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RESEARCH

Drivers of microhabitat use and vegetation structure selection by the woodland dormouse (*Graphiurus murinus*) in a riverine forest

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Abstract
Arboreal small mammals are of particular concern due to their reliance on forest habitats, which are declining, notably in Africa. Most dormice species (Rodentia, Gliridae) are arboreal or semi-arboreal and may serve as indicators of forest habitat quality. However, the ecological requirements of several African dormice species remain poorly understood. We aimed to understand what factors drive the use of microhabitat features and which features are selected by woodland dormice *Graphiurus murinus* in a riverine *Combretum* forest in South Africa. We hypothesized that season, individual traits, residency status, connectivity, and vegetation structure and cover influence microhabitat choice. We collected capture–mark–recapture data across four seasons and assessed microhabitat features using a grid of 192 traps set at various heights. Generalized linear and generalized mixed models and comparative tests were used to assess microhabitat use and selection. Dormice were less captured during winter and where only same-sex individuals were present. Microhabitats with a higher number of dormice neighbours and those with animals with longer residency time were more frequently used. Dormice used more well-connected areas, trunks and canopies; favouring higher, denser and more connected vegetation cover. The species predominantly utilized *Combretum caffrum*, *Rhus* spp., and *Gymnosporia heterophylla*, preferring the latter two tree species. The significance of riverine *Combretum* forest structure for dormice microhabitat use and selection was evident. We suggest management practices potentially relevant to maintain dormice populations (e.g., preventing vegetation gaps larger than 50% per 100 m^2) by balancing potential alterations on forest density and structure (e.g., climate change).

Keywords Arboreal rodents · Capture–mark–recapture · Connectivity · Gliridae · South Africa

Introduction

Forests cover 31% of the Earth's land surface and are lost at an annual rate of 1.2%, particularly in Africa and Latin America (UN 2021). These losses have increased habitat fragmentation and led to reductions in biodiversity of up to 75% (Haddad et al. 2015). Riverine forests may often act as movement corridors and offset fragmentation effects on animal populations (Anderson and Jenkins 2006). However, these forests have declined over the past decades mainly due to lower rainfall (Swemmer et al. 2023). Climate change may especially affect riverine forests due to their reliance

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on water availability (Eeley et al. 1999) and so compromise management efforts to their conservation (Swemmer et al. 2023). Currently, riverine forests provide protection against extreme weather conditions (Carvalho et al. 2024a). During dry seasons, these forests are increasingly utilized by larger herbivores (Varty 1988), which may alter the forest structure (Pringle et al. 2023) and affect the associated small mammal communities (Keesing 2000).

Arboreal small mammals are a group of particular concern because they primarily depend on forests (Fedyń et al. 2021). Several dormice species (family Gliridae) are arboreal or semi-arboreal (Holden-Musser et al. 2016) and are considered indicators of forest habitat quality (Fedyń et al. 2021). Forest fragmentation may affect genetic variability and compromise dispersal of dormice even when forest fragments are partially connected (Bani et al. 2017). Dormice populations are more genetically isolated and unstable in smaller forest fragments compared to continuous forests (e.g., hazel dormouse *Muscardinus avellanarius*, Bani et al. 2017; edible dormice *Glis glis*, Moska et al. 2023).

The woodland dormouse *Graphiurus murinus* is considered a proxy for other less abundant and more elusive arboreal glirid species (Youlatos et al. 2015). This species and all dormice (except for the desert dormouse *Selevinia betpakdalaensis*) have several adaptations for semi-arboreal and arboreal locomotion (Holden-Musser et al. 2016). More specifically, hallucal grasping enables dormice to use small branches efficiently (*G. murinus*; Youlatos et al. 2015). Those adaptations may have allowed for a disproportionate use (considering their availability) at a fine scale of these habitat features in forests, that is microhabitat selection *sensu* Johnson (1980). Individuals' ability to use and select available microhabitat features is crucial for species persistence in specific habitats (Varner and Dearing 2014). Understanding microhabitat choice is essential for guiding effective management actions for species conservation (Kearny et al. 2023). The significance of microhabitat features for biodiversity conservation becomes even more pronounced during periods of climate change (Ridell et al. 2021). Animals that can use different structures at a fine scale may find small refuges that better protect them from drastic temperature shifts due to climate change (Ridell et al. 2021). For example, small mammals that use underground burrows are less exposed to climate change compared to birds because those structures are more insulated than tree and bush canopies (Carvalho et al. 2014; Ridell et al. 2021). However, arboreal or semi-arboreal dormice that hibernate in shallow ground nests, experience decreases in survival and fertility due to warmer and wetter winters (e.g., hazel dormouse *Muscardinus avellanarius*; Combe et al. 2023). These changes impact adults during winter and juveniles throughout the year (Combe et al. 2023).

Although more than half of the extant Gliridae species belong to the genus *Graphiurus*, there is little information on their microhabitat use and selection in forests (Lamani 2014; Fedyń et al. 2021). Specifically, studies on the microhabitat use by *G. murinus* often either failed to capture enough animals to conduct a thorough analysis (Richard et al. 2022) or were limited to ground-level traps in tropical habitats (Fitzherbert et al. 2007). Moreover, these studies mostly account for microhabitat use and fail to include microhabitat selection (used versus available). Additionally, information on features that may influence microhabitat use by this species is lacking.

In this study, we aim to understand what factors affect microhabitat use and which microhabitat features are selected by *G. murinus* in a riverine *Combretum* forest in the Great Fish River Nature Reserve (GFRNR) in South Africa. Riverine *Combretum* forests are highly important for *G. murinus* in our study area. Studies on small mammals conducted in this reserve either failed to find this species in other habitats (e.g., Kryštufek et al. 2007; Lagesse and Thondhlana 2016) or only found it very close to these forests' borders (Z. J. K. Madikiza & E. Do Linh San, pers. obs.). We used capture–mark–recapture data to investigate our hypotheses that (1) season, (2) individual traits, (3) residency status, (4) connectivity and (5) vegetation structure and cover may influence microhabitat use. Additionally, we assessed which vegetation features were selected by this species. Given that *G. murinus* undergo torpor bouts under lower temperatures (Mzilikazi et al. 2012), we predicted that captures would decrease in winter, similarly to what was found in other studies (Madikiza et al. 2010a). Females have smaller home ranges than males (Madikiza et al. 2011), and juveniles stay with their mothers long after weaning (Madikiza 2017). Therefore, we expected that sex, age, and proximity between individuals would affect microhabitat use. Finally, as this species primarily uses forest habitats and is seldom captured on the ground (Madikiza et al. 2010a; Richard et al. 2022), we predicted that higher, denser, and well-connected vegetation would be more frequently used and selected.

Understanding how *G. murinus* uses and selects microhabitat features is crucial for developing guidelines for forest management to prevent local extinctions. This is particularly relevant for riverine forests, which already serve as refuges for several species (e.g., Carvalho et al. 2014, 2024a, b). Management should adopt specific guidelines, especially during habitat alterations due to climate change or other factors, such as the reintroduction of large herbivores in protected areas.

Methods

Study area

This study was conducted in the Great Fish River Nature Reserve (GFRNR), Eastern Cape Province, South Africa (Fig. 1). The reserve has 445 km^2 of undulating terrain ranging from 170 to 600 m a.s.l. (Birch 2000). The climate is warm temperate (Cfa) according to the Koppen-Geiger classification (Beck et al. 2018). Minimum temperatures range from −3 °C to 18 °C and maximum temperatures are above 22 °C (and may reach 40 °C in summer) (Palmer et al. 1988). Mean annual rainfall is 434 mm, with peaks in mid and late spring (October/November) and late summer and early autumn (February/March) (Palmer et al. 1988).

Our study site (33º 07' S, 26º 40' E) is located on the southwestern part of the reserve in a stretch of riverine *Combretum* forest (Madikiza and Do Linh San 2020). This riverine forest (< 100 m wide) is mainly fed by an underground water table; surface water occurs temporarily and only after heavy rains (Madikiza et al. 2010a). This forest is dominated by stands of Cape bushwillows *Combretum caffrum*, which usually rot from inside allowing dormice to use their numerous holes and hollows as nest sites (Madikiza 2017). Other trees present at the study site are notably *Ziziphus mucronata*, *Olea europaea* ssp. *africana*, *Gymnosporia heterophylla*, *Vachellia karroo*, *Acalypha glabrata*, *Schotia afra*, and *Rhus* spp. In addition to shoots of those trees, several tall shrubs also form a dense layer of understory vegetation such as *Azima tetracantha*, *Carissa bispinosa* ssp. *bispinosa*, *Ehretia rigida*, and *Scutia myrtina* (Madikiza et al. 2019). The study site crosses a matrix of Bushclump Karroid Thicket. This patch contrasts with the dense riverine forest by being a semi-open habitat (Fig. 1) mainly composed of *Rhus* spp. and *Scutia myrtina* bushclumps and a karroid herbaceous layer.

Study species

Listed as Least Concern (Holden-Musser et al. 2016), the woodland dormouse *Graphiurus murinus* was traditionally mapped from Ethiopia to South Africa, though recent

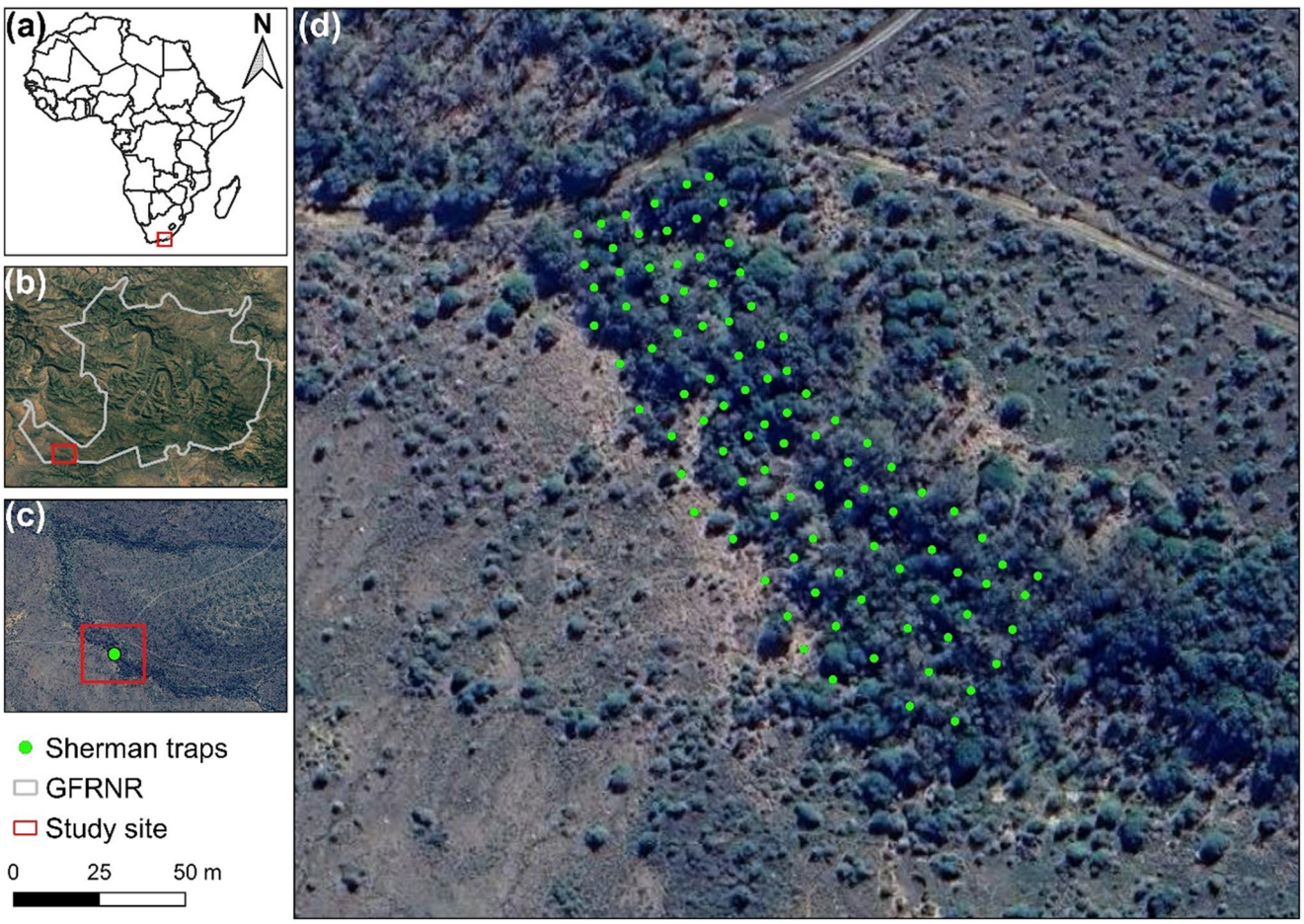


Fig. 1 Study area location in (**a**) South Africa in (**b**) the southwestern part of the Great Fish River Nature Reserve (GFRNR). The inset (**c**) shows the riverine *Combretum* forest at a larger extent. The inset (**d**) shows the relative positions of trap stations at the Junction 9 study site

genomic evidence suggests the true species is restricted to Southern Africa within a wider complex (Onditi et al. 2026). It is semi-arboreal, occurs at low densities (Madikiza et al. 2016), and can be easily caught if traps are set above ground (Madikiza et al. 2010a). This species primarily inhabits forest habitats (Kryštufek et al. 2007; Madikiza et al. 2010a) and is rarely found in wooded savanna, grasslands, cultivated crops, and fallow fields (Odhiambo et al. 2005; Fitzherbert et al. 2007; Mayamba et al. 2019). Therefore, *G. murinus* is a good indicator species for assessing forest fragmentation and connectivity.

Graphiurus murinus is predominantly insectivorous but also consumes fruits (Lamani 2014) and may act as a pollinator and seed disperser (Ssali and Sheil 2019). This species hibernates under low temperatures and/or food deprivation and can undergo torpor bouts of at least 8 consecutive days in winter (Mzilikazi et al. 2012; Eto et al. 2022). *Graphiurus murinus* is primarily nocturnal, using hollow trunks and branches or similar cavities as nests during the day (e.g., in *Combretum* trees; Lamani 2011). Individual home ranges in this species (average home range size (±SD): 2514 ± 1205 m^2) overlap greatly, suggesting a promiscuous mating system (Madikiza et al. 2011). Females typically have one or two litters per year, depending on rainfall and food availability, and offspring remain with their mothers long after weaning (Madikiza et al. 2019). Litters have an average (±SD) of 3.88 ± 0.81 young which can be born from the second half of October until mid-February (Madikiza et al. 2019).

Data collection

Graphiurus murinus were sampled every season, from June 2011 to April 2012. We used 192 Sherman live-traps (8 × 9 × 23 cm) arranged in a rectangular grid of 96 stations of two traps each (16 rows × 6 lines × 2 traps). Trap stations were spaced at 10 m intervals from each other (Fig. 1). At each station, traps were placed at different heights (within a 2 m radius), depending on the microhabitat features available (average (±SD) height of trap placement: 1.00 ± 0.75 m). Altogether, we conducted 4 trapping sessions of 5 consecutive nights, totalling 3840 trap-nights. Trap bait was a mixture of rolled oats and sunflower oil. Traps were checked in the morning and late afternoon–early evening.

Captured dormice were anaesthetized using diethyl ether and then sexed, aged, weighed, marked, and released at the same trap station. We remained at the trap station until the animal had fully recovered from the anaesthetic and moved to a safe location (e.g., a tree hole or higher branches). Age (adult/juvenile) was determined based on weight (23–34 g for adults) and fur characteristics (Skinner and Chimimba 2005). All animals that were less than one year old and had not yet experienced their first hibernation were regarded as juveniles (Madikiza et al. 2019). Commonly dormice become sexually active only after their first hibernation (Hutchins et al. 2003). Each dormouse was marked in one or two ears with a unique code using single-digit spiked tattoo numbers attached to forceps (Hauptner Herberholz, Solingen, Germany).

Microhabitat features included structural characteristics of vegetation assessed at a fine scale considering the home range of the species (Morris 1987; Brehm and Mortelliti 2021). We sampled microhabitat features for each trap at the station point (height, structural type and vertical position, and plant species) and in a 100 m^2 quadrat centred on each trap (inradius = 5 m; adapted from Hille and Mortelliti 2010; vegetation cover and vegetation connectivity to adjacent quadrats) (Table 1). We assessed vegetation cover, at four different height classes to account for understory and canopy cover: vegetation cover at < 10 cm; vegetation cover at [10–50 cm[; vegetation cover at [50–150 cm[; vegetation cover at > 150 cm. Vegetation cover was recorded at each height class in five percentage classes: class 0: 0%; class 1:]0–25%[; class 2: [25–50%[; class 3: [50–75%[; class 4: [75–100%]. We divided the 100 m^2 quadrat into four equal parts to assess vegetation connectivity to adjacent quadrats (i.e. connectivity between trees and shrubs from one quadrat to the next) according to five classes (similar to vegetation cover classes): class 0: no connections; class 1: connectivity in 1/4 quadrat; class 2: connectivity in 2/4 quadrat; 3: connectivity in 3/4 quadrat; class 4: connectivity in 4/4 quadrat.

Data analysis

Drivers of the frequency of microhabitat use

Capture–recapture data for *Graphiurus murinus* collected during the 3840 trap-nights were merged per trap per season totalizing 768 occasions (192 traps × 4 seasons). We used the total number of captures per trap per season as response variable to analyse *G. murinus* frequency of microhabitat use. We considered the trap station and the surrounding 100 m^2 quadrat as a proxy for microhabitat (adapted from Morris 1987; Brehm and Mortelliti 2021). We grouped 17 drivers (explanatory variables) into five "functional" groups according to their expected influence on *G. murinus*. We analysed the effects of those five "functional" groups on the number of captures per trap: (1) "season"; (2) individual traits ("age", "sex" and "weight"); (3) residency status ("days" and "neighbours"); (4) connectivity ("vegetation connectivity", "distance from nearest forest edge" and "distance from main road"); (5) vegetation structure and cover ("type and position", "tree and bush species", "vegetation cover at < 10 cm", "vegetation cover at [10–50 cm[", "vegetation cover at [50–150 cm[", "vegetation cover at > 150 cm", and

Table 1 Response variable, random effects and explanatory variables used in the analysis of (1) drivers of the frequency of microhabitat use and of (2) microhabitat selection by woodland dormice *Graphiurus murinus*. "na" stands for not applicable

Variable	Definition	Type	Units
Response variable (1)			
Captures (1)	number of captures	discrete	[0, 4]
Random effects(1)			
Trap (1)	trap identification	nominal	na
Vegetation connectivity [a] (1,2)	vegetation connectivity to adjacent quadrats (class 0: 0%; class 1:]0–25%[; class 2: [25–50%[; class 3: [50–75%[; class 4: [75–100%])	ordinal[a]	(%)[a]
Explanatory variables(1,2)			
Season(1)			
Season	winter; spring; summer; autumn	nominal	na
Individual traits(1)			
Age	adult/juvenile (1/0)	binary	(1/0)
Sex	only females; only males; both sexes; none	nominal	na
Weight	weight	continuous	(g)
Residency status(1)			
Days	average number of days since the first capture	continuous	na
Neighbours	average number of animals captured on neighbouring traps	continuous	na
Connectivity(1,2)			
Vegetation connectivity [a] (1,2)	vegetation connectivity to adjacent quadrats (class[b])	ordinal[a]	(%)[a]
Distance to nearest forest edge (1)	minimum distance from trap to limit of the riverine forest	continuous	(cm)
Distance to main road (1)	minimum distance from trap to road bisecting the riverine forest	continuous	(cm)
Vegetation structure and cover(1,2)			
Tree and bush species (1,2)	plant species at trap location (*Combretum caffrum*; *Gymnosporia heterophylla*; *Olea europaea*; *Rhus* spp.; *Vachellia karroo*; *Ziziphus mucronata*; other; none)	nominal	na
Type and position (1,2)	structural type and vertical position at trap location (canopy; trunk; log; bush; ground cover; ground open)	nominal	na
Vegetation cover at < 10 cm (1,2)	vegetation cover at < 10 cm (class[b])	ordinal[a]	(%)
Vegetation cover at [10–50 cm[(1,2)	vegetation cover at [10–50 cm[(class[b])	ordinal[a]	(%)
Vegetation cover at [50–150 cm[(1,2)	vegetation cover at [50–150 cm[(class[b])	ordinal[a]	(%)
Vegetation cover at > 150 cm (1,2)	vegetation cover at > 150 cm (class[b])	ordinal[a]	(%)

Each variable was assessed seasonally and either used (1) in the modelling procedures to assess the drivers of frequency of microhabitat use, (2) in the assessment of microhabitat selection or (1,2) in both parts of the analysis. [a] Vegetation cover and connectivity were estimated visually and used as classes (ordinal variable) for the modelling procedures to assess the drivers of frequency of microhabitat use, and as % values (discrete variable) to assess microhabitat selection. [b] Classes are the same as those shown for the variable "vegetation connectivity" in the random effects

"trap height"). Well-connected areas are more frequently used by small mammals (Galantinho et al. 2020). Therefore, we used two random effects—"trap identification" and "vegetation connectivity"—to account for possible correlations between observations. Variables and random effects are summarized in Table 1.

We modelled the effect of each variable group on the number of captures using generalized linear models (GLM) and generalized mixed models (GLMM) with a Poisson distribution. We followed Zuur et al. (2009) for model building and validation and Burnham and Anderson (2002) for model selection. Collinearity, autocorrelation, and dispersion were calculated for the full model of each variable group. Collinearity was assessed using the variation inflation factor (VIF) and variables were discarded whenever VIF > 3. Autocorrelation was evaluated using Moran's I. We calculated the

dispersion parameter (Φ) to assess the need for using other modelling methods (e.g., negative binomial or zero-inflated models) if Φ > 1.5.

The candidate model set for each group included all possible combinations of non-collinear variables. We used Akaike's Information Criterion corrected for small samples (AICc) to rank models within each group. Full models with random effects (GLMM) were discarded for each group whenever presenting convergence problems or a higher AICc than models without random effects (GLM). Details for random effects are only presented in the results section if included in the model procedure.

We proceeded with the analysis whenever the best model explained considerably more variation in the number of captures than the null model (ΔAICc > 4 between best model and null model). We used model averaging to estimate parameters and associated unconditional standard errors (SE) whenever a subset of competing models existed at ΔAICc < 4 from the best model. When model averaging was used, we report the relative importance of each variable (*w*+), i.e., the sum of Akaike weights (*w*) of all models of each set where the variable was included. Therefore, a variable's relative importance increases with its weight. However, we considered a variable to have low support if the 95% confidence interval for its estimate included zero. Additionally, we used Bonferroni's correction to assess differences among categories, accounting for multiple comparisons, whenever a categorical variable was considered to significantly affect the number of captures (Dalgaard 2002; Zuur et al. 2009). Bonferroni's correction is only presented in the results section whenever it does not support model interpretation. Detailed results for model building, selection, validation, autocorrelation, and Bonferroni's correction are presented as Online Resource 1.

Microhabitat selection

Habitat selection is the disproportionate use of habitat features considering their availability (Johnson 1980). Habitat selection studies with small mammals have focused on macrohabitat and/or microhabitat scales (e.g., Novillo et al. 2017; Brehm and Mortelliti 2021). We were interested in microhabitat selection within the home range of the animals. We evaluated microhabitat features at each capture location and compared them with what was available at the neighbouring traps. We considered the median distance between two consecutive capture locations (captures of the same animal on consecutive days) across all animals to determine the neighbouring traps of each capture location. Moreover, for each capture location, we only evaluated microhabitat features of neighbouring traps that did not capture *Graphiurus murinus*.

We evaluated the selection of eight variables used to characterise microhabitat struture: "type and position", "tree and bush species", "vegetation cover at < 10 cm", "vegetation cover at [10–50 cm[", "vegetation cover at [50–150 cm[", "vegetation cover at > 150 cm", "trap height", and "vegetation connectivity". "Type and position" and "tree and bush species" were used as categorical variables and their selection were assessed by the number of times a capture was included in a class that was the same or different from the most frequent class in the neighbourhood. To identify which classes were selected, we used the One-proportion Z-test (when more than 10 observations in both classes) and the Exact Test of Goodness of Fit (when less than 10 observations in a class) to assess if the number of captures in the different class was significantly higher than in the same class. We calculated the selection for the remaining six variables according to the formula (Eq. (1) adapted from Brehm and Mortelliti 2021):

$$Selection\ of\ X\ = \frac{X_{l_i} - \bar{X}_{n_i}}{sd\ (X_{n_i})} \quad (1)$$

where X is one of the six variables studied, X_{l_i} is the value of X at the capture location i, and $\bar{X}_{n_i}$ and $sd\ (X_{n_i})$ are the mean value and the standard deviation, respectively, of variable X at the available neighbourhood traps of the capture location i. Thus, a positive selection value means that the value of the variable at the place of capture is greater than at its neighbourhood, i.e., *G. murinus* have selected higher values of that variable (negative selection values mean the opposite). We used the Wilcoxon signed-rank test to determine if the value for each variable at the capture location was significantly higher (positive selection) or lower (negative selection) than its mean value at neighbourhood traps.

Statistical analyses were conducted in R version 4.0.1 (R Core Team 2020). GLMM and GLM were implemented using function "glmer" from package "lme4" version 1.1–23 (Bates et al. 2015) and function "glm" from package "stats" version 4.0.1 (R Core Team 2020), respectively. We assessed collinearity using function "vif" from package "car" version 3.0–8 (Fox and Weisberg 2019) and spatial autocorrelation using package "spdep" version 1.1–3.1 (Bivand and Wong 2018). We used package "MuMIn" version 1.43.17 to implement model averaging (Barton 2020). Functions "emmeans" and "pairs" from package "emmeans" version 1.11.2-8.2 were used to perform Bonferroni's correction (Lenth 2025). We used the function "binom.test" and the function "prop.test" from package "stats" version 4.0.1 (R Core Team 2020) for the Exact Test of Goodness of Fit and for the One-proportion Z-test, respectively. Function "wilcox.test" from package MASS version 7.3–51.6 (Venables

and Ripley 2002) in R was used to compute the Wilcoxon signed-rank test. We considered all differences significant whenever $P \leq 0.05$.

Results

During 3840 trap-nights, we captured 27 different individuals of *Graphiurus murinus* on 110 capture occasions. We captured 18 males (nine adults, nine juveniles) and nine females (five adults, three juveniles, one as a juvenile and later as an adult). Animals were captured on average four times (4.07 ± 3.30; mean ± SD) by 32.29% of all traps. However, only one animal was captured more than once in the same trap in the same season. The median distance travelled on consecutive nights was 25.47 m ($n = 98$; range: 0–75.06 m).

Drivers of the frequency of microhabitat use

Although most captures of *Graphiurus murinus* occurred in summer (3.64% in winter, 19.09% in spring, 40.91% in summer and 36,36% in autumn), this season's effect on capture rate was similar to that of spring and autumn but significantly higher than that of winter (Table 2). Winter was associated with a significant decrease of 85.61% in capture rate when compared to autumn (Table 2).

Our model for the individual traits group suggested that the number of captures decreased significantly when only females (51.62% less) or only males (50.98% less) were captured compared to captures of both sexes in the same trap during each season (Table 2). Captures of both sexes included also both age groups (adults and juveniles) on 62.50% occasions, while capturing only juveniles or only adults occurred on 18.75% occasions (for each age group). Age was discarded from model building to ensure models for the individual traits group had no collinearity problems (VIF < 3, Online Resource 1, Table 1.5). The positive effect of weight on the number of captures had a low support on the averaged model (95% CI for estimates included zero; Table 2).

Each additional day an animal spent in the area and each additional neighbour were associated with an increase in capture numbers per trap of 0.75% and 43.17%, respectively (Table 2).

Vegetation connectivity above 50% between the capture site and adjacent sites significantly increased capture numbers, while the effect of vegetation connectivity below

Table 2 Models of the estimated effects on the number of captures of woodland dormice *Graphiurus murinus* of "Season" (GLMM; "vegetation connectivity" as random effect; "autumn" as reference category for "season"), "Individual traits" (averaged GLM; "both" as reference category for "sex"), "Residency status" (GLM) and "Connectivity" (averaged GLM; "0%" as reference category for "vegetation connectivity"). We show standard errors (SE) and 95% confidence intervals (CI) for each variable or category. The relative importance ($w+$) is shown for variables included in averaged models (otherwise "na" stands for not applicable). Estimates for explanatory variables whose 95% CI excluded zero are in bold. Exponent notation (a to b) means multiplication by: $a = 10^4$; $b = 10^3$; $c = 10^1$; $d = 10^{-1}$; $e = 10^{-2}$; $f = 10^{-3}$; $g = 10^{-4}$; $h = 10^{-5}$

	Estimate	SE	CI	$w+$
Season				
(Intercept)	−2.01	0.43	(−3.12, −1.06)	
Season				na
spring	−0.43	0.27	(−0.99, 0.10)	
summer	0.22	0.22	(−0.21, 0.66)	
winter	**−1.94**	**0.53**	**(−3.15, −1.01)**	
Individual traits				
(Intercept)	7.57^{d}	2.96^{d}	(1.76^{d}, 1.34)	
Sex				**1.00**
female	$\mathbf{-7.26^{d}}$	$\mathbf{2.51^{d}}$	**(−1.22, −2.34[d])**	
male	$\mathbf{-7.13^{d}}$	$\mathbf{2.30^{d}}$	**(−1.17, −2.61[d])**	
none	-2.61^{c}	7.27^{b}	(-1.43^{a}, 1.42^{a})	
Weight (g)	3.63^{h}	8.07^{f}	(-3.06^{e}, 3.08^{e})	0.27
Residency status				
(Intercept)	−2.69	0.16	(−3.03, −2.38)	
Days	$\mathbf{7.46^{f}}$	$\mathbf{6.30^{g}}$	**(6.21^{f}, 8.69^{f})**	na
Neighbours	**0.36**	**0.12**	**(0.12, 0.59)**	na
Connectivity				
(Intercept)	−3.75	0.47	(−4.67, −2.83)	
Vegetation connectivity				**1.00**
]0–25%[	−0.36	0.82	(−1.97, 1.24)	
[25–50%[	**1.27**	**0.46**	**(0.37, 2.17)[§]**	
[50–75%[	**1.81**	**0.44**	**(0.95, 2.67)**	
[75–100%]	**2.35**	**0.44**	**(1.48, 3.22)**	
Distance to main road	2.20^{f}	2.26^{f}	(-3.79^{g}, 7.23^{f})	0.64
Distance to nearest forest edge	9.74^{f}	1.31^{e}	(-6.34^{f}, 4.38^{e})	0.52

[§] contrast with reference level non-significant (Bonferroni's correction, $z = -2.736$, $p > 0.05$)

25% did not have a strong support (95% CI includes zero; Table 2). Although the positive effect of vegetation connectivity in class [25–50%[had a strong support (95% CI exclude zero; Table 2), post-hoc Bonferroni's correction did not consider its effect as significantly different when compared to the absence of connectivity while accounting for multiple comparisons (class 0% vs. class [25–50%[, z = −2.736, $p > 0.05$, Online Resource 1, Table 1.8). Altogether, vegetation connectivity in classes [50–75%[and [75–100%] were associated with an increase on the number of captures of 508.47% and 947.04%, respectively (Table 2). The increase in the number of captures when increasing the distances to the nearest forest edge or to the main road did not have a strong support (both 95% CI included zero; Table 2).

The type of vegetation (and position) and its cover above 150 cm were the most important variables on model selection and averaging for the effects of vegetation structure and cover on the number of captures (Table 3; Online Resource 1, Table 1.4). Vegetation cover from 50 to 150 cm ($w+ = 0.66$) had more than half of the importance of both vegetation type (and position) ($w+ = 1.00$) and cover above 150 cm ($w+ = 1.00$). However, only the effect of "type and position" had significant support (95% CI did not include zero): "canopy" and "trunk" were associated with an increase of the number of captures of 413.24% and 331.99%, respectively, when compared to "ground open". Vegetation cover < 10 cm was not considered relevant (models including this variable are at ΔAICc > 4 from the best model; Online Resource 1, Table 1.4). "Tree and bush species" were discarded from model building to ensure models for the vegetation structure and cover group had no collinearity problems (VIF < 3).

Microhabitat selection

Graphiurus murinus selected higher and more connected traps where vegetation cover was greater above 50 cm and lower below 10 cm when compared with neighbouring traps (less than 25.47 m away). Those differences between capture locations and their neighbourhoods were significant for trap height (V = 4506, $P = 7.34^{-06}$), vegetation connectivity (V = 5041.5, $P = 6.35^{-11}$), vegetation cover < 10 cm (V = 2360.5, $P < 0.05$), vegetation cover 50–150 cm (V = 3303, $P < 0.05$), and vegetation cover above 150 cm (V = 4029.5, $P < 0.001$).

In 73.64% of all capture occasions, animals were trapped in a "tree or bush species" class different from the most frequent class in the neighbouring traps. Animals were mostly captured on *Combretum caffrum*, *Rhus* spp. and *Gymnosporia heterophylla* on 27.27%, 19.09% and 14.55% of the trapping occasions, respectively. *Combretum caffrum*, *Rhus* spp. and *G. heterophylla* were selected over the most common species in the neighbourhood on 46.67%, 85.71% and 93.75% of those trapping occasions (Fig. 2a; Online Resource 2, Table 2.1). For these three most used species, the differences between the occasions when the capture location was on a species similar or different from the most

Table 3 Model of the estimated effects on the number of captures of woodland dormice *Graphiurus murinus* of "Vegetation structure and cover" (averaged GLM). We show standard errors (SE), 95% confidence intervals (CI) and relative importance ($w+$) for each variable. Estimates for explanatory variables whose 95% CI excluded zero are in bold. The reference category is "ground open" for "type and position" and "0%" for each of the vegetation cover at each height

	Estimate	SE	CI	$w+$
(Intercept)	−18.16	662.38	(−1318.48, 1282.16)	
Type and position				**1.00**
bush	−0.21	0.85	(−1.88, 1.46)	
canopy	**1.64**	**0.51**	**(0.64, 2.63)**	
ground cover	0.58	0.62	(−0.63, 1.79)	
log	0.85	0.72	(−0.55, 2.26)	
trunk	**1.46**	**0.51**	**(0.46, 2.47)**	
Vegetation cover at > 150 cm				1.00
]0–25%[	13.75	662.37	(−1286.56, 1314.07)	
[25–50%[	13.52	662.37	(−1286.80, 1313.83)	
[50–75%[	14.19	662.37	(−1286.12, 1314.51)	
[75–100%]	15.05	662.37	(−1285.27, 1315.37)	
Vegetation cover at [50–150 cm[				0.66
]0–25%[	0.43	0.92	(−1.45, 2.76)	
[25–50%[	0.70	0.97	(−0.93, 3.07)	
[50–75%[	0.96	1.07	(−0.53, 3.44)	
[75–100%]	1.00	1.11	(−0.52, 3.56)	
Height (m)	−0.11	0.18	(−0.66, 0.15)	0.42
Vegetation cover at [10–50 cm[				0.12
]0–25%[	−0.07	0.26	(−1.54, 0.32)	
[25–50%[	−0.02	0.15	(−0.97, 0.62)	
[50–75%[	−0.07	0.25	(−1.44, 0.24)	
[75–100%]	−0.08	0.26	(−1.47, 0.13)	

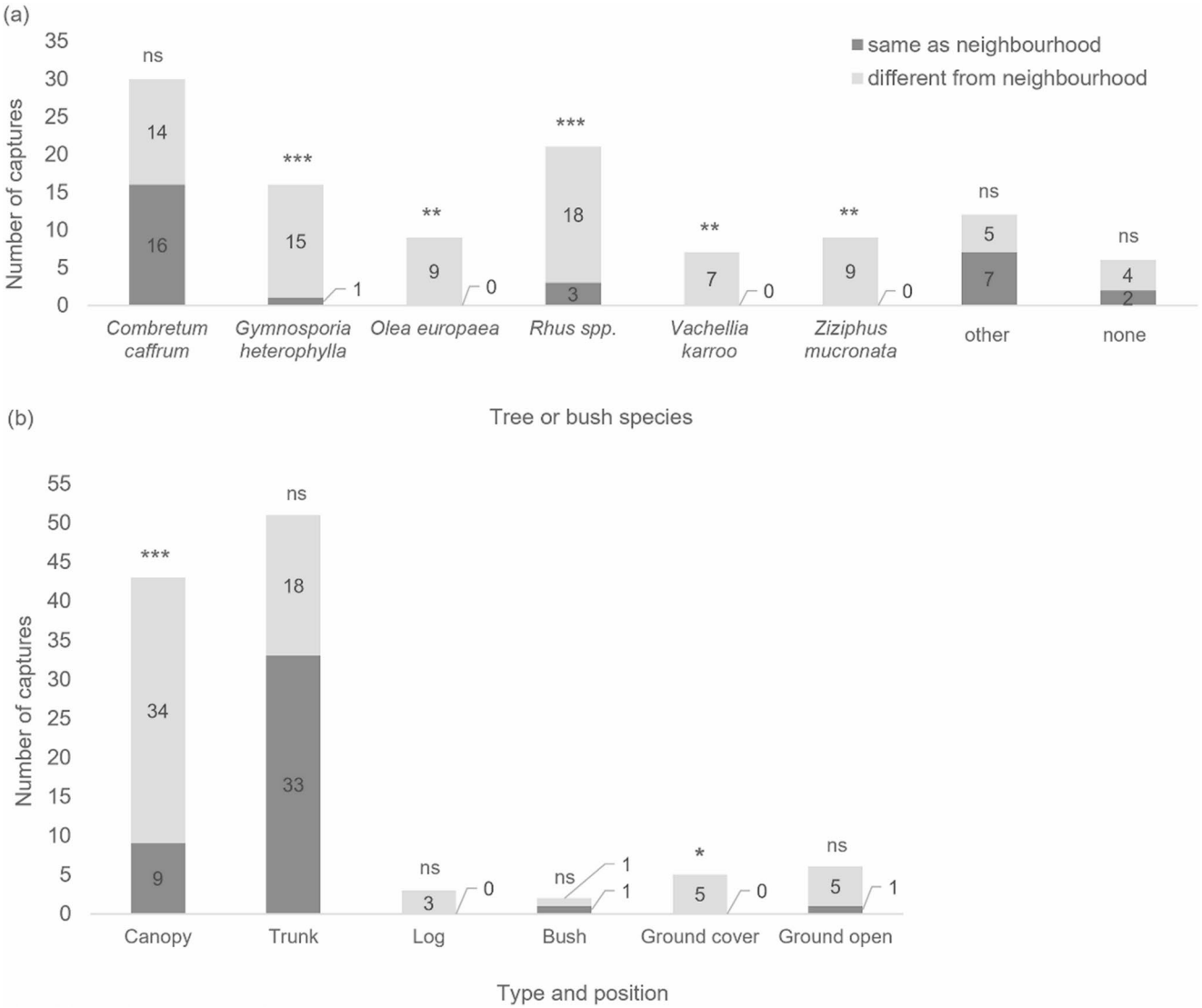


Fig. 2 Selection of (**a**) tree or bush species and (**b**) type and position by woodland dormice *Graphiurus murinus* during their nocturnal activity periods. Each bar represents the number of captures per (**a**) plant species or (**b**) type and position class. Bars account for the number of occasions that each class at the capture location was the "same" as (dark grey) or "different" from (light drey) the most frequent class (mode) at the neighbourhood traps (less than 25.47 m away from capture location). Significance levels refer to Exact Test of Goodness of Fit or One-proportion Z-test results assessing if the number of captures in the "different" class was significantly higher than in the "same" class. Significance levels are shown on top of each stacked bar as: (ns) non-significant; (*) $P<0.05$; (**) $P<0.01$; (***); $P<0.001$

frequent one in the neighbourhood was only significant for *Rhus* spp. ($P<0.001$) and for *G. heterophylla* ($P<0.001$) (Fig. 2a).

Animals were caught in traps located in a "type and position" different from the most frequent class in the neighbourhood on 60% of all captures. Animals were mostly captured in "trunk" and "canopy" on 46.36% and 39.09% of capture occasions, respectively. "Trunk" and "canopy" were selected over the most common structures in the neighbourhood on 16.36% and 30.91% of those trapping occasions (Fig. 2b; Online Resource 2, Table 2.2). For these two most used classes, captures on a different class of "type or position" from the most frequent one in the neighbourhood were significantly higher than in the same class only for "canopy" ($P<0.001$) (Fig. 2a).

Discussion

In riverine *Combretum* forests, *Graphiurus murinus* tended to use less microhabitats in winter and where only same-sex individuals were present. Conversely, this species used more microhabitats with a higher number of neighbours and that are used by animals with longer residency times. *Graphiurus*

murinus used more well-connected microhabitats (sampling quadrats), trunks and canopies. They favoured higher, denser and more connected vegetation cover. *Graphiurus murinus* predominantly utilized *Combretum caffrum*, *Rhus* spp., and *Gymnosporia heterophylla*, with a preference for the latter two tree species when compared with what is available in the neighbourhood. These findings corroborate our hypotheses that season, individual traits, residency status, habitat connectivity, and vegetation structure and cover influence this species' microhabitat choice.

Drivers of the frequency of microhabitat use

Graphiurus murinus were significantly less captured during winter, likely due to their torpor bouts lasting up to 8 days under cold weather (Mzilikazi et al. 2012). Although a previous study found all *G. murinus* torpid in nest boxes during winter (Mzilikazi et al. 2012), younger animals tend to move between torpor bouts and could therefore be captured in this study. In winter, *Muscardinus avellanarius* can undergo torpor bouts of up to 30 days (Holden-Musser et al. 2016) and change hibernacula multiple times (Gubert et al. 2023). Captures increasing during the other seasons aligns with *G. murinus* breeding season, from mid-spring to summer, resulting in the recruitment of juveniles, particularly in summer (Madikiza et al. 2019). During the breeding season, males increase their movements in search of receptive females, who become receptive asynchronously (Madikiza et al. 2011). Increased foraging efforts in search of food and hibernacula in preparation for winter torpor may also account for the higher number of captures observed during autumn (Mzilikazi et al. 2012; Gubert et al. 2023).

Microhabitats where only same-sex individuals were present, were used significantly less by *G. murinus* suggesting that they could be searching for a sexual partner (Ruf and Bieber 2020). However, 62.5% of the occasions when both sexes were captured involved adults and juveniles. Juvenile *G. murinus* often remain with their mothers long after weaning (Madikiza and Do Linh San 2020), likely increasing protection against predators and learning opportunities. Juveniles of other dormice species may also share sleeping sites with adult females (e.g., Eurasian forest dormouse *Dryomys nitedula*; Juškaitis and Keturka 2017) and with adult males (e.g., *Glis glis*, Ruf and Bieber 2020). Sleeping associations may mean that animals can move as a group in search of sleeping sites. In fact, *D. nitedula* can change sleeping sites together during the day (Juškaitis and Keturka 2017). Additionally, *G. murinus* used significantly more microhabitats with a higher number of neighbours. *Graphiurus murinus* demonstrates high tolerance and home range overlap among individuals, likely reflecting a promiscuous mating system (Madikiza et al. 2011) similar to *M. avellanarius* (Juškaitis et al. 2020). The abundant food and nesting sites in the riverine *Combretum* forest may also allow females to have a clumped distribution (Madikiza et al. 2011). Dormice females can indeed tolerate the close presence of other females as suggested by the documented nest sharing among breeding females in *Eliomys quercinus* (European garden dormouse; Viñals et al. 2017), D. *nitedula* (Juškaitis and Keturka 2017), and *G. glis* (Pilastro et al. 1996). Additionally, resident *G. murinus* females maintain nest sites and may reproduce twice a year (Madikiza et al. 2019). Altogether, animals that remain in the area for longer periods may enhance their number of social connections (e.g., dyadic sleeping associations, Madikiza 2017), which is reflected in the higher use of microhabitats with a higher number of neighbours. Therefore, social connections may account for *G. murinus* using significantly more microhabitats used by animals with longer residency time.

Microhabitats with vegetation connectivity above 50% were significantly more used, likely because *G. murinus* are semi-arboreal and are only rarely captured on the ground (Madikiza et al. 2010a; Richard et al. 2022). These findings suggest that *G. murinus* dispersal ability may be hampered where vegetation connectivity is lower than 50% what may compromise population persistence. In fact, although the most arboreal dormice species use the ground to some extent, they have a limited dispersal ability (e.g., *M. avellanarius*, Dietz et al. 2018). Forest connectivity and adequate habitat diversity are crucial for the presence of *M. avellanarius* (Dietz et al. 2018). Genetic studies show that *G. glis* populations are more isolated and unstable in smaller patches compared to continuous forests (Moska et al. 2023). Therefore, vegetation connectivity facilitates daily foraging and dispersal, thus ensuring the long-term viability of dormice populations.

The presence of trunks or canopies significantly increased microhabitat use by *G. murinus*. Arboreal and semi-arboreal dormice have morphological and physiological adaptations for climbing trunks and moving along thinner branches of canopies (Holden-Musser et al. 2016). *Graphiurus murinus* manoeuvrability and the high availability of tree hollows may account for its absence in Cape genet *Genetta tigrina* diet in our study area (Plaatjie et al. 2024). Conversely, *G. murinus* was one of the most frequent small mammal prey for *G. tigrina* in a coastal habitat (Roberts et al. 2007) where tree hollows are less frequent. Additionally, other dormice species commonly use tree hollows as nests (Holden-Musser et al. 2016). *Muscardinus avellanarius* spends most of its time in trees and only uses ground nests during hibernation (Gubert et al. 2022). The Japanese dormouse *Glirulus japonicus* frequently uses tree hollows and only rarely resorts to underground nests (Shibata et al. 2004). In our study area, *G. murinus* resting sites were predominantly

located in hollow trunks and branches of *C. caffrum* trees, with only one (out of 183 resting sites) located underground (Lamani 2011).

Microhabitat selection

Graphiurus murinus significantly selected microhabitats with higher vegetation and connectivity, as well as those featuring "canopy". This finding at the fine scale aligns with studies that show that forest connectivity at larger scales is a major preditor of the presence of other dormice species contributing to their persistence (*Muscardinus avellanarius*, Dietz et al. 2018; *Glis glis*, Moska et al. 2023). *Graphiurus murinus* showed a significant preference for microhabitats with higher and denser vegetation cover above 50 cm, while selecting areas with less vegetation cover below 10 cm. In a miombo forest, *G. murinus* were more frequently captured in mature woodlands with over 30% canopy cover and open understory vegetation (Fitzherbert et al. 2007). In our study area, out of all traps with 75–100% cover above 150 cm, 27.92% had 0% cover below 10 cm, while 29.44% had 75–100% cover. Thus, *G. murinus* may select safer microhabitats above, from where they can observe potential predators (e.g., small carnivores and snakes; Roberts et al. 2007; Holden 2013) below, rather than selecting microhabitats with dense vegetation cover at all heights. However, the effect of ground vegetation cover might vary depending on the landscape context and among different dormice species. For instance, *G. murinus* were only found in fallow fields before cattle disturbance (Mayamba et al. 2019). These fallow fields, surrounded by cultivated land, resembled natural forests with dense ground vegetation cover before being disturbed by cattle (Mayamba et al. 2019). Although height and vegetation cover were significantly more selected, they did not strongly influence microhabitat use. Therefore, *G. murinus* selected microhabitats with greater heights and vegetation cover than what was generally available, but their frequency of use depended on other factors previously described. Specifically, canopies may be selected and frequently used regardless of their height and vegetation cover (Table 3). *Glis glis* also selects forest areas with higher trees and denser canopies and understory (Milazzo et al. 2003). Altough *Eliomys quercinus* may be less arboreal than most dormice (Holden-Musser et al. 2016), it rarely uses forest paths without tree cover or understory (Erhardt et al. 2025). Nevertheless *Muscardinus avellanarius* selects areas of forest with well-lit understory because shrubs and trees provide food at different times in the year (Bright and Morris 1996).

Graphiurus murinus were predominantly captured on *Combretum caffrum*, *Rhus* spp., and *Gymnosporia heterophylla*, significantly selecting the latter two species. At our study site, these three species have arboreal structures, and *C. caffrum* typically has holes and hollow trunks used as nesting sites by *G. murinus* (Madikiza et al. 2010b). The dominance of *C. caffrum* in our study area likely accounts for the lack of significant selection for this species and for "trunk" when compared with its availability in the neighbourhood. *Gymnosporia heterophylla* and *Rhus* spp. are less common and the former has a very structured and rough bark with several crevices which probably eases climbing and provides safe nest sites. *Graphiurus murinus* can also use *Rhus* spp. as resting sites (Lamani 2011). Many dormice species select tree holes as nests sites (Holden-Musser et al. 2016). However, *Muscardinus avellanarius*, though also spending most of their time in trees, choose shallow nests in the ground during the hibernation period (Gubert et al. 2022, 2023). *Eliomys quercinus* can use nests in tree cavities (Holden-Musser et al. 2016) but also selects nests among rocks under the ground of forests (Bertolino and Cordero di Montemozolo 2007).

Strengths, limitations and future research

We assessed microhabitat use and selection by *Graphiurus murinus* in a single study site, which may limit the scope of our inferences and recommendations due to potential pseudoreplication. Nonetheless, results accounting for pseudoreplication should not be disregarded (Davies and Gray 2015). We employed 192 traps, considered spatial autocorrelation (microhabitat use analysis) and discarded neighbourhood traps that captured *G. murinus* (microhabitat selection analysis). Overall, our findings provide scientific evidence that can be adapted for managing similar species and habitats. Additionally, our study serves as a baseline for population monitoring in the event of future habitat changes.

Telemetry could have been more suitable for assessing additional microhabitats used by each animal inside and outside the riverine forest. Nevertheless, capture–mark–recapture allowed us to gather data on more animals over a longer period and at a lower cost than telemetry (Gomez et al. 2011). This method has been successfully used in microhabitat studies with small mammals (e.g., Brehm and Mortelliti 2021; Galantinho et al. 2020, 2022). However, our data were not robust enough to further assess differences in habitat selection among individuals. These individual differences may impact the species' ability to adapt to new circumstances (Northrup et al. 2022), such as habitat fragmentation and climate change. Therefore, future studies should be conducted in areas with varying landscapes and climates to assess differences in microhabitat use and selection. Such studies should consider using telemetry and dataloggers to measure temperature, humidity, and rainfall. This knowledge would guide management to ensure microhabitat availability and, consequently, species persistence.

Management recommendations

Our findings provide guidelines for management aiming for the conservation of arboreal dormice and riverine forests.

Currently, *G. murinus* is classified as Least Concern, so our recommendations will depend on the management goals for a specific area. In protected areas, at riverine forests (1) vegetation gaps larger than 50% per 100 m² must be prevented; (2) taller and older trees with hollow trunks and vegetation cover especially above 150 cm must be maintained. Additionally, we recommend keeping the riverine forest's width above 50 m (minimum width at our study site), where the terrain permits, by planting tree species that are significantly used or selected by *G. murinus*: *Combretum caffrum*, *Gymnosporia heterophylla*, and *Rhus* spp. Concurrently, *G. murinus* populations should be monitored to adjust management practices in the event of major habitat alterations (death of trees due to water scarcity or to the planned reintroduction of elephants; Gaylard et al. 2021).

Conclusions

Vegetation, season, individual traits, and residency status significantly influence the microhabitat choices of *Graphiurus murinus*. Riverine *Combretum* forests and dormice populations should be closely monitored, to ensure their maintenance (e.g., planting selected trees). Management for *G. murinus* conservation will be particularly relevant to balance alterations in vegetation structure and cover due to the introduction of large herbivores (e.g., elephants) or to climate changes. Our recommendations are crucial for the persistence of arboreal and semi-arboreal small rodents, and possibly for some small carnivores, which are mostly associated to riverine *Combretum* forests in our study area (e.g., *Genetta tigrina*; Carvalho et al. 2024b), and should be applied to similar areas.

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Data availability The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Materials and Code availability Not applicable.

Declarations

Ethics approval Our handling procedures were approved by the Ethics Committee of the University of Fort Hare (Ethical clearance Nr SAN051SGEB02).

Consent to participate Not applicable.

Competing interests The authors declare no competing interests.

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