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Species richness and ecology of tree squirrels in low altitude forests from Yoko Forest Reserve, Democratic Republic of the Congo

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Because of their arboreal lifestyle, the diversity and life history of squirrels in low-altitude Afrotropical forests are currently under-researched. Following a 72-day inventory using traditional traps, we provide insights into the diversity and population dynamics of tree squirrels of the Yoko Forest Reserve, Democratic Republic of the Congo. Out of seven squirrel species recorded, *Funisciurus anerythrus* was the most abundant and ubiquitous species in the habitats surveyed, followed by two sympatric taxa potentially belonging to a species complex of *Funisciurus* cf. *bayonii*; one previously unidentified *Funisciurus* sp., as well as *Protoxerus stangeri*, *Heliosciurus rufobrachium* and *Paraxerus* cf. *boehmi*. Statistics on species richness based on incidence data estimated eight squirrel species, indicating that our inventory was likely nearly complete. We show that 9 days are sufficient to sample >87% of species, confirming that 12–15 days are sufficient to sample the representative species richness of rodents colonising a given habitat in Afrotropical forests. Diversity appeared higher in secondary forests and fallow lands than in primary forests. The sex ratio for *Funisciurus anerythrus* favoured males. All species appeared to reproduce throughout the year, but for most, reproduction was less intensive during the sub-dry season (December, January, February, June, July and August) compared to the rainy season (March, April, May, September, October and November).

Keywords: bush squirrel, Congo Basin, diversity, ecology, giant squirrel, life history, rope squirrel, sun squirrel

Supplementary material: supplementary information is available online at https://doi.org/10.1080/15627020.2026.2725966

Introduction

The Congo Basin contains the second largest expanse of tropical rainforest in the world and comprises several distinct ecoregions that support exceptional levels of biodiversity (Van de Perre et al. 2019). Despite its global importance, much of the fauna inhabiting these forests remains poorly documented, particularly small mammals, for which the species diversity, distribution and ecology are still insufficiently understood (Dinerstein et al. 2017).

Among African small mammals, tree squirrels (Sciuridae) constitute an ecologically important group because they contribute to seed dispersal, seed predation and forest regeneration, while also serving as prey for numerous predators (Emmons 1980; Steiner and Huettmann 2023). Nevertheless, their arboreal habits make them difficult to observe and capture, resulting in relatively few ecological studies across Central African forests. Consequently, fundamental aspects of their diversity, habitat use, population dynamics and reproductive ecology remain largely unknown, particularly in the Congo Basin (Katuala 2009; Baelo et al. 2018, 2025).

Interest in African tree squirrels has recently increased because several species, particularly rope squirrels (*Funisciurus* spp.) and sun squirrels (*Heliosciurus* spp.), have been implicated as potential reservoirs or hosts of zoonotic pathogens, including the mpox virus (Khodakevich et al. 1987; Curaudeau et al. 2023; Kinganda et al. 2025; Leendertz et al. 2025). Understanding their ecology, habitat preferences and life-history traits is therefore important, not only for biodiversity conservation, but also for improving our understanding of wildlife-associated disease transmission at the human–wildlife interface.

The Yoko Forest Reserve, a 6 975 ha protected lowland rainforest located approximately 32 km east of Kisangani in the Democratic Republic of the Congo, represents one of the few remaining relatively well-preserved forests in the central Congo Basin. However, ecological information on its squirrel community remains scarce.

Here, we investigated the species richness and ecology of tree squirrels inhabiting the Yoko Forest Reserve and adjacent fallow lands. Using data collected during eight

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trapping campaigns conducted between 2020 and 2022 across the rainy and sub-dry seasons, we assess species richness, abundance, habitat preferences and reproductive activity of rope squirrels (*Funisciurus*), sun squirrels (*Heliosciurus*), bush squirrels (*Paraxerus*) and giant squirrels (*Protoxerus*). Our study provides one of the first comprehensive ecological assessments of tree squirrels from lowland forests of the central Congo Basin and contributes baseline information for future conservation, ecological and epidemiological research.

Materials and methods

Study area

Yoko Forest Reserve (Figure 1) (0.29638° N, 25.28722° E, ±428 m), located in a low-altitude evergreen rainforest region of the Democratic Republic of the Congo, has vegetation mainly composed of mixed forests containing the main habitat type characteristic of tropical forests. Squirrels were collected in mature habitats (primary and secondary forests) of all types and degraded forest (fallow land) where the local population practices agriculture, not far from human settlements (Shutsha et al. 2017). Yoko has an equatorial climate. Daily temperatures vary between 20 and 30 °C, with an annual average close to 25 °C. Annual rainfall varies between 1 500 and 2 000 mm, with an average of 1 750 mm (Boyemba 2011). Temperatures remain high almost all year round and there is no dry season. The climate is classified as Af (tropical rainforest climate): a humid tropical climate with average monthly temperatures >18 °C, no winter season, and heavy rainfall during almost every month of the year (Peel et al. 2007).

Trapping

Trapping was carried out during four sampling campaigns in the rainy season (October 2020, April 2021, October 2021 and April 2022) and four campaigns during the sub-dry season (July 2020, January 2021, July 2021 and January 2022) (Supplementary Table S1). For each campaign, 75 traditional traps (TTs; Supplementary Figure S1) were installed, at the rate of 25 TTs per habitat. These traps were baited with ripe palm nuts (*Elaeis guineensis*) and placed at heights ranging from 0.32 to 7.37 m (average height 1.58 ± 1.29 m).

In each habitat type, the TTs were installed and left in place for 9 days, resulting in a total of 72 sampling days (36 per season). Surveys were carried out once daily, between 09:00 and 13:00, and traps were repaired and rebaited as necessary. At each capture point, ecological data (e.g. habitat type and trap height) for the capture site were also recorded.

This study is one of several studies seeking to understand the biology and reservoir ecology of mpox. However, as TTs are not selective, the other rodents captured were used for other studies; for the present study, only squirrels were considered.

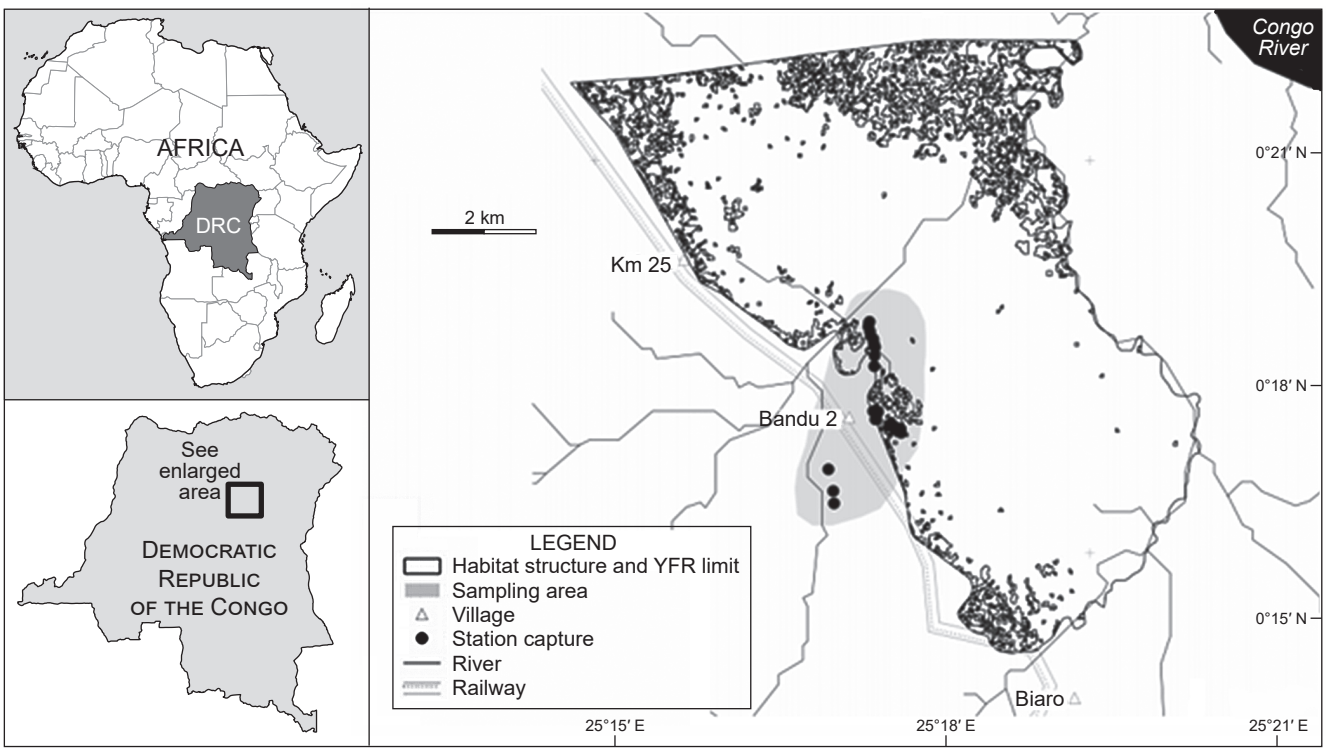


Figure 1: Squirrel sampling area. Squirrels were sampled in fallow lands located along the periphery of the reserve as well as in forest habitats within the Yoko Forest Reserve (YFR), Democratic Republic of the Congo (DRC). The light grey-shaded area indicates the location where the traps were deployed

Molecular data acquisition and specimen identification

Molecular data acquisition and specimen identification are discussed in detail by Baelo et al. (2025). Briefly, the captured squirrels were first examined for external morphological criteria. Sex was determined by external observation. Data collection on reproductive status was performed in the laboratory. After examining the specimens, we euthanised the live-captured squirrels with an overdose of isoflurane, following the American Society of Mammalogists guidelines for euthanasia (Sikes et al. 2016), before collecting blood on Whatman filter paper and organ samples (tongue, kidney, liver, lung, spleen and colon) and faeces. Samples were collected and stored in either 70%–94% ethanol or DNA/RNA later.

We used DNA barcoding to confirm the morphological identification of the specimens. We performed the extraction, amplification, purification and alignment of cytochrome *b* fragment sequences at the Royal Belgian Institute of Natural Sciences in Brussels. The Nucleospin Tissue Mini Kit was used according to the manufacturer's instructions (Machery-Nagel, Düren, Germany), with overnight pre-lysis incubation instead of 1–3 h, and 1 min elution at 70 °C instead of room temperature. We amplified a mitochondrial gene fragment using the universal cytochrome *b* primers L14723 and H15915 (Montgelard et al. 2002) with Promega MasterMix PCR following the manufacturer's instructions (Promega, Madison, WI, USA). Initial denaturation was performed at 94 °C for 3 min, followed by 35 cycles at 94 °C for 1 min, 52 °C for 1 min, and 72 °C for 1 min. Final extension was performed at 72 °C for 7 min.

We purified the amplified products using the Thermo Fisher ExoSAP-IT PCR Cleanup Reagent (Thermo Fisher Scientific, Santa Clara, CA, USA) and sent them to Macrogen (Amsterdam, The Netherlands) for Sanger sequencing. Finally, we manually cleaned the sequences based on the chromatograms and aligned them using the MAFFT algorithm in Geneious 2019.2.3. This alignment included internally generated *Funisciurus* sequences, as well as two *Paraxerus* sequences serving as an outgroup. Only samples from squirrels of the genus *Funisciurus* underwent genetic testing, and when a taxon represents a species complex or its taxonomy is unclear, we use the term confer (cf.) in our identifications.

Specific richness and diversity

Habitat diversity was assessed using the Shannon–Wiener index, the Simpson index and the evenness index (Krebs 1994). We assessed species richness in the form of species accumulation curves, based on the cumulative number of species captured and using statistical estimates based on incidence with 100 randomisations in EstimateS software (version 9.1.0) (Colwell and Elsensohn 2014). Analyses were performed first for all seasons (72 days) and then for each season, i.e. one for the rainy season (36 days) and one for the sub-dry season (36 days). The values of the estimators were compared using first-order Jackknife (Jackknife 1; Burnham and Overton 1978, 1979), Chao 2 with bias correction (Chao 1987), an abundance-based coverage estimator (ICE) (Chao et al. 2006) and Bootstrap richness estimator (Smith and van Bell 1984). Two estimators were plotted, Jackknife 1 and Chao 2, and evaluated as generally performing well (Williams et al. 2007).

Reproduction analysis

Determining the exact age of small mammals is traditionally based on weighing the lens of the eye, examining the fusion of the skull bones or assessing the wear on the molars (Dapson 1980; Wilson and Mittermeier 2019). These advanced techniques were not used, but a preliminary indication was obtained by categorising individuals into three age classes based on body weight and examination of their reproductive system. As a result, the following three age classes were identified (Amundala et al. 2008): (1) juveniles are immature individuals, characterised by the absence of criteria indicating sexual maturity; (2) subadults are individuals in which one of the criteria for sexual maturity is detected (testicles in the process of scrotalisation, perforated vagina, undeveloped mammary glands and absence of uterine embryo); and (3) adults are older individuals who are generally heavier and in which all criteria for sexual maturity are observed.

In males, the testicles are abdominal in young individuals, undergoing recrudescence in subadults, and scrotal and well developed in adults. In females, when the vagina is open, the individual is sexually active. Adults with developed mammary glands are either pregnant or lactating. The analysis is best done when the animal is fresh, by applying slight pressure to the mammary gland, which often causes milk to flow out, proving that the female is lactating or about to do so. Internal examination of females allows the condition of the uterus to be described: embryos in pregnant adults, resorbed or scarred in lactating adults, normal in subadults, and thread-like and thin in juveniles.

Results

Species richness

A total of 92 squirrels were captured over a total trapping effort of 5 400 trap-nights, with 1 800 trap-nights per habitat. The overall capture success rate was 1.7%. In total, seven species belonging to four genera were recorded.

During each of the nine-day sampling sessions, 87.5% of the total number of species were sampled (captured and estimated). The number of species sampled during these eight 9-day capture sampling sessions (i.e. 72 days of capture from four sampling sessions (36 days) for each season) is seven. Estimates of species richness were lower for the sub-dry seasons (Table 1, Figure 2b). However, the overall composition of the most frequently encountered species during the wet and dry seasons was identical, except for the single *Funisciurus* individual that was captured during the wet season. Estimates of species richness during the wet seasons were similar across all sampling periods (Table 1, Figure 2a), but the 95% confidence intervals were much lower. Overall, the cumulative number of species captured converged with statistical estimates of seven to eight species (Chao 2, 95% confidence interval) (Table 1, Figure 2c).

Specific diversity and abundance per habitat type

A total of seven species (*F. anerythrus*, *Funisciurus*

Table 1: Observed and estimated squirrel species richness during the dry season, wet season and the entire sampling period in the Yoko Forest Reserve

Field session	Day	Number of species sampled	Number of species estimated			
			Jackknife 1	± Chao 2	ICE	Bootstrap
Dry season	36	7	7.99 ± 0.9	7.32 ± 0.9 (7.02–12.84)	7.33 ± 0.0	7.4 ± 0.0
Wet season	36	6	6.0 ± 0.0	6.00 ± 0.5 (6.0–7.33)	6.00 ± 0.0	6.0 ± 0.0
Cumulative	72	7	7.99 ± 0.9	7.00 ± 0.52 (7.0–8.51)	7.33 ± 0.0	7.4 ± 0.0

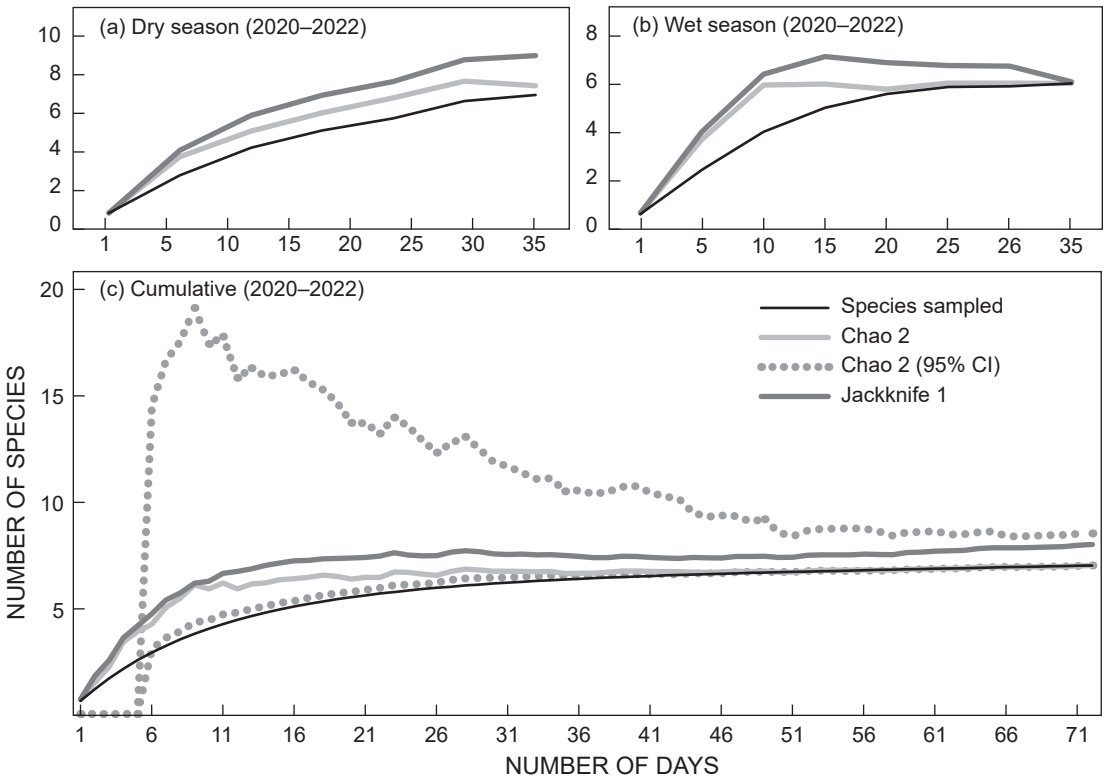


Figure 2: Species richness of squirrels in Yoko Forest Reserve (represented by species accumulation curves) based on the number of species sampled (black) and statistically estimated using the Jackknife 1 and Chao 2 methods. (a) Rainy season: October 2020–April 2021–October 2021 and April 2022; (b) sub-dry season: July 2020, January 2021, July 2021 and January 2022; and (c) cumulative data for the entire period, 2020–2022 (72 days). The dotted lines show the 95% confidence interval for Chao 2

sp., *F.* cf. *bayonii*_sp1, *F.* cf. *bayonii*_sp2, *H. rufobrachium*, *P.* cf. *boehmi* and *P. stangeri*) were observed (Table 2). The *F.* cf. *bayonii*_sp1 and *F.* cf. *bayonii*_sp2, lineages most likely represent two distinct species within the *F.* cf. *bayonii* complex. Although they are morphologically indistinguishable, they exhibit marked genetic divergence, suggesting the presence of cryptic species within this taxonomic complex. *Funisciurus anerythrus* was the most frequently captured species, representing 30 of the 92 individuals sampled (32.61%), followed by *P. stangeri*, with 22 individuals (23.91%). The species *F.* cf. *bayonii*_sp2 and *H. rufobrachium* were represented by 13 specimens (14.13% each). The other species were less well represented: *F.* cf. *bayonii*_sp1 (seven individuals, 7.61%), *P.* cf. *boehmi* (six individuals, 6.52%) and *Funisciurus* sp. (one individual, 1.09%) (Table 2). The majority of individuals were captured in most human-impacted environments, fallow land (36/92 individuals, 39.13%) and secondary forests (33/92 individuals, 35.86%). Primary forests provided only 23 individuals (25%) (Table 2). Fallow land appears to be the preferred habitat of *F. anerythrus* and the *F.* cf. *bayonii* complex, whereas *H. rufobrachium*, *P. stangeri*, *P.* cf. *boehmi* and *Funisciurus* sp. prefer forest environments (Table 2).

Table 2 also presents the diversity indices for the entire study area and for the three habitats surveyed. The diversity calculated using the Shannon index shows that the secondary forest is more diverse (H' = 1.747 and $1 - D$ = 0.819) than the fallow land (H' =1.187 and $1 - D$ = 0.614) and the primary forest (H' =1.158 and $1 - D$ = 0.601). The probability of capturing two squirrels belonging to two different species is slightly higher in secondary forests (E = 0.975), followed by fallow land (E = 0.737) and primary forests (E = 0.72).

Table 2: Species composition, relative abundance and diversity indices of squirrels across three habitat types in the Yoko Forest Reserve

Species/genus	Primary forest	Secondary forest	Fallow land	Total	Relative abundance
Funisciurus anerythrus (Thomas, 1890)	2	8	20	30	32.61
Funisciurus sp. (Trouessart, 1880)	1	0	0	1	1.09
Funisciurus cf. *bayonii*_sp1	0	4	3	7	7.61
Funisciurus cf. *bayonii*_sp2	1	3	9	13	14.13
Heliosciurus rufobrachium (Waterhouse, 1842)	6	6	1	13	14.13
Paraxerus cf. *boehmi* (Reichenow, 1886)	0	6	0	6	6.52
Protoxerus stangeri (Waterhouse, 1843)	13	6	3	22	23.91
Total	**23**	**33**	**36**	**92**	
Percentage	**25**	**35.86**	**39.13**		
Shannon–Wiener (*H*′)	**1.158**	**1.747**	**1.187**		
Simpson (1 − *D*)	**0.601**	**0.819**	**0.614**		
Equitability (*E*)	**0.72**	**0.975**	**0.737**		

Reproduction

For each species surveyed, the sex ratio (males/females) for species caught in the traps favoured males. However, in *P.* cf. *boehmi*, the sex ratio favoured females (Table 3). For each species, seasonal variation in reproductive activity was observed between males and females. Table 4 shows that a total of 68 sexually active individuals were recorded, including 55 males (80.9%) and 13 females (19.1%). Sexually active females were more numerous during the sub-dry season (nine individuals) than during the rainy season (four individuals), whereas males exhibited the opposite pattern, with slightly higher reproductive activity during the rainy season (36 individuals) than during the sub-dry season (19 individuals).

Among females, reproductive activity was therefore more pronounced during the sub-dry season. This pattern was mainly driven by *P. stangeri* (three sexually active females), *F.* cf. *bayonii*_sp1 (two), *F.* cf. *bayonii*_sp2 (two), and *P.* cf. *boehmi* (two), all of which were recorded exclusively during this period. In contrast, *H. rufobrachium* exhibited reproductive activity only during the rainy season (three females), while *F. anerythrus* was represented by only one sexually active female, also captured during the rainy season. No sexually active females were recorded for *Funisciurus* sp. These findings suggest that, for most of the species examined, female reproduction tends to be concentrated during the sub-dry season, although some species exhibit different reproductive strategies (Table 4).

In males, reproductive activity was observed during both seasons, indicating a relatively continuous reproductive capacity throughout the year. *Funisciurus anerythrus* showed almost identical numbers of sexually active males during the rainy season (nine individuals) and the sub-dry season (10 individuals), suggesting year-round reproductive activity. *Heliosciurus rufobrachium* also displayed stable reproductive activity, with four sexually active males recorded in each season. In contrast, *P. stangeri* was observed exclusively during the rainy season (12 males), whereas *F.* cf. *bayonii*_sp2 showed greater reproductive activity during the rainy season (seven vs one male). Conversely, *F.* cf. *bayonii*_sp1 was slightly more active during the sub-dry season (three vs two males). These differences indicate that reproductive seasonality varies among species, but overall, males remain reproductively active over a longer period than females (Table 4).

Table 3: Sex ratio of squirrel species captured in the Yoko Forest Reserve

Species	Female (F)	Male (M)	M/F
Funisciurus anerythrus	1	29	29.00
Funisciurus sp.	0	1	–
Funisciurus cf. *bayonii*_sp1	2	5	2.50
Funisciurus cf. *bayonii*_sp2	4	9	2.25
Heliosciurus rufobrachium	3	10	3.33
Paraxerus cf. *boehmi*	4	2	0.50
Protoxerus stangeri	5	17	3.40

Table 4: Seasonal reproductive activity of sexually mature male and female squirrels captured during the rainy (RS) and sub-dry (SDS) seasons in the Yoko Forest Reserve

Species	Females		Males	
	RS	SDS	RS	SDS
Funisciurus anerythrus	1	0	9	10
Funisciurus sp.	0	0	1	0
Funisciurus cf. *bayonii*_sp1	0	2	2	3
Funisciurus cf. *bayonii*_sp2	0	2	7	1
Heliosciurus rufobrachium	3	0	4	4
Paraxerus cf. *boehmi*	0	2	1	1
Protoxerus stangeri	0	3	12	0
Total	4	9	36	19

Sex distribution differed from one habitat to another (Table 5). Capture success was consistently higher for males than females regardless of habitat type, with 18 and five individuals recorded in primary forest, 22 and 11 In secondary forest, and 33 and three in fallow land, respectively (Table 5).

Reproduction occurred during both rainy (March, April, May, September, October and November) and sub-dry seasons (December, January, February, June, July and August), although it appears to be higher during the rainy season. All three age classes (adults, subadults and juveniles) were present during all seasons. During the dry season, the proportion of pregnant females was

7.69% in *F.* cf. *bayonii*_sp2 (Figure 3a). During the same season, the proportion of lactating females was 15.38% each for *F.* cf. *bayonii*_sp1 and *P.* cf. *boehmi*, while for *F.* cf. *bayonii*_sp2 and *P. stangeri* it was 7.69% each (Figure 3a). However, no young females of *F.* cf. *bayonii*_sp1 were captured, and the proportion for F. cf. *bayonii*_sp2, *P.* cf. *boehmi* and *P. stangeri* was 7.69%, 15.38% and 23.07%, respectively (Figure 3a). During the rainy season, the proportion of pregnant females was 16.6% in *F. anerythrus*, and no other pregnant females of other species were captured (Figure 3b). During the same rainy season, the proportion of lactating females in *H. rufobrachium* was 33.33%, and no other lactating females of other species were sampled. The proportion of young females of *F.* cf. *bayonii*_sp2, *H. rufobrachium* and *P. stangeri* was 16.66% each (Figure 3b). Litter sizes are generally small (1–3 embryos). No pregnant females were observed in the other species during the two seasons (Figure 3).

Sexually mature males were recorded in all squirrel species during both seasons, although their frequency varied among species (Figure 4). During the sub-dry season (Figure 4a), *F. anerythrus* exhibited the highest proportion of sexually mature males (38.46%), followed by *H. rufobrachium* (15.38%) and *F.* cf. *bayonii*_sp1 (11.53%). In contrast, *P. stangeri* was represented exclusively by juvenile individuals during this period. Juveniles were most frequently observed in *F. anerythrus* (19.23%), whereas they were absent from several other species. During the rainy season (Figure 4b), *P. stangeri* became the species with the highest proportion of sexually mature males (25.53%), followed by *F. anerythrus* (19.14%) and *F.* cf. *bayonii*_sp2 (14.89%). Juvenile males were also recorded in several species, including *P. stangeri* (8.51%),

Table 5: Distribution of male (M) and female (F) squirrels among primary forest, secondary forest and fallow habitats in the Yoko Forest Reserve

Species	Primary forest		Secondary forest		Fallow land	
	F	M	F	M	F	M
Funisciurus anerythrus	0	2	1	7	0	20
Funisciurus cf. *bayonii*_sp1	0	0	1	3	1	2
Funisciurus cf. *bayonii*_sp2	1	0	2	1	1	8
Heliosciurus rufobrachium	0	6	2	4	1	0
Paraxerus cf. *boehmi*	0	0	4	2	0	0
Funisciurus sp.	0	1	0	0	0	0
Protoxerus stangeri	4	9	1	5	0	3
Total	5	18	11	22	3	33

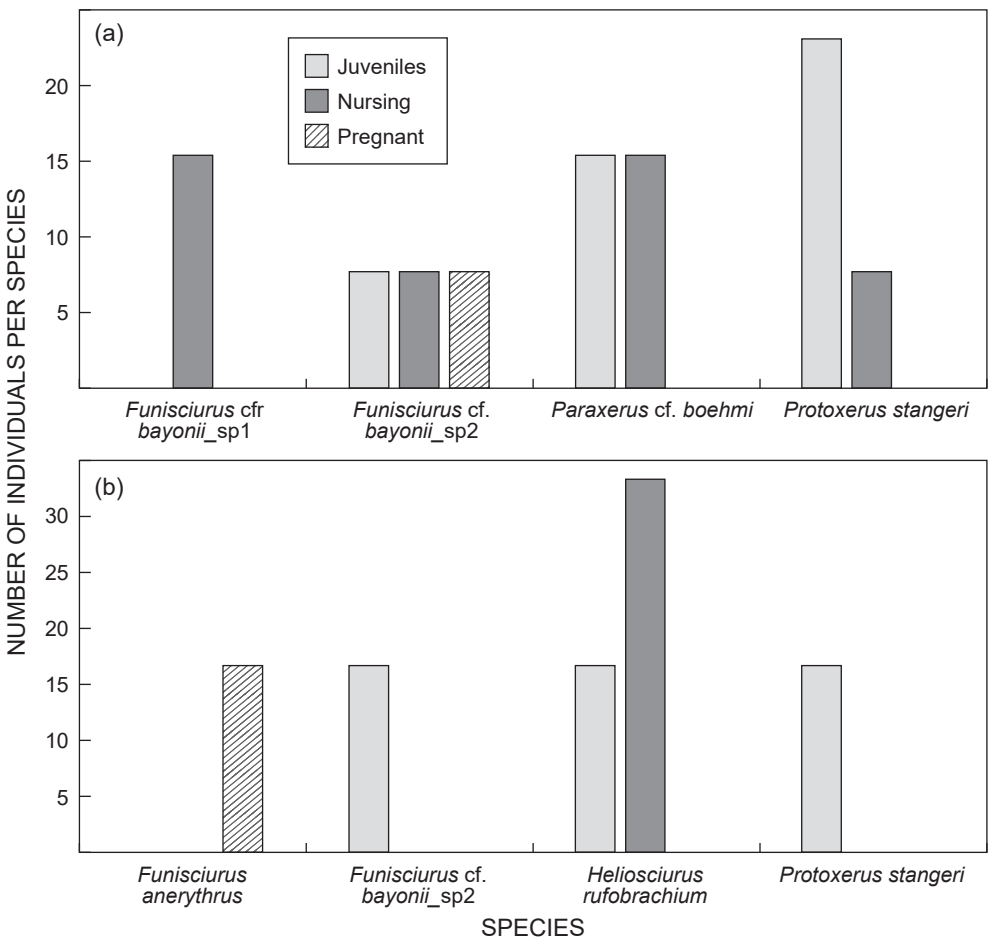


Figure 3: Proportion of female reproductive classes of species inventoried during the sub-dry season (a) and rainy season (b)

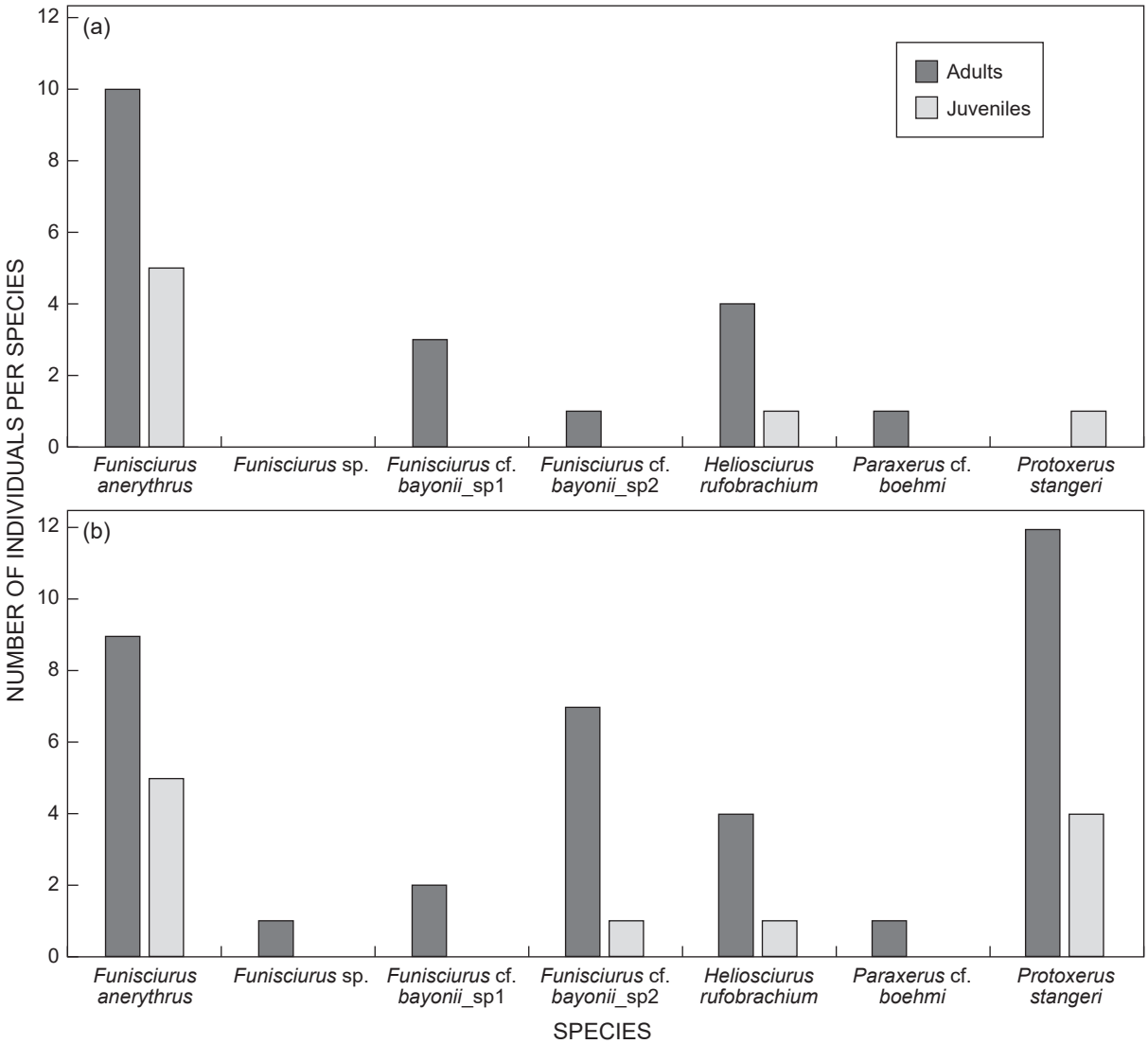


Figure 4: Seasonal distribution of juvenile and sexually mature male squirrels among species sampled in the Yoko Forest Reserve during the sub-dry (a) and rainy seasons (b). Dark grey columns = sexually mature males; pale grey columns = juveniles

F. anerythrus (10.63%), *F.* cf. *bayonii*_sp2 (2.12%), and *H. rufobrachium* (2.12%). In contrast, no juvenile males were observed in *P.* cf. *boehmi*, *F.* cf. *bayonii*_sp1 or *Funisciurus* sp.

Discussion

This study provides one of the first comprehensive ecological assessments of tree squirrels in a lowland tropical rainforest of the central Congo Basin. The captured squirrels were first examined based on external morphological criteria followed by molecular identification. We documented seven squirrel species belonging to four genera, partly corroborating the findings reported by Thorington et al. (2012) and the observations of Baelo et al. (2018) from the Kisangani region.

Furthermore, species richness estimators indicated that the local squirrel community comprises approximately seven to eight species. These findings suggest that our inventory detected most of the species occurring within the study area. However, some species inhabiting the upper canopy or naturally occurring at low densities may have remained undetected, as traps were deployed only up to a maximum height of 7.37 m. Similar limitations have been reported in surveys of arboreal mammals in tropical forests, where capture success declines markedly with increasing use of the forest canopy (Emmons 1980)

The molecular confirmation of species identity also highlights the taxonomic complexity of Central African squirrels. Two sympatric but genetically distinct taxa belonging to the *F.* cf. *bayonii* complex could not be separated using external morphology alone, supporting previous evidence that the taxonomy of African rope squirrels remains incompletely resolved (Baelo et al. 2025). Likewise, the occurrence of an unidentified *Funisciurus* species and *P.* cf. *boehmi* outside their currently recognised distributions suggests that the geographic ranges of several squirrel taxa may require reassessment. These

observations reinforce the need for integrative taxonomic studies combining morphology, molecular data and broad geographic sampling throughout the Congo Basin.

Species accumulation curves indicated that approximately 87.5% of the squirrel fauna was sampled during each 9-day trapping session. Unlike previous studies on terrestrial rodents and shrews from the Kisangani region, which generally reported higher species richness during the rainy season (Amundala 2013; Gambalemoke 2014), seasonal differences in squirrel species richness were limited. This probably reflects the predominantly arboreal ecology of squirrels, whose detectability appears to be influenced more strongly by habitat characteristics than by seasonal variation.

Habitat type had a stronger influence on squirrel abundance than season. Secondary forests and fallow lands supported the highest abundance and diversity, whereas primary forest yielded fewer captures. *Funisciurus anerythrus* was the most abundant and widespread species, particularly in fallow lands, confirming its ecological plasticity previously reported in the Kisangani region (Baelo et al. 2018). Likewise, the *F.* cf. *bayonii* complex was largely associated with anthropogenic habitats. These environments probably provide abundant food resources, including oil palm fruits and other seeds, together with structurally heterogeneous vegetation offering numerous feeding and shelter opportunities.

In contrast, *P. stangeri*, *H. rufobrachium*, *P.* cf. *boehmi* and the unidentified *Funisciurus* species were predominantly associated with forest habitats, consistent with published ecological accounts (Thorington et al. 2012; Thomas et al. 2019). The relatively low capture success in primary forest is unlikely to indicate lower abundance alone. Rather, it probably reflects methodological limitations, as many canopy specialists regularly forage above the maximum trapping height used in this study.

The ecological distribution of *F. anerythrus* deserves particular attention because this species frequently occurred in fallow lands located close to human settlements. Since rope squirrels have been implicated as potential reservoirs of the mpox virus (Khodakevich et al. 1987; Schulze et al. 2020; Curaudeau et al. 2023; Leendertz et al. 2025) and are commonly hunted for bushmeat, frequent contact between humans and squirrels may increase opportunities for zoonotic transmission. Although our study did not investigate pathogen prevalence directly, the ecological patterns observed here provide useful information for future surveillance programmes integrating wildlife ecology and public health.

Overall, these results suggest that the squirrel species studied do not exhibit strictly seasonal reproduction. Males remain sexually active throughout the year, with a slight predominance during the rainy season, whereas females display a more seasonal reproductive pattern, with activity occurring primarily during the sub-dry season. This difference between the sexes may reflect distinct reproductive strategies, with males maintaining continuous reproductive readiness to maximise mating opportunities, while females tend to synchronise reproduction with environmental conditions that are most favourable for gestation, parturition and offspring survival. However, this interpretation should be treated with caution because of the small sample sizes recorded for some species, which may limit the detection of robust seasonal reproductive patterns. These findings are consistent with previous studies on African murid rodents, particularly those of Amundala et al. (2008) and Katuala et al. (2008) conducted in the Kisangani region.

The occurrence of reproductive females, lactating females, sexually mature males and juveniles during both the rainy and sub-dry seasons indicates that tree squirrels reproduce throughout the year in the Yoko Forest Reserve (Figures 3 and 4, Table 4). However, seasonal changes in the proportion of sexually mature males and juveniles suggest that reproductive intensity varies between seasons and differs among species (Figure 4). Females (lactating and pregnant) were sampled more frequently during the sub-dry season (Figure 3), indicating seasonal fluctuations in reproductive intensity rather than strict reproductive seasonality. Similar reproductive patterns have been reported for several African tropical forest rodents, whose breeding is continuous but reaches its highest intensity during the wetter periods, when food resources are most abundant (Delany 1972; Dudu 1997; Katuala et al. 2005; Makundi et al. 2007; Katandukila et al. 2013). Although the number of reproductive females recorded in this study was relatively low, our findings support the hypothesis that tropical forest squirrels exhibit an opportunistic reproductive strategy, characterised by continuous breeding with seasonal peaks in reproductive activity rather than a complete cessation of reproduction.

This study provides one of the first comprehensive ecological assessments of tree squirrels in the lowland forests of the Yoko Forest Reserve and improves our understanding of squirrel diversity in the central Congo Basin. We documented seven species, including two sympatric genetically distinct lineages within the *F.* cf. *bayonii* complex and one unidentified *Funisciurus* species, emphasising that the taxonomy and distribution of Central African squirrels remain incompletely resolved. Species richness estimates indicate that our sampling captured most of the local squirrel community, with habitat emerging as the primary driver of squirrel abundance and diversity. Secondary forests and fallow lands supported higher abundance and diversity than primary forests, where capture success was probably limited by the predominantly arboreal habits of several species. *Funisciurus anerythrus* was the most abundant and widespread species, whereas *P. stangeri*, *H. rufobrachium*, *P.* cf. *boehmi* and the unidentified *Funisciurus* species were mainly associated with forest habitats. Seasonal variation had little influence on species richness, although females (both breastfeeding and pregnant) were sampled more frequently during the semi-dry season, while remaining detectable throughout the year. Overall, our findings provide an important ecological baseline for future taxonomic, ecological and conservation studies and underline the value of integrating ecological surveys with molecular approaches to better understand squirrel diversity and distribution in the Congo Basin. Considering the increasing evidence that several African squirrel species may act as reservoirs of zoonotic pathogens, including the mpox virus, this knowledge will also contribute to wildlife disease surveillance and public health initiatives in the region.

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Data availability – The generated and/or analysed datasets can be made available for research purposes upon request to the corresponding author.

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Ethics approval – Research permits were obtained through the Centre de Surveillance de la Biodiversité at the University of Kisangani. Samples exported to Belgium were authorised under a Nagoya export permit issued by the Congolese Ministry of the Environment and Sustainable Development (MEDD): 018/ANCCB-RDC/SG EDD/BTB/07/2022, 021/SG-EDD/BTB/ANCCB-RDC/08/2023, 011/ANCCB-RDC/SG EDD/BTB/2023. Permission to import the samples into Belgium was granted by the Federal Agency for the Safety of the Food Chain (FASFC): 2022DBP504, 2023DBP370, 2023DBP371, 2024DBP424.

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References

Amundala D. 2013. Ecologie de population des Rongeurs (Rodentia, Mammalia) dans une perspective de gestion des espèces nuisibles aux cultures dans la région de Kisangani (R.D. Congo) [Population ecology of rodents (Rodentia, Mammalia) with a view to managing crop pests in the Kisangani region (DR Congo)]. PhD thesis. Université de Kisangani, Democratic Republic of the Congo.

Amundala D, Kennis J, Leirs H, Dudu AM. 2008. Farmer survey in the hinterland of Kisangani (Democratic Republic of Congo) on rodent crop damage and rodent control techniques used. *Mammalia* 72: 192–197. https://doi.org/10.1515/MAMM.2008.034.

Baelo P, Asimonyio J, Amundala N, Akaibe D, Gambalemoke S, Verheyen E, Laudisoit A, Bongo G, Ngbolua K. 2018. Preliminary inventory of squirrels (Sciuridae, Rodentia) of Kisangani region in the Democratic Republic of the Congo. *American Journal of Zoology* 1(1): 15–19. https://doi.org/10.11648/j.ajz.20180101.13.

Baelo P, Fourchault L, Laurent N, Mande C, Laudisoit A, Amundala N, Temidayo SG, Gembu GC, Mariën J, Gryseels S et al. 2025. Reassessing the diversity and distribution of African rope squirrels (*Funisciurus* Trouessart, 1880). bioRxiv preprint. Available at https://doi.org/10.1101/2025.08.25.672055.

Boyemba B. 2011. Ecologie de *Pericopsis elata* (Harms) Van Meeuwen (Fabaceae), arbre de forêt tropicale africaine à répartition agrégée [Ecology of *Pericopsis elata* (Harms) Van Meeuwen (Fabaceae), a tropical African rainforest tree with an aggregate distribution]. PhD thesis, Université Libre de Bruxelles, Belgium.

Burnham KP, Overton WS. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65(3): 625–633. https://doi.org/10.1093/biomet/65.3.625.

Burnham KP, Overton WS. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60(5): 927–936. https://doi.org/10.2307/1936861.

Chao A. 1987. Estimating the population size for capture–recapture data with unequal catchability. *Biometrics* 43(4): 783–791. https://doi.org/10.2307/2531532.

Chao A, Chazdon R, Colwell R, Shen TJ. 2006. Abundance-Based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62(2): 361–371. https://doi.org/10.1111/j.1541-0420.2005.00489.x.

Colwell RK, Elsensohn JE. 2014. EstimateS turns 20: statistical estimation of species richness and shared species from samples, with non-parametric extrapolation. *Ecography* 37(6): 609–613. https://doi.org/10.1111/ecog.00814.

Curaudeau M, Besombes C, Nakouné E, Fontanet A, Gessain A, Hassanin A. 2023. Identifying the most probable mammal reservoir hosts for Monkeypox virus based on ecological niche comparisons. *Viruses* 15(3): 727. https://doi.org/10.3390/v15030727.

Dapson RW. 1980. Guidelines for statistical usage in age-estimation technics. *Journal of Wildlife Management* 44(3): 541–548. https://doi.org/10.2307/3808001.

Delany MJ. 1972. The ecology of small rodents in tropical Africa. *Mammal Review* 2(1): 1–42. https://doi.org/10.1111/j.1365-2907.1972.tb00155.x.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R et al. 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67(6): 534–545. https://doi.org/10.1093/biosci/bix014.

Dudu A, Verhagen R, Gevaerts H, Verheyen W. 1997. Population structure and reproductive cycle of *Praomys jacksoni* (De Winton, 1897) and first data on the reproduction of *P. misonnei* Van der Straeten & Dieterlen, 1987 and *P. mutoni* Van der Straeten & Dudu, 1990 (Muridae) from Masako forest (Kisangani, Zaïre). *Belgian Journal of Zoology* 127(Suppl. 1): 67–70.

Emmons LH. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* 50(1): 31–54. https://doi.org/10.2307/2937245 .

Gambalemoke M. 2014. Phylogénie et biodiversité des Musaraignes (Soricomorpha, Crocidurinae) en Cuvette Congolaise (Kisangani, RDC) [Phylogeny and biodiversity of shrews (Soricomorpha, Crocidurinae) in the Congo Basin (Kisangani, DRC)]. PhD thesis, Université de Kisangani, Democratic Republic of the Congo.

Katandukila JV, Faulkes CG, Chimimba CT Bennett NC. 2013. Reproduction in the East African root rat (*Tachyoryctes splendens*; Rodentia: Spalacidae) from Tanzania: the importance of rainfall. *Journal of Zoology* 291(4): 258–268. Print ISSN 0952-8369. https://doi:10.1111/jzo.12067.

Katuala GB. 2009. Biodiversité et biogéographie des Rongeurs Myomorphes et Sciuromorphes (Rodentia, Mammalia) de

quelques blocs forestiers de la Région de Kisangani (R D Congo) [Biodiversity and biogeography of myomorph and sciuromorph rodents (Rodentia, Mammalia) in selected forest blocks of the Kisangani region (DR Congo)]. PhD thesis, Université de Kisangani, Democratic Republic of the Congo.

Katuala GB, Hart JA, Hutterer R, Leirs H, Dudu A. 2005. Biodiversity and ecology of small mammals (rodents and shrews) of the "Reserve de Faune à Okapis", Democratic Republic of the Congo. *Belgian Journal of Zoology* 135(Suppl. 1): 191–196.

Katuala P, Kennis J, Nicolas V, Wendelen W, Hulselmans J, Verheyen E, van Houtte N, Dierckx T, Dudu A, Leirs H. 2008. The presence of *Praomys*, *Lophuromys*, and *Deomys* species (Muridae, Mammalia) in the forest blocks separated by the Congo River and its tributaries (Kisangani region, Democratic Republic of Congo). *Mammalia* 72(3): 223–228. https://doi.org/10.1515/MAMM.2008.044.

Khodakevich L, Szczeniowski M, Nambu-ma-Disu, Jezek Z, Marennikova S, Nakano J, Meier F. 1987. Monkeypox virus in relation to the ecological features surrounding human settlements in Bumba zone, Zaire. *Tropical and Geographical Medicine* 39(1): 56–63.

Kinganda-Lusamaki E, Amuri-Aziza A, Fernandez-Nuñez N, Makangara-Cigolo J-C, Pratt C, Vakaniaki EH, Hoff NA, Luakanda-Ndelemo G, Akil-Bandali P, Nundu SS et al. 2025. Clade I mpox virus genomic diversity in the Democratic Republic of the Congo, 2018–2024: predominance of zoonotic transmission. *Cell* 188(1): 4–14.E6. https://doi.org/10.1016/j.cell.2024.10.017.

Krebs CJ. 1994. *Ecology: the experimental analysis of distribution and abundance* (4th edn). New York: HarperCollins College Publishers.

Leendertz F, Riutord-Fe C, Schlotterbeck J, Lagostina L, Kouadio L, Herridge H, Jochum M, Noma N, López-Morales A, Hoffmann D et al. 2025. Fire-footed rope squirrels (*Funisciurus pyrropus*) are a reservoir host of monkeypox virus (*Orthopoxvirus monkeypox*). ResearchSquare preprint. Available at https://doi.org/10.21203/rs.3.rs-6322223/v1.

Makundi RH, Massawe AW, Mulungu LS. 2007. Reproduction and population dynamics of *Mastomys natalensis* Smith, 1834 in an agricultural landscape in the Western Usambara Mountains, Tanzania. *Integrative Zoology* 2(4): 233–238. https://doi:10.1111/j.1749-4877.2007.00063.x.

Montgelard C, Bentz S, Tirard C, Verneau O, Catzeflis FM. 2002. Molecular systematics of Sciurognathi (Rodentia): the mitochondrial cytochrome *b* and 12S rRNA genes support the Anomaluroidea (Pedetidae and Anomaluridae). *Molecular Phylogenetics and Evolution* 22(2): 220–233. https://doi.org/10.1006/mpev.2001.1056.

Peel MC, Finlayson BL, Mahon TA. 2007. Updated world map of the Köppen–Geiger climate classification. *Hydrology and Earth System Sciences* 11(5): 1633–1644. https://doi.org/10.5194/hess-11-1633-2007.

Schulze V, Lurz PW, Ferrari N, Romeo C, Steele MA, Marino S, Vittoria MM, Calvignac SS, Schlottau K, Beer M et al. 2020. Search for polyoma-, herpes-, and bornaviruses in squirrels of the family Sciuridae. *Virology Journal* 17: 42. https://doi.org/10.1186/s12985-020-01310-4.

Shutsha RE, Asimonyio JA, Omatoko JM, Kambale JLK, Angoyo RA, Lomba CB, Ndjele NB, Ngbolua K. 2017. Etudes floristique, phytosociologique et phytogéographique de la végétation herbacée et du sous-bois de la réserve forestière de la Yoko (Province de la Tshopo, RD Congo) [Floristic, phytosociological and phytogeographical studies of the herbaceous vegetation and the underwood of the Yoko reserve forest (Tshopo Province, DR Congo)]. *International Journal of Innovation and Scientific Research* 29(2): 119–136 [in French with English abstract].

Sikes RS, Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97(3): 663–688. https://doi.org/10.1093/jmammal/gyw078.

Smith EP, van Belle G. 1984. Nonparametric estimation of species richness. *Biometrics* 40(1): 119–129. https://doi.org/10.2307/2530750.

Steiner M, Huettmann F. 2023. *Sustainable squirrel conservation*. Cham: Springer. https://doi.org/10.1007/978-3-031-23547-4_1.

Thomas HH, Best LT, Agwanda B. 2019. *Heliosciurus rufobrachium* (Rodentia: Sciuridae). *Mammalian Species* 51(978): 61–69. https://doi.org/10.1093/mspecies/sez010.

Thorington RWJ, Koprowski JL, Steele MA, Whatton JF. 2012. *Squirrels of the world*. Baltimore: John Hopkins University Press. https://doi.org/10.1353/book.17238.

Van de Perre F, Leirs H, Verheyen E. 2019. Paleoclimate, ecoregion size, and degree of isolation explain regional biodiversity differences among terrestrial vertebrates within the Congo Basin. *Belgian Journal of Zoology* 149: 23–42. https://doi.org/10.26496/bjz.2019.28.

Williams VL, Witkowski ETF, Balkwill K. 2007. The use of incidence-based species richness estimators, species accumulation curves, and similarity measures to appraise ethnobotanical inventories from South Africa. *Biodiversity and Conservation* 16: 2495–2513. https://doi.org/10.1007/s10531-006-9026-9.

Wilson DE, Mittermeier RA (eds). 2019. *Handbook of the mammals of the world, vol. 8: Insectivores, sloths and colugos*. Barcelona: Lynx Edicions.

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