N.J., Doggart N.H., Fjeldså J., Howell K.M., Kilahama F.B., Loader S.P., Lovett J.C., Mbilinyi B., Menegon M., Moyer D.C., Nashanda E., Perkin A., Rovero F., Stanley W.T. & Stuart S.N. 2007: The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. — *Biological Conservation* 134: 209–231, https://doi.org/10.1016/j.biocon.2006.08.015.

Caplow S., Putri A.A.D. & Kweka D.L. 2014: Piloting REDD in Zanzibar through community forest management, Tanzania. — In: Sills E.O., Atmadja S.S., de Sassi C., Duchelle A.E., Kweka D.L., Resosudarmo I.A.P. & Sunderlin W.D. (eds.), *REDD+ on the ground: A case book of subnational initiatives across the globe*: 234–244. Center for International Forestry Research (CIFOR), Bogor.

Coates D.J., Byrne M. & Moritz C. 2018: Genetic diversity and conservation units: Dealing with the species-population continuum in the age of genomics. — *Frontiers in Ecology and Evolution* 6: 165, https://doi.org/10.3389/fevo.2018.00165.

Ebinger C., Djomani Y.P., Mbede E., Foster A. & Dawson J.B. 1997: Rifting Archaean lithosphere: The Eyasi-Manyara-Natron rifts, East Africa. — *Journal of the Geological Society* 154: 947–960, https://doi.org/10.1144/gsjgs.154.6.0947.

Foster J.B. 1964: Evolution of mammals on islands. — *Nature* 202: 234–235.

Garnett S.T., Johnston C.E., Bowles P., Christidis L., Conix S., Duckworth J.W., Lien A., Zachos F.E. & Witteveen J. 2026: Evaluating the use of taxonomy in the IUCN Red List. — *Conservation Biology* 40: e70306, https://doi.org/10.1111/cobi.70306.

Grimshaw J.M., Cordeiro N.J. & Foley C.A.H. 1995: The mammals of Kilimanjaro. — *Journal of East African Natural History* 84: 105–139, https://doi.org/10.2982/0012-8317(1995)84[105:tmok]2.0.co;2.

Groves C.P. 2008: *Extended family: Long lost cousins. A personal look at the history of primatology*. — Conservation International, Arlington.

Hahn H. 1934: Die Familie der Procaviidae. — *Zeitschrift für Säugetierkunde* 9: 207–358.

Hara K. 2025: Root-like formation of upper incisors in captive rock hyrax (*Procavia capensis*). — *Mammal Study* 50: 405–412, https://doi.org/10.3106/ms2024-0025.

Hemp A. 2001: Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro. Part II: Habitat selection. — *Plant Biology* 3: 493–523.

Hemp A. 2005: Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. — *Global Change Biology* 11: 1013–1023, https://doi.org/10.1111/j.1365-2486.2005.00968.x.

Hemp A. 2006a: Vegetation of Kilimanjaro: Hidden endemics and missing bamboo. — *African Journal of Ecology* 44: 305–328, https://doi.org/10.1111/j.1365-2028.2006.00679.x.

Hemp A. 2006b: Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. — *Plant Ecology* 184: 27–42, https://doi.org/10.1007/s11258-005-9049-4.

Hending D. 2025: Cryptic species conservation: A review. — *Biological Reviews* 100: 258–274, https://doi.org/10.1111/brv.13139.

Hill A.P., Prince P., Piña Covarrubias E., Doncaster C.P., Snaddon J.L. & Rogers A. 2018: AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. — *Methods in Ecology and Evolution* 9: 1199–1211, https://doi.org/10.1111/2041-210X.12955.

Hoeck H., Rovero F., Cordeiro N.J., Butynski T.M., Perkin A.W. & Jones T. 2015: *Dendrohyrax validus*. — *The IUCN Red List of Threatened Species* 2015: e.T136599A21288090, https://doi.org/10.2305/iucn.uk.2015-2.rlts.t136599a21288090.en.

IUCN Standards and Petitions Committee 2024: *Guidelines for using the IUCN Red List Categories and Criteria*. Version 16. — Standards and Petitions Committee of the IUCN Species Survival Commission, https://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Kershenbaum A., Kershenbaum A. & Blaustein L. 2011: Rock hyrax (*Procavia capensis*) den site selection: Preference for artificial sites. — *Wildlife Research* 38: 244–248, https://doi.org/10.1071/WR10228.

Kingdon J. 1990: *Island Africa*. — Collins, London.

Kingdon J. 1997: *The Kingdon field guide to African mammals*. — Academic Press, San Diego.

Kukkonen M. & Käyhkö N. 2014: Spatio-temporal analysis of forest changes in contrasting land use regimes of Zanzibar, Tanzania. — *Applied Geography* 55: 193–202, https://doi.org/10.1016/j.apgeog.2014.09.013.

Kundaeli J.N. 1976: Distribution of tree hyrax (*Dendrohyrax validus validus* True) on Mt Kilimanjaro, Tanzania. — *African Journal of Ecology* 14: 253–264, https://doi.org/10.1111/j.1365-2028.1976.tb00241.x.

Lalis A., Baylac M., Cosson J.F., Makundi R.H., Machang'u R.S. & Denys C. 2009: Cranial morphometric and fine scale genetic variability of two adjacent *Mastomys natalensis* (Rodentia: Muridae) populations. — *Acta Theriologica* 54: 171–181.

Lawes M.J., Mealin P.E. & Piper S.E. 2000: Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented Afromontane forest in South Africa. — *Conservation Biology* 14: 1088–1098, https://doi.org/10.1046/j.1523-1739.2000.99120.x.

Lê S., Josse J. & Husson F. 2008: FactoMineR: An R package for multivariate analysis. — *Journal of Statistical Software* 25: 1–18, https://doi.org/10.18637/jss.v025.i01.

Leskinen J., Pohjonen V.M. & Ali M.S. 1997: *Woody biomass inventory of Zanzibar islands*. — Forest and Park Service, Vantaa.

Liu J., Slik F., Zheng S. & Lindenmayer D.B. 2022: Undescribed species have higher extinction risk than known species. — *Conservation Letters* 15: e12876, https://doi.org/10.1111/conl.12876.

Lomolino M.V. 2005: Body size evolution in insular vertebrates: Generality of the island rule. — *Journal of Biogeography* 32: 1683–1699, https://doi.org/10.1111/j.1365-2699.2005.01314.x.

Louw E., Louw G.N. & Retief C.P. 1972: Thermolability, heat tolerance and renal function in the dassie or hyrax, *Procavia capensis*. — *Zoologica Africana* 7: 451–469, https://doi.org/10.1080/00445096.1972.11447455.

Lovett J.C. 1998: Eastern Tropical African Centre of Endemism: A candidate for World Heritage Status. — *Journal of East African Natural History* 87: 359–366, https://doi.org/10.2982/0012-8317(1998)87[359:etacoe]2.0.co;2.

Mace G.M. 2004: The role of taxonomy in species conservation. — *Philosophical Transactions of the Royal Society B: Biological Sciences* 359: 711–719, https://doi.org/10.1098/rstb.2003.1454.

Mace G.M., Collar N.J., Gaston K.J., Hilton-Taylor C., Akçakaya H.R., Leader-Williams N., Milner-Gulland E.J. & Stuart S.N. 2008: Quantification of extinction risk: IUCN's system for classifying threatened species. — *Conservation Biology* 22: 1424–1442, https://doi.org/10.1111/j.1523-1739.2008.01044.x.

Matschie P. 1893: Über anscheinend neue afrikanische Säugethiere. — S*itzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1893: 107–114.

McDonald M.M., Cunneyworth P.M.K., Anderson A.G. & Wroblewski E. 2022: Mitochondrial genetic diversity and divergence dating of Angolan colobus monkeys (*Colobus angolensis*) in the eastern forests of Kenya and Tanzania: Implications for subspeciation and reconstructing historical biogeography. — *American Journal of Primatology* 84: e23384, https://doi.org/10.1002/ajp.23384.

Meiri S., Dayan T. & Simberloff D. 2006: The generality of the island rule reexamined. — *Journal of Biogeography* 33: 1571–1577, https://doi.org/10.1111/j.1365-2699.2006.01523.x.

Moyano S.R., Cassini G.H. & Giannini N.P. 2019: Skull ontogeny of the hyraxes *Procavia capensis* and *Dendrohyrax arboreus* (Procaviidae: Hyracoidea). — *Journal of Mammalian Evolution* 26: 317–331, https://doi.org/10.1007/s10914-017-9424-7.

National Oceanic and Atmospheric Administration 2024: *Is sea level rising*? — https://oceanservice.noaa.gov/facts/sealevel.html.

Nonnotte P., Guillou H., Le Gall B., Benoit M., Cotten J. & Scaillet S. 2008: New K-Ar age determinations of Kilimanjaro volcano in the North Tanzanian diverging rift, East Africa. — *Journal of Volcanology and Geothermal Research* 173: 99–112, https://doi.org/10.1016/j.jvolgeores.2007.12.042.

Oates J.F., Woodman N., Gaubert P., Sargis E.J., Wiafe E.D., Lecompte E., Dowsett-Lemaire F., Dowsett R.J., Gonedelé Bi S., Ikemeh R.A., Djagoun C.A.M.S., Tomsett L. & Bearder S.K. 2022: A new species of tree hyrax (Procaviidae: *Dendrohyrax*) from West Africa and the significance of the Niger–Volta interfluvium in mammalian biogeography. — *Zoological Journal of the Linnean Society* 194: 527–552, https://doi.org/10.1093/zoolinnean/zlab029.

Oksanen J., Simpson G.L., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Solymos P., Stevens M.H.H., Szoecs E., Wagner H., Bedward M., Bolker B., Borcard D., Carvalho G., De Caceres M., Durand S., Evangelista H.B.A., Hannigan G., Hill M.O., Lahti L., Martino C., Ouellette M.-H., Ribeiro Cunha E., Smith T., Stier A., Ter Braak C.J.F. & Weedon J. 2025: *vegan: Community Ecology Package*, version 2.7-2. — https://doi.org/10.32614/CRAN.package.vegan.

Parmentier E., Scalbert R., Raick X., Gache C., Frédérich B., Bertucci F. & Lecchini D. 2022: First use of acoustic calls to distinguish cryptic members of a fish species complex. — *Zoological Journal of the Linnean Society* 195: 964–975, https://doi.org/10.1093/zoolinnean/zlab056.

Pihlström H., Hemp C., Hemp A., Knapp L., Witting O., Bearder S.K., Kilawe C.J. & Rosti H. 2025: Notes on tree hyraxes, dwarf galagos, and other mammals in the West and East Usambara Mountains, Tanzania. — *Journal of East African Natural History* 114: 66–79.

Pozzi L., Disotell T.R., Bearder S.K., Karlsson J., Perkin A. & Gamba M. 2019: Species boundaries within morphologically cryptic galagos: Evidence from acoustic and genetic data. — *Folia Primatologica* 90: 279–299, https://doi.org/10.1159/000496972.

Prendergast M.E., Rouby H., Punnwong P., Marchant R., Crowther A., Kourampas N., Shipton C., Walsh M., Lambeck K. & Boivin N.L. 2016: Continental island formation and the archaeology of defaunation on Zanzibar, eastern Africa. — *PLoS ONE* 11: e0149565, https://doi.org/10.1371/journal.pone.0149565.

R Core Team 2025: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, https://www.R-project.org/.

Roberts D. 2001: *Geographic variation in the loud calls of tree hyrax* Dendrohyrax validus *(True 1890) in the Eastern Arc Mountains, East Africa: Taxonomic and conservation implications*. — MSc thesis, University of Reading, Reading.

Roberts D., Topp-Jørgensen E. & Moyer D. 2013: *Dendrohyrax validus* Eastern tree hyrax. — In: Kingdon J., Happold D., Hoffmann M., Butynski T., Happold M. & Kalina J. (eds.), *Mammals of Africa. Volume I: Introductory chapters and Afrotheria*: 158–161. Bloomsbury Publishing, London.

Rodgers W.A., Hall J., Mwasumbi L., Swai I. & Vollesen K. 1986: *The conservation status and values of Ngezi Reserve, Pemba Island, Tanzania*. — Forest Conservation Group, University of Dar es Salaam, Dar es Salaam.

Rodrigues A.S.L., Pilgrim J.D., Lamoreux J.F., Hoffmann M. & Brooks T.M. 2006: The value of the IUCN Red List for conservation. — *Trends in Ecology & Evolution* 21: 71–76, https://doi.org/10.1016/j.tree.2005.10.010.

Rosti H. 2023: Behavioral ecology and conservation biology of nocturnal mammals of the Taita Hills, Kenya. — *Dissertationes Helsingiensis* 102/2023, University of Helsinki, Helsinki.

Rosti H., Pihlström H., Bearder S., Pellikka P. & Rikkinen J. 2020: Vocalization analyses of nocturnal arboreal mammals of the Taita Hills, Kenya. — *Diversity* 12: 473,

https://doi.org/10.3390/d12120473.

Rosti H., Heiskanen J., Loehr J., Pihlström H., Bearder S., Mwangala L., Maghenda M., Pellikka P. & Rikkinen J. 2022: Habitat preferences, estimated abundance and behavior of tree hyrax (*Dendrohyrax* sp.) in fragmented montane forests of Taita Hills, Kenya. — *Scientific Reports* 12: 6331, https://doi.org/10.1038/s41598-022-10235-7.

Rosti H., Pihlström H., Rottcher N., Bearder S., Mwangala L., Maghenda M. & Rikkinen J. 2023a: Species identity and behavior of cave-dwelling tree hyraxes of the Kenyan coast. — *Ecology and Evolution* 13: e9693, https://doi.org/10.1002/ece3.9693.

Rosti H., Pihlström H., Bearder S., Maeda E., Loehr J., Räsänen M., Mwangala L., Maghenda M., Pellikka P. & Rikkinen J. 2023b: Seasonal and diel variations in the acoustic communication of tree hyraxes in Taita Hills, Kenya. — *Mammalian Biology* 104: 1–14, https://doi.org/10.1007/s42991-023-00370-7.

Rosti H., Hemp A., Pihlström H., Kilawe C.J., Witting O., Knapp L. & Hemp C. 2025: Adapted to deforestation? Eastern tree hyraxes (*Dendrohyrax validus*) in crevices in Pare Mountains, Tanzania. — *African Journal of Ecology* 63: e70134, https://doi.org/10.1111/aje.70134.

Said M.S., Msanya B.M., Semoka J.M. & Maliondo S.M.S. 2017: Tidal trends and magnitude of Chwaka and Uzi Bays as a proxy of seawater intrusion in Jozani Groundwater Forest, Zanzibar, Tanzania. — *American Journal of Agriculture and Forestry* 4: 168–177.

Sebastián-González E. & Pérez-Granados C. 2025: Geographic variation in acoustic signals in wildlife: A systematic review. — *Journal of Biogeography* 52: e15116, https://doi.org/10.1111/jbi.15116.

Seibt U., Hoeck H. & Wickler W. 1977: *Dendrohyrax validus* True, 1890 in Kenia. — *Zeitschrift für Säugetierkunde* 42: 115–118.

Snowdon C.T. 1989: Vocal communication in New World monkeys. — *Journal of Human Evolution* 18: 611–633, https://doi.org/10.1016/0047-2484(89)90097-3.

Swynnerton G.H. & Hayman R.W. 1950: A check list of the land mammals of the Tanganyika Territory and the Zanzibar Protectorate. — *Journal of the East Africa Natural History Society* 20: 274–392.

Tam J., Lagisz M., Cornwell W. & Nakagawa S. 2022: Quantifying research interests in 7,521 mammalian species with h-index: A case study. — *GigaScience* 11: giac074, https://doi.org/10.1093/gigascience/giac074.

Tanzania National Bureau of Statistics & Office of the Chief Government Statistician Zanzibar 2022: *The 2022 Population and Housing Census: Administrative units population distribution report*. — National Bureau of Statistics and Office of the Chief Government Statistician, Tanzania.

Taylor C.R. & Sale J.B. 1969: Temperature regulation in the hyrax. — *Comparative Biochemistry and Physiology* 31: 903–907, https://doi.org/10.1016/0010-406x(69)91799-x.

True F.W. 1890: Description of two new species of mammals from Mt. Kilima-Njaro, East Africa. — *Proceedings of the United States National Museum* 13: 227–229, https://doi.org/10.5479/si.00963801.814.227.

Vogel Ely C., Bordignon S.A.D.L., Trevisan R. & Boldrini I.I. 2017: Implications of poor taxonomy in conservation. — *Journal for Nature Conservation* 36: 10–13, https://doi.org/10.1016/j.jnc.2017.01.003.

Wilkins M.R., Seddon N. & Safran R.J. 2013: Evolutionary divergence in acoustic signals: Causes and consequences. — *Trends in Ecology & Evolution* 28: 156–166, https://doi.org/10.1016/j.tree.2012.10.002.

Zhang Y. & Wiens J.J. 2026: Cryptic species are widespread across vertebrates. — *Proceedings of the Royal Society B: Biological Sciences* 293: 20252377, https://doi.org/10.1098/rspb.2025.2377.