



**HAL**  
open science

# Lodge-building in rodents: relationships with ecological and natural history factors

J. Qiu, C. Schradin

► **To cite this version:**

J. Qiu, C. Schradin. Lodge-building in rodents: relationships with ecological and natural history factors. *Journal of Zoology*, 2024, 324 (2), pp.177-186. 10.1111/jzo.13207 . hal-04833522

**HAL Id: hal-04833522**

**<https://cnrs.hal.science/hal-04833522v1>**

Submitted on 12 Dec 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Lodge-building in rodents: relationships with**  
2 **ecological and natural history factors**

3

4 Qiu, J.<sup>1,2</sup> & Schradin, C.<sup>1,2</sup>

5

6 <sup>1</sup>School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, South Africa.

7 <sup>2</sup> Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

8

9 **PUBLISHED AS**

10 Qiu, J. & C. Schradin (2024) Lodge-building in rodents: relationships with ecological and  
11 natural history factors. *Journal of Zoology*, **324**, 177.

12

13

14 Short title:

15 **Ecological and natural history of lodge-building**

16 **rodents**

17

18

19 **Abstract**

20 Mouse-like rodents often take cover in natural shelters or burrow underground where they build  
21 simple nests. A few species build extensive shelters above ground, called lodges, mounds or  
22 houses. Here we present the first phylogenetically controlled comparative study on the  
23 ecological factors of habitat heterogeneity, environmental aridity and fire risk related to nesting  
24 habits in mouse-like rodents (Myomorpha, 326 genera). 20 species from 7 genera were found  
25 to build lodges, and they mainly occur in arid environments with low fire risk. Most lodge-  
26 building species (14 out of 20) belong to the packrats (genus *Neotoma*), which in phylogeny  
27 only represent one event of evolution of lodge building and therefore limit the statistical power  
28 of the phylogenetically controlled analysis. The Bayesian phylogenetic mixed-effects models  
29 show a phylogenetic signal of 0.43 for 515 Myomorpha species. Under this moderate to strong  
30 phylogenetic relatedness, we did not find specific factors being associated to the evolution of  
31 sheltering habit in Myomorpha. We suggest studying the importance of aridity combined with  
32 low fire risk for lodge building on the species level, for example by studying the limits of  
33 species distribution ranges depending on these factors.

34

35 **Keywords:**

36 Myomorpha; lodge; shelter; phylogenetic; aridity; fire

37

## 38 **Introduction**

39 Many animals construct external structures as an adaptation against the harshness of the local  
40 environment. Such structures extend beyond the individuals' body and are thus one example  
41 of extended phenotypes (Dawkins, 2016; Woods et al., 2021). Eusocial insects such as termites,  
42 ants and bees build nests that offer protection for hundreds to millions of individuals (Lüscher,  
43 1961; Korb, 2003; Hölldobler & Wilson, 2009), many fish and bird species construct nests  
44 during the breeding season to incubate and raise their offspring (Barber, 2013). Among  
45 mammals, apes build leaf nests for sleeping (Prasetyo et al., 2009), bears prepare dens for  
46 hibernation (Diedrich, 2011), and rodents are famous for constructing burrow systems (Kinlaw,  
47 1999, Hayes, Chesh & Ebensperger, 2007). The protective nature of external structures could  
48 be especially important for small animals as they often face high predation risk (Erlinge et al.,  
49 1983; Lima et al., 2001; Leahy et al., 2016, Deeming, 2023) and are prone to thermal stress  
50 (Blanckenhorn, 2000; Klockmann, Günter & Fischer, 2017).

51 As the largest order in mammals, rodents show a high diversity in ecological niches occupied  
52 and in shelter usage. Some use natural shelters such as tree holes and rock crevices, in which  
53 they build simple nests, or create their own architecture, most commonly underground burrows  
54 (Frank & Layne, 1992, Zhang, Zhang & Liu, 2003, Hayes, Chesh & Ebensperger, 2007), or/and  
55 relatively rare aboveground shelters (Whitford & Steinberger, 2010). Burrows offer protection  
56 for their nest, and for some species below ground foraging opportunities (Kinlaw, 1999, Zhang,  
57 Zhang & Liu, 2003). Fewer species build shelters above ground, which are called houses  
58 (Birkenholz, 1963), middens (Campos, Boeing & Throop, 2019) or lodges (Vermeulen, 1988,  
59 Wolhuter et al., 2022). Lodge building in rodents is rare and could represent an adaptation to  
60 specific environments.

61 Lodges are structures built above ground, usually made of plant material, offering protection  
62 for the nest which lays inside (Jackso et al., 2002). Beavers (*Castor spp.*) are famous for  
63 building extensive lodges inside ponds they create with beaver dams (Baker & Hill, 2003).  
64 North American packrats (*Neotoma spp.*) use urine, plant and animal materials to build  
65 middens above ground, which are extremely sturdy and can last for thousands of years after  
66 being abandoned (Betancourt, Devender & Martin, 2021). Bush Karoo rats (*Otomys*  
67 *unisulcatus*) from South Africa and greater stick-nest rats (*Leporillus conditor*) from Australia  
68 build extensive stick lodges which offer protection against the arid and hot climate (Vermeulen  
69 et al., 1988; Copley, 1999; Moseby & Bice, 2004; Robinson, 1975). For small rodents, lodges

70 are energetically expensive to build but can offer protection for generations (Vermeulen & Nel,  
71 1988; Onley et al., 2022).

72 Specific climate conditions can make the investment of lodge building adaptive. For example,  
73 the temperature inside the lodges of bush Karoo rats from semi-deserts in South Africa varies  
74 less than ambient environment: the temperature inside is higher than outside in cold winter  
75 nights, and lower in hot summer days (Du Plessis, Kerley & Winter, 1992). Water vapor  
76 pressure inside lodges is 64-74% in summer and 56-83% in winter, both varies less and is  
77 always higher than in the outside arid environment (Du Plessis et al., 1992). If lodges generally  
78 offer a favourable micro-climate, they may be especially adaptive in environments with  
79 extreme temperatures and aridity. Lodges built in arid and hot habitats may offer protection  
80 against the harsh ambient conditions, but the high temperatures and lack of rainfall can create  
81 low fuel moisture in such habitats. The dry plant material used to build these lodges is highly  
82 flammable and therefore vulnerable to wildfires (Kerley & Erasmus, 1992, Jackson, Bennett &  
83 Spinks, 2004). If lodges burn, then instead of offering protection they might represent a deadly  
84 trap. This leads to the prediction that lodges occur mainly in arid environments with low fire  
85 risk.

86 Ecological factors and natural history shape evolution, but how they influence and interplay  
87 with the evolution of lodge-building behaviour is less clear. Ecological factors that can  
88 influence the evolution of lodge building include fire risk, aridity, and habitat heterogeneity.  
89 As sheltering habit may evolve as an adaptation to specific habitats, species that occur in  
90 multiple types of habitats may develop either a consistent sheltering habit that is universally  
91 adaptive to all the habitats they live in or the ability to show multiple sheltering habits  
92 depending on the local environment. Regarding natural history factors, the protective nature of  
93 lodges could be especially important for animals with small body sizes, as they are more  
94 sensitive to thermal stress (Blanckenhorn, 2000; Klockmann, Günter & Fischer, 2017), or  
95 alternatively, a larger body size may bring advantages in carrying building materials and in  
96 defending their precious lodges against competitors. Considering the overlap of food sources  
97 and building materials, plant-based diet can be expected to facilitate lodge building and  
98 maintenance, animals feeding on green plant materials may be more efficient in collecting  
99 sticks, and the food remains can contribute as building materials (Betancourt, Devender &  
100 Martin, 2021). Lodges may offer protection against the heat during the day for nocturnal  
101 species, or offer protection against predators for diurnal species (Betancourt, Devender &  
102 Martin, 2021). In sum, the natural history factors of body size, diet and activity pattern might

103 influence the evolution of lodge building. Despite these potential influences, how this distinct  
104 trait in sheltering habit may differentiate these lodge-building species from their relatives in  
105 ecological and natural history remains unknown.

106 We conducted a comparative study focusing on sheltering habits for mouse-like rodents  
107 (suborder Myomorpha) to determine what ecological and natural history factors were  
108 associated to lodge building. The extreme arid environment where the lodge building may be  
109 adaptive often associated with high climate fire risk, which puts the flammable lodges at risk.  
110 Specifically, we predicted that (1) lodge building is more common in arid environments as an  
111 adaption to highly variable or extreme ambient temperature/humidity and (2) lodge building is  
112 more common in areas with low fire risk.

113

## 114 **Methods**

### 115 *Database on shelter use*

116 We established a database on shelter use for mouse-like rodents (suborder Myomorpha). We  
117 searched for information of 1655 species of Myomorpha (classified by IUCN 2022) in the  
118 “*Handbook of the Mammals of the World. Vol. 7. Rodents II*” (Wilson et al., 2017) and found  
119 information on shelter use for 532 species (seven families, 201 genera). For 11 species, the  
120 description in the book was not clear enough to determine sheltering type (e.g., it was stated  
121 they use shelters without stating the type of shelter, or it was not stated whether they  
122 constructed shelters or used shelters constructed by other species), such that we searched for  
123 additional information online (publications, photos of the shelters), allowing us to add seven  
124 additional species into the database (included in the 532 species, for references see comment  
125 column in ESM S1). Shelter type was categorized as natural shelter (nests inside dense  
126 vegetation, rock crevices, tree holes, or shelters build by other species), burrows, and lodges  
127 (shelters above ground constructed by sticks and other materials). Because some species can  
128 use more than one types of shelter, we classified shelter use into seven categories: lodge,  
129 burrow, natural, lodge + burrow, lodge + natural, burrow + natural, lodge + burrow + natural.

### 130 *Natural history variables*

131 As important natural history variables that may affect preferred sheltering types and the ability  
132 of shelter construction (see introduction), we recorded body mass and length, diet and activity

133 patterns from the “*Handbook of the Mammals of the World. Vol. 7. Rodents II*” (Wilson et al.,  
134 2017). Habitat type was obtained from the species description in the IUCN Red List of  
135 Threatened Species. Habitat heterogeneity was then calculated as the total number of habitats  
136 occupied per species (Olivier et al., 2022, Qiu et al., 2022). Table 1 summarises the categories  
137 of these variables.

#### 138 *Aridity*

139 Aridity was estimated based on the Koppen-Geiger climate classification map (Beck et al.,  
140 2018), which presents global climate classification maps from 1980 to 2016. Based on  
141 threshold values and seasonality of monthly air temperature and precipitation, the Koppen-  
142 Geiger system classifies global climate into five main classes: tropical, arid, temperate, cold  
143 and polar (Beck et al, 2018). To focus on aridity, we coded the arid areas as one and non-arid  
144 areas as zero. By comparing this map with species distribution polygons, we could determine  
145 how much of the species distribution area falls into the arid climate classification. The levels  
146 of aridity for each species was then calculated by the percentage of arid area in each species  
147 distribution polygon, ranging from zero (no distribution in arid climate) to one (totally  
148 distributed in arid climate).

149 Species distribution information was obtained from the IUCN Red List of Threatened  
150 Species, based on definitions of presence, areas coded as “extant”, “probably extant”,  
151 “possibly extant” were considered as the distribution area of the species. From the 516  
152 species included in the phylogenetic model, the distribution of 12 species contained areas  
153 where the species were introduced (category “Extant & Introduced” in the IUCN). Only three  
154 species had considerable introduced area (Polynesian rat, *Rattus exulans*; House rat, *Rattus*  
155 *rattus*; Oriental house rat, *Rattus tanezumi*). ), We included these areas in this study because  
156 (1) the species would not be able to become resident in introduced area if they are not pre-  
157 adapted to the local environments and (2) origin and introduced area were sometimes difficult  
158 to distinguish, and natural dispersal may be involved, especially for globally spread species  
159 such as the house mouse (*Mus musculus*), for which the IUCN Red List of Threatened  
160 Species gives no information about their native origin.

#### 161 *Fire risk*

162 We were interested to know if species building lodges do not occur in areas that frequently  
163 burnt (high fire risk). Thus, we calculated fire risk by the proportion of historically burnt area

164 in this study. The data was produced by a data mining process using MODIS burnt area  
165 product Collection 6 (MCD64A1, <https://lpdaac.usgs.gov/products/mcd64a1v006/>). The  
166 entire product is available under the umbrella of the Global Wildfire Information System  
167 (GWIS, Boschetti et al, 2022), which provides numerous data services to report and forecast  
168 the global activity of wildfire. With this global burnt area map, we used all data available  
169 from 2001 to 2020, information was given by tile (smallest special unit that sum up the fire  
170 event and burnt area of each fire, 0.25\*0.25 degree). Burnt area was acquired daily with  
171 accuracy of one hectare, overlapping in the same area was counted separately (see Artés et al.  
172 2019 for more details).

173 By comparing the species distribution ranges with this fire dataset, we were able to obtain the  
174 cumulated burnt area from 2001 to 2020 (km<sup>2</sup>, cumulated data of 20 years) in each species  
175 distribution range. Specifically, for each species, the tiles from the fire map that had its  
176 centroid intersect located within the species distribution polygon were selected to add up to  
177 the burnt area, multiple fires events from the same tile of the 20 years were included. This  
178 value was then divided by species distribution range (km<sup>2</sup>) to get a comparable fire risk  
179 between species. (see ESM S2 for detailed calculation).

#### 180 *Statistical analysis*

181 Phylogenetic comparative analyses were conducted in R v.3.6.1, using the R packages brms  
182 (Bürkner. 2017; Bürkner. 2018), RStan (Stan Development Team. 2020) and Rethinking  
183 (McElreath. 2020). The modelling and R code were adapted from Jaeggi et al 2020 and Qiu et  
184 al 2022. Habitat heterogeneity, aridity and fire risk were included in the Bayesian phylogenetic  
185 mixed-effects model to estimate whether they have an influence on the evolution of shelter use.  
186 Aridity was weakly correlated with fire risk (Pearson's  $r = -0.02$ ), we therefore included them  
187 as independent variables in the model. We conducted an alternative model to test for the  
188 potential interaction between aridity and fire risk, which did not give any significance  
189 differences; therefore, we excluded the interaction from the main model. The phylogenetic  
190 relationships and their uncertainty were represented by a sample of 100 phylogenetic trees,  
191 downloaded from the phylogeny subsets of online database VertLife  
192 (<http://vertlife.org/phylosubsets/>), which produce distributions of trees with subsets of taxa  
193 (Jetz et al., 2012.) Phylogenetic signal ( $\lambda$ ) was calculated as the proportion of random factors  
194 variance captured by the phylogenetic random effects, representing the tendency of related  
195 species to resemble each other more than species drawn at random from the same tree. The



196 model employs a categorical error distribution, fitted with two Markov Chain Monte Carlo  
197 (MCMC) chains, undergoing a total of 2000 iterations each, with the first 1000 iterations in  
198 each chain designated as burn-in to allow for parameter convergence. The shelter categories  
199 were combined to simplify the model and increase statistical power: For, the main analysis, we  
200 used three categories: natural shelter (natural), burrows (burrow, burrows + natural) and lodge  
201 (lodge, lodge + burrow, lodge + natural). As some lodge-building species also dig burrows, we  
202 ran an additional phylogenetic analysis with four categories: natural shelter (natural), burrows  
203 (burrow, burrows + natural), lodge (lodge, lodge + natural), burrow + lodge.

204

## 205 **Results**

### 206 *Shelter usage*

207 Out of the 532 species of Myomorpha with available data, 145 species use natural shelters, 320  
208 species dig burrows and 14 species construct lodges, with the remaining 53 species having  
209 more than one form of shelter use: 47 species use natural shelters and dig burrows, one species  
210 construct lodges and use natural shelters, five species construct lodges and dig burrows. No  
211 species use three types of shelters at the same time, reducing the shelter usage categories to six  
212 for statistical analysis (Fig. 1). In total we found 20 species that build lodges. Of these, three  
213 species (Round-tailed muskrat, *Neofiber alleni*; Common muskrat, *Ondatra zibethicus*; Water  
214 mouse, *Xeromys myoides*) are semi-aquatic and construct lodges upon or nearby water, the  
215 other 17 species are terrestrial and construct dry lodges on the ground (for species details see  
216 ESM S1). 14 of 20 lodge building species belongs to the packrat (*Neotoma*), a lodge-building  
217 genus. One exception in this genus is *N. mexicana*, which generally does not build lodges and  
218 was thus recorded as non-lodge building in our data source. However, it's important to note  
219 that they can use lodges build by other species and were reported to be capable of building  
220 lodges inside natural shelters such as rock cracks (Cornely & Baker, 1986).

### 221 *Description of natural history and ecological factors*

222 The majority species were herbivorous, and this was more pronounced in lodge-building  
223 species (ESM Fig S3.1; lodge 89%, burrow 54%, natural 56%). Most species were nocturnal  
224 independent of shelter use (ESM Fig S3.2). The most common habitat was forest (270 species),  
225 followed by shrubland (240 species), grassland (216 species) and artificial (191 species). Mean  
226 habitat heterogeneity was two and did not differ between the species with different sheltering

227 habit (ESM Fig S3.3). Lodge-building species had a lower body length/mass ratio than others  
228 (ESM Table S3; lodge:  $1.2 \pm 1.07$ ; burrow  $2.4 \pm 1.5$ ; natural  $2.2 \pm 1.39$ ).

229 The mean aridity of lodge-building species was higher than species that dig burrows or live in  
230 natural shelters (lodge:  $0.566 \pm 0.416$ ; burrow:  $0.426 \pm 0.406$ ; natural:  $0.158 \pm 0.260$ ; Fig. 2,  
231 ESM Table S3). Fire risk was lowest where lodge-builders occur (lodge:  $0.210 \pm 0.324$ ,  
232 burrow:  $0.725 \pm 2.231$ ; natural:  $0.720 \pm 1.345$ ; Fig. 2, ESM Table S3).

### 233 *Phylogenetic comparative analyses*

234 The phylogenetic signal ( $\lambda=0.43$ ) was moderate to high for the 515 Myomorpha species in the  
235 model. Phylogenetic distribution showed six independent evolutionary origins of lodge  
236 building behaviour (Fig. 3). In the phylogenetically controlled analysis the associations of  
237 lodge building with ecological factors (habitat heterogeneity, aridity and fire risk) were non-  
238 significant (Fig. 4). The additional model with 4 categories gave similar results (ESM Fig. S4).

239

## 240 **Discussion**

241 We studied whether lodge building rodents occur especially in harsh arid areas with low fire  
242 risk, which would benefit them with a mild micro-climate within the lodge without the risk that  
243 their lodge becomes a deadly burning trap. Our descriptive results correspond with this  
244 hypothesis: lodge building species occur in arid areas with low fire risk. Lodge building is a  
245 conspicuous behaviour, but worldwide only 20 myomorph rodent species (4% of studied  
246 species) have been reported to build lodges. However, when controlling for phylogeny, neither  
247 aridity nor fire severity remained as a significant predictor for the evolution of lodge building.  
248 This is probably due to the fact that most lodge species belong to one single genus, the packrats  
249 (*Neotoma* spp.), reducing the number of independent evolutionary origins to only six. Two  
250 evolutionary pathways for lodge building did not associate with low aridity, which were species  
251 building lodges nearby water, as is also known for several species of another rodent suborder,  
252 the Castorimorpha (Beavers, Baker & Hill, 2003).

253 Wildfires directly threaten the survival of a variety of animals (Jolly et al., 2022). Small  
254 mammals cannot run away from wildfires but seek protection in shelters (Ford *et al.*, 1999).  
255 Observations suggest that not many rodents can escape from wildfires unless protected by  
256 underground burrows (Howard, Fenner & Childs, 1959). Wildfires can kill rodents directly and  
257 reduce their survival probability after fires. As fire destroy above ground shelters, they

258 additionally increase predation risk (Pastro, 2013). Lodges are usually made of dry plant  
259 material in environment with low humidity and are thus vulnerable to fire. Fire vulnerability  
260 has been observed in packrats (*Neotoma* spp.), which are reluctant to vacate their lodges and  
261 likely die under fire event (Howard et al., 1959; Simons, 1991). Although some lodge-building  
262 species can dig burrows underneath their lodges, this cannot protect their expensive and  
263 flammable lodges from being burnt down. A burning lodge would likely kill the rodent hiding  
264 in it, and even if it survives, it would loss its protecting shelter.

265 Our study points to two strategies for lodge-building species to avoid fire. Three semi-aquatic  
266 species build lodges near water, making fire unlikely to ignite their wet lodges. Similar tactics  
267 are observed in non-myomorph rodents such as the two species of beavers (*Castor spec.*),  
268 which construct lodges near waters with sticks and branches (Baker & Hill, 2003). Most lodge-  
269 building species (17 of 20) in Myomorpha habituated in arid environments, based on the hot  
270 weather with low humidity, they face a relatively high theoretical fire sensitivity. However, the  
271 actual fire risk was very low for lodge building species, probably because their arid  
272 environments had little fuel available to support wildfires. Many arid environments are  
273 associated with low plant productivity (Turner & Randall, 1989; Miranda et al., 2009; Yue et  
274 al., 2020), which does not provide a lot of natural shelters but also makes fires unlikely to  
275 spread: if a fire starts, it simply runs out due to patches without any burnable material  
276 (McLaughlin & Bowers, 1982; Pausas & Keeley, 2021). For example, the bush Karoo rat  
277 (*Otomys unisulcatus*) occurs in the arid and hot Succulent Karoo of South Africa, where  
278 wildfires cannot spread as there is not sufficient plant material, but it does not occur in South  
279 African savannah habitat, where wildfires occur regularly (Kruger et al., 2006).

280 The dataset we used to calculate fire risk was based on daily observed fires with threshold  
281 100×100m (by hectare) for a period of 20 years, such that fires that occur in intervals longer  
282 than 20 years were not represented. The dataset does allow for the detection of relatively small  
283 fires, however, fires with burnt areas smaller than 1ha were not represented. Even in areas with  
284 a high fire risk, there might be pocket areas that were less burnt, and in areas with low fire risk,  
285 small fires might occur in patches with sufficient fuel., Whether such local environmental  
286 characteristics influence species distribution would be interesting to study, especially to  
287 understand the variation in distribution of a species within its distribution range.

288 Our descriptive results agree with the hypothesis that lodge-building species are more likely  
289 distributed in arid environments with low fire risk, but these effects were not significant when

290 controlled for phylogeny. Phylogenetically controlled models take the evolutionary relatedness  
291 of species into account (Hadfield & Nakagawa, 2010), and the 20 lodge-building species fall  
292 into seven genera (two of them closely related) of two (seven in total) myomorph families.  
293 Most (14 of 20) of the lodge-building species are packrats (*Neotoma* spp.), such that their data  
294 are phylogenetically dependent, representing only one independent evolutionary transition.  
295 While only approximately 1/3 of myomorph species had data on shelter usage, the use of lodges  
296 is very conspicuous and our data source has probably reported for most species that do build  
297 lodges. Thus, it is unlikely increase the statistical power of our analysis by including more  
298 species that build lodges. In summary, our result suggests lodge-building species often  
299 distribute in areas characterized by low fire risk, during evolutionary processes, they may have  
300 persisted in areas with less incidence of large and intense fires, possibly due to low fuel loads.

301 Two evolutionary transitions to lodge building occurred in species living in wetlands and along  
302 waterways. These species (*Neofiber alleni*, *Ondatra zibethicus*, *Xeromys myoides*) live in  
303 regions with an overall three times higher fire risk compared to the other lodge-building species  
304 (0.63 vs. 0.21, see ESM S1, column “fire risk”). However, within these habitats they choose  
305 aquatic niches for lodge building which significantly reduces the likelihood of their lodges  
306 being burnt down. Therefore, these species suggest another possibility for the evolution of  
307 lodge building. The vulnerability of lodges to fire could be reduced by either (i) the  
308 environment being too wet to allow lodges to ignite, or (ii) the environment has low primary  
309 productivity and does not produce sufficient fuel to maintain fires.

310 Based on the result of this study, we suggest future studies on lodge-building rodents should  
311 focus on specific species to test whether aridity combined with low fire risk is associated with  
312 the limitation of their distribution range, for example, this would predict that the range of lodge-  
313 building species ends where fire risk increases, or that in these areas they use different shelters  
314 than lodges. In addition, studies on specific species also help capturing the effect of short and  
315 patched fires with smaller spatial and time scales, which are likely underestimated in studies  
316 conducted in global scale. Most lodge-building species are folivores (*Otomys*, *Leporillus*, many  
317 species of *Neotoma*), some eat seeds and fruits (*Mus spicilegus*, *Neotoma phenax*) and one even  
318 eats invertebrates (*Xeromys myoides*; see ESM S1, column “Diet”). The mainly folivores diet  
319 is consistent with their sheltering habit as lodges are mainly constructed with plant material  
320 and thus also offer a food source directly at the shelter. Our descriptive results suggested that  
321 lodge-building species have larger body size (body mass/length ratio) than those living in  
322 natural shelters or burrows, which may bring advantages for them to construct and defend their

323 lodge against other rodents (Schradin & Pillay, 2005; Schradin, 2005). As these descriptive  
324 results are not controlled by phylogeny, we cannot determine to what extent the association is  
325 biased by their phylogenetic relatedness. It would be interesting to have further investigation  
326 on the natural history traits commonly shared by lodge builders and the potential interaction  
327 with ecological factors, for example if lodge-builders becomes larger when faces high  
328 interspecific competition for their lodges. Therefore, studies comparing the body size between  
329 lodge-building species with sympatric non-lodge building rodent species would be useful to  
330 test this potential association.

331

### 332 **Conclusions**

333 Our study investigated possible associations between ecology, natural history and sheltering  
334 habits in mouse-like (myomorph) rodents. The descriptive result suggests that lodge-building  
335 species are mostly herbivorous, tend to have larger body size than those who live in burrows  
336 or natural shelters, and are more likely to occur in arid environment with low fire risk.  
337 However, lodge-building remains a rare sheltering strategy for mouse-like rodents (3.7% of  
338 species), and the high relatedness between those species makes it difficult to test these  
339 associations in phylogenetically controlled studies. In sum, the associations found in our study  
340 should be tested rather on a species than comparative level. For example, a previous study on  
341 bush Karoo rats suggested that their distribution was limited by wildfire (Kerley & Erasmus,  
342 1992). We suggest to study lodge building rodents such as the South African bush Karoo rat or  
343 the Australian stick-lodge rat toto test the predictions: (1) lodge builder are larger than other  
344 sympatric rodents, and (2) lodge builders have a species distribution range restricted by aridity  
345 (species distribution more arid than area around it) and (3) fire risk.

346

### 347 **Acknowledgements**

348 This study was supported by a Wits-CNRS joint PhD fellowship.

349 We thank Dr. Tomas Artés for sharing his knowledge helping us understand and process data  
350 from their wildfire dataset. We are thankful to the comments of the 3 referees that have  
351 significantly improved our manuscript. Lindelani Makuya and Siyabonga Sangweni helped  
352 improving the writing on the manuscript.

353

354 **Author Contributions Statement**

355 Jingyu Qiu collected and analysed the data, designed methodology and led the writing of the  
356 manuscript. Carsten Schradin conceived the ideas and designed methodology. All authors  
357 contributed critically to the drafts and gave final approval for publication.

358 **References**

- 359 Artés, T., Oom, D., de Rigo, D., Durrant, T.H., Maianti, P., Libertà, G. & San-Miguel-Ayanz,  
360 J. (2019). A global wildfire dataset for the analysis of fire regimes and fire behaviour.  
361 *Sci Data* 6, 296.
- 362 BAILEY, V. (1931). Mammals of New Mexico. N. Amer. Fauna, 53: 1-412. *Bailey153N. Amer.*  
363 *Fauna*.
- 364 Baker, B. W., and E. P. Hill. 2003. Beaver (*Castor canadensis*). Pages 288-310 in G. A.  
365 Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild Mammals of North*  
366 *America: Biology, Management, and Conservation*. Second Edition. The Johns  
367 Hopkins University Press, Baltimore, Maryland, USA.
- 368 Barber, I. (2013). The Evolutionary Ecology of Nest Construction: Insight from Recent Fish  
369 Studies. *Avian Biology Research* 6, 83–98.
- 370 Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A. & Wood, E.F.  
371 (2018). Present and future Köppen-Geiger climate classification maps at 1-km  
372 resolution. *Sci Data* 5, 180214.
- 373 Betancourt, J.L., Van Devender, T.R. & Martin, P.S. (2021). *Packrat middens: the last 40,000*  
374 *years of biotic change*. University of Arizona Press.
- 375 Birkenholz, D.E. (1963). A study of the life history and ecology of the round-tailed muskrat  
376 (*Neofiber alleni* True) in north-central Florida. *Ecological Monographs* 33, 255–280.
- 377 Blanckenhorn, W.U. (2000). The evolution of body size: what keeps organisms small? *The*  
378 *quarterly review of biology* 75, 385–407.
- 379 Boschetti, L., Sparks, A., Roy, D.P., Giglio, L., San-Miguel-Ayanz, J. (2022). GWIS national  
380 and sub-national fire activity data from the NASA MODIS Collection 6 Burned Area  
381 Product in support of policy making, carbon inventories and natural resource  
382 management, developed under NASA Applied Sciences grant #80NSSC18K0400,  
383 Using the NASA Polar Orbiting Fire Product Record to Enhance and Expand the Global  
384 Wildfire Information System (GWIS).
- 385 Bürkner P. C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal*  
386 *of Statistical Software* 80, 1–28.
- 387 Bürkner P. C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The*  
388 *R Journal* 10(1), 395-411.
- 389 Campos, H., Boeing, W.J. & Throop, H.L. (2019). Decaying woodrat (*Neotoma* spp.) middens  
390 increase soil resources and accelerate decomposition of contemporary litter. *Journal of*  
391 *Arid Environments* 171, 104007.

392 Copley, P. (1999). Natural histories of Australia's stick-nest rats, genus *Leporillus* (Rodentia :  
393 Muridae). *Wildl. Res.* 26, 513–539.

394 Cornely, J.E. & Baker, R.J. (1986). *Neotoma mexicana*. *Mammalian species* 1–7.

395 Dawkins, R. (2016). *The extended phenotype: The long reach of the gene*. Oxford University  
396 Press.

397 Deeming, D. C. (2023) Nest construction in mammals: a review of the patterns of construction  
398 and functional roles. *Philosophical Transactions of the Royal Society B: Biological*  
399 *Sciences*, 378, 20220138.

400 Diedrich, C.G. (2011). An overview of the ichnological and ethological studies in the Cave  
401 Bear Den in Urşilor Cave (Western Carpathians, Romania). *Ichnos* 18, 9–26.

402 Du Plessis, A., Kerley, G.I. & Winter, P.D. (1992). Refuge microclimates of rodents: a surface  
403 nesting *Otomys unisulcatus* and a burrowing *Parotomys brantsii*. *Acta Theriologica* 37,  
404 351–358.

405 Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I.N., Nilsson, T.,  
406 von Schantz, T. & Sylvén, M. (1983). Predation as a Regulating Factor on Small Rodent  
407 Populations in Southern Sweden. *Oikos* 40, 36–52.

408 Ford, W.M., Menzel, M.A., McGill, D.W., Laerm, J. & McCay, T.S. (1999). Effects of a  
409 community restoration fire on small mammals and herpetofauna in the southern  
410 Appalachians. *Forest ecology and management* 114, 233–243.

411 Frank, P.A. & Layne, J.N. (1992). Nests and daytime refugia of cotton mice (*Peromyscus*  
412 *gossypinus*) and golden mice (*Ochrotomys nuttalli*) in south-central Florida. *American*  
413 *Midland Naturalist* 21–30.

414 Hadfield, J.D. & Nakagawa, S. (2010). General quantitative genetic methods for comparative  
415 biology: phylogenies, taxonomies and multi-trait models for continuous and categorical  
416 characters. *Journal of Evolutionary Biology* 23, 494–508.

417 Hayes, L.D., Chesh, A.S. & Ebensperger, L.A. (2007). Ecological Predictors of Range Areas  
418 and Use of Burrow Systems in the Diurnal Rodent, *Octodon degus*. *Ethology* 113, 155–  
419 165.

420 Hölldobler, B. & Wilson, E.O. (2009). *The Superorganism – The Beauty, Elegance and*  
421 *Strangeness of Insect Societies*. 1er édition. New York: W. W. Norton & Company.

422 Howard, W.E., Fenner, R.L. & Childs, H.E. (1959). Wildlife survival in brush burns.

423 IUCN. 2022. The IUCN Red List of Threatened Species. Version 2022-2.  
424 <https://www.iucnredlist.org>.



425 Jackso, T.P., Roper, T.J., Conradt, L., Jackson, M.J. & Bennett, N.C. (2002). Alternative refuge  
426 strategies and their relation to thermophysiology in two sympatric rodents, *Parotomys*  
427 *brantsii* and *Otomys unisulcatus*. *Journal of Arid Environments* 51, 21–34.

428 Jackson, T.P., Bennett, N.C. & Spinks, A.C. (2004). Is the distribution of the arid-occurring  
429 otomyine rodents of southern Africa related to physiological adaptation or refuge type?  
430 *Journal of Zoology* 264, 1–10.

431 Jaeggi, A.V., Miles, M.I., Festa-Bianchet, M., Schradin, C. & Hayes, L.D. (2020). Variable  
432 social organization is ubiquitous in Artiodactyla and probably evolved from pair-living  
433 ancestors. *Proceedings of the Royal Society B* 287, 20200035.

434 Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity  
435 of birds in space and time. *Nature* 491, 444–448.

436 Jolly, C.J., Dickman, C.R., Doherty, T.S., van Eeden, L.M., Geary, W.L., Legge, S.M.,  
437 Woinarski, J.C.Z. & Nimmo, D.G. (2022). Animal mortality during fire. *Global*  
438 *Change Biology* 28, 2053–2065.

439 Kerley, G.I. & Erasmus, T. (1992). Fire and the range limits of the bush Karoo rat *Otomys*  
440 *unisulcatus*. *Global ecology and biogeography letters* 11–15.

441 Kinlaw, A. (1999). A review of burrowing by semi-fossorial vertebrates in arid environments.  
442 *Journal of Arid Environments* 41, 127–145.

443 Klockmann, M., Günter, F. & Fischer, K. (2017). Heat resistance throughout ontogeny: body  
444 size constrains thermal tolerance. *Global Change Biology* 23, 686–696.

445 Korb, J. (2003). Thermoregulation and ventilation of termite mounds. *Naturwissenschaften* 90,  
446 212–219.

447 Kruger, F.J., Forsyth, G.G., Kruger, L.M., Slater, K., Le Maitre, D.C. & Matshate, J. (2006).  
448 Classification of veldfire risk in South Africa for the administration of the legislation  
449 regarding fire management.

450 Leahy, L., Legge, S.M., Tuft, K., McGregor, H.W., Barmuta, L.A., Jones, M.E. & Johnson,  
451 C.N. (2016). Amplified predation after fire suppresses rodent populations in Australia’s  
452 tropical savannas. *Wildl. Res.* 42, 705–716.

453 Lima, M., Julliard, R., Stenseth, N.CHR. & Jaksic, F.M. (2001). Demographic dynamics of a  
454 neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic  
455 factors. *Journal of Animal Ecology* 70, 761–775

456 Lüscher, M. (1961). Air-conditioned Termite Nests. *Scientific American* 205, 138–147.

457 McElreath R. (2020) Statistical rethinking: A Bayesian course with examples in R and Stan.  
458 Chapman and Hall/CRC.

- 459 McLaughlin, S.P. & Bowers, J.E. (1982). Effects of Wildfire on A Sonoran Desert Plant  
460 Community. *Ecology* 63, 246–248.
- 461 Miranda, J. de D., Padilla, F.M., Lázaro, R. & Pugnaire, F.I. (2009). Do changes in rainfall  
462 patterns affect semiarid annual plant communities? *Journal of Vegetation Science* 20,  
463 269–276.
- 464 Moseby, K.E. & Bice, J.K. (2004). A trial re-introduction of the Greater Stick-nest Rat  
465 (*Leporillus conditor*) in arid South Australia. *Ecological Management & Restoration* 5,  
466 118–124.
- 467 Olivier, C.A., Martin, J.S., Pilisi, C., Agnani, P., Kauffmann, C., Hayes, L., Jaeggi, A.V. &  
468 Schradin, C. (2022). Primate social organization evolved from a flexible pair-living  
469 ancestor. *bioRxiv* 2022.08. 29.505776.
- 470 Onley, I.R., Austin, J.J., Mitchell, K.J. & Moseby, K.E. (2022). Understanding dispersal  
471 patterns can inform future translocation strategies: A case study of the threatened  
472 greater stick-nest rat (*Leporillus conditor*). *Austral Ecology* 47, 203–215.
- 473 Pastro, L. (2013). The effects of wildfire on small mammals and lizards in The Simpson Desert,  
474 Central Australia.
- 475 Pausas, J.G. & Keeley, J.E. (2021). Wildfires and global change. *Frontiers in Ecology and the*  
476 *Environment* 19, 387–395.
- 477 Prasetyo, D., Ancrenaz, M., Morrogh-Bernard, H.C., Utami Atmoko, S.S., Wich, S.A. & van  
478 Schaik, C.P. (2009). Nest building in orangutans. *Orangutans: Geographical Variation*  
479 *in Behavioral Ecology, Oxford University Press, Oxford* 269–277.
- 480 Qiu, J., Olivier, C.A., Jaeggi, A.V. & Schradin, C. (2022). The evolution of marsupial social  
481 organization. *Proceedings of the Royal Society B* 289, 20221589.
- 482 Robinson, A.C. (1975). The sticknest rat, *Leporillus conditor*, on Franklin Island, Nuyts  
483 Archipelago, South Australia. *Australian Mammalogy* 1, 319–327.
- 484 Schradin, C. (2005). Nest-Site Competition in Two Diurnal Rodents from the Succulent Karoo  
485 of South Africa. *Journal of Mammalogy* 86, 757–762.
- 486 Schradin, C. & Pillay, N. (2005). Demography of the striped mouse (*Rhabdomys pumilio*) in  
487 the succulent karoo. *Mammalian Biology* 70, 84–92.
- 488 Simons, L.H. (1991). Rodent dynamics in relation to fire in the Sonoran Desert. *Journal of*  
489 *Mammalogy* 72, 518–524.
- 490 Stan Development Team. (2020) RStan: the R interface to Stan. R package version 2.21.2.
- 491 Turner, F.B. & Randall, D.C. (1989). Net production by shrubs and winter annuals in Southern  
492 Nevada. *Journal of Arid Environments* 17, 23–36.

493 Vermeulen, H.& N. (1988). The bush Karoo rat *Otomys unisulcatus* on the Cape West coast.  
494 *African Zoology* 23, 103–111.

495 Whitford, W.G. & Steinberger, Y. (2010). Pack rats (*Neotoma* spp.): keystone ecological  
496 engineers? *Journal of Arid Environments* 74, 1450–1455.

497 Wilson, D.E., Lacher, T.E., Jr & Mittermeier, R.A. eds. (2017). Handbook of the Mammals of  
498 the World. Vol. 7. Rodents II. Lynx Editions, Barcelona.

499 Wolhuter, L., Thomson, J., Schradin, C. & Pillay, N. (2022). Life history traits of free-living  
500 bush Karoo rats (*Otomys unisulcatus*) in the semi-arid Succulent Karoo. *Mamm Res* 67,  
501 73–81.

502 Woods, H.A., Pincebourde, S., Dillon, M.E. & Terblanche, J.S. (2021). Extended phenotypes:  
503 buffers or amplifiers of climate change? *Trends in Ecology & Evolution* 36, 889–898.

504 Yue, K., Jarvie, S., Senior, A.M., Van Meerbeek, K., Peng, Y., Ni, X., Wu, F. & Svenning, J.-  
505 C. (2020). Changes in plant diversity and its relationship with productivity in response  
506 to nitrogen addition, warming and increased rainfall. *Oikos* 129, 939–952.

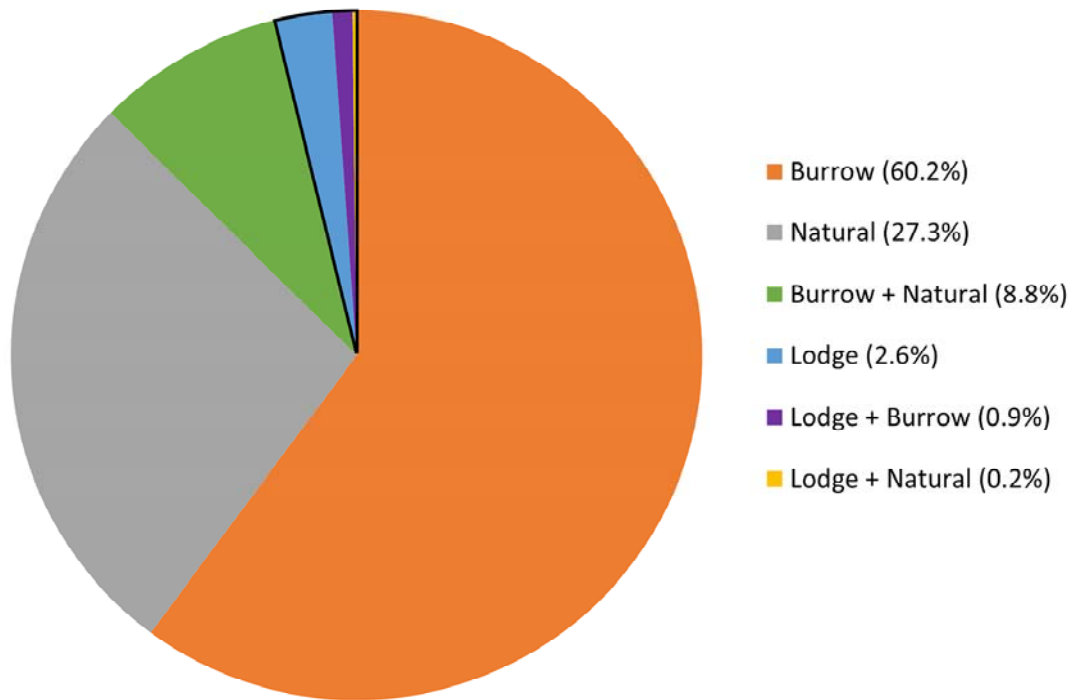
507 Zhang, Y., Zhang, Z. & Liu, J. (2003). Burrowing rodents as ecosystem engineers: the ecology  
508 and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems  
509 on the Tibetan Plateau. *Mammal Review* 33, 284–294.

510

511

512

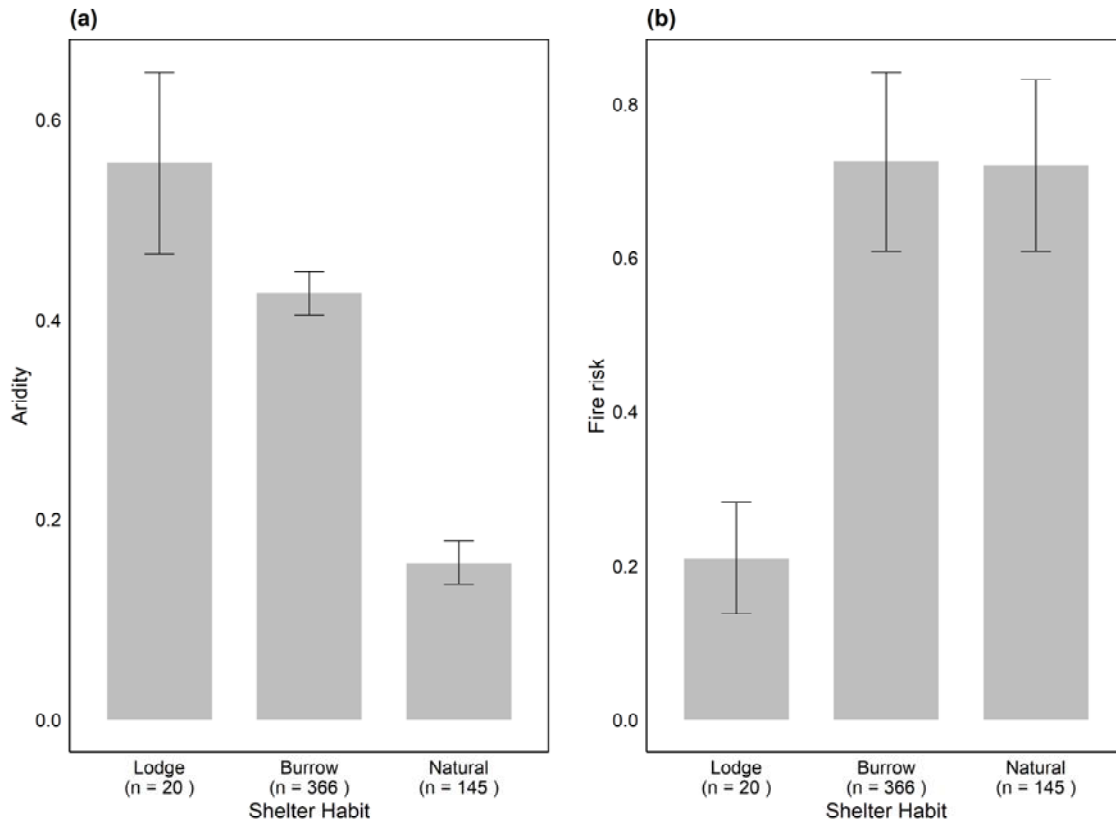
513



514

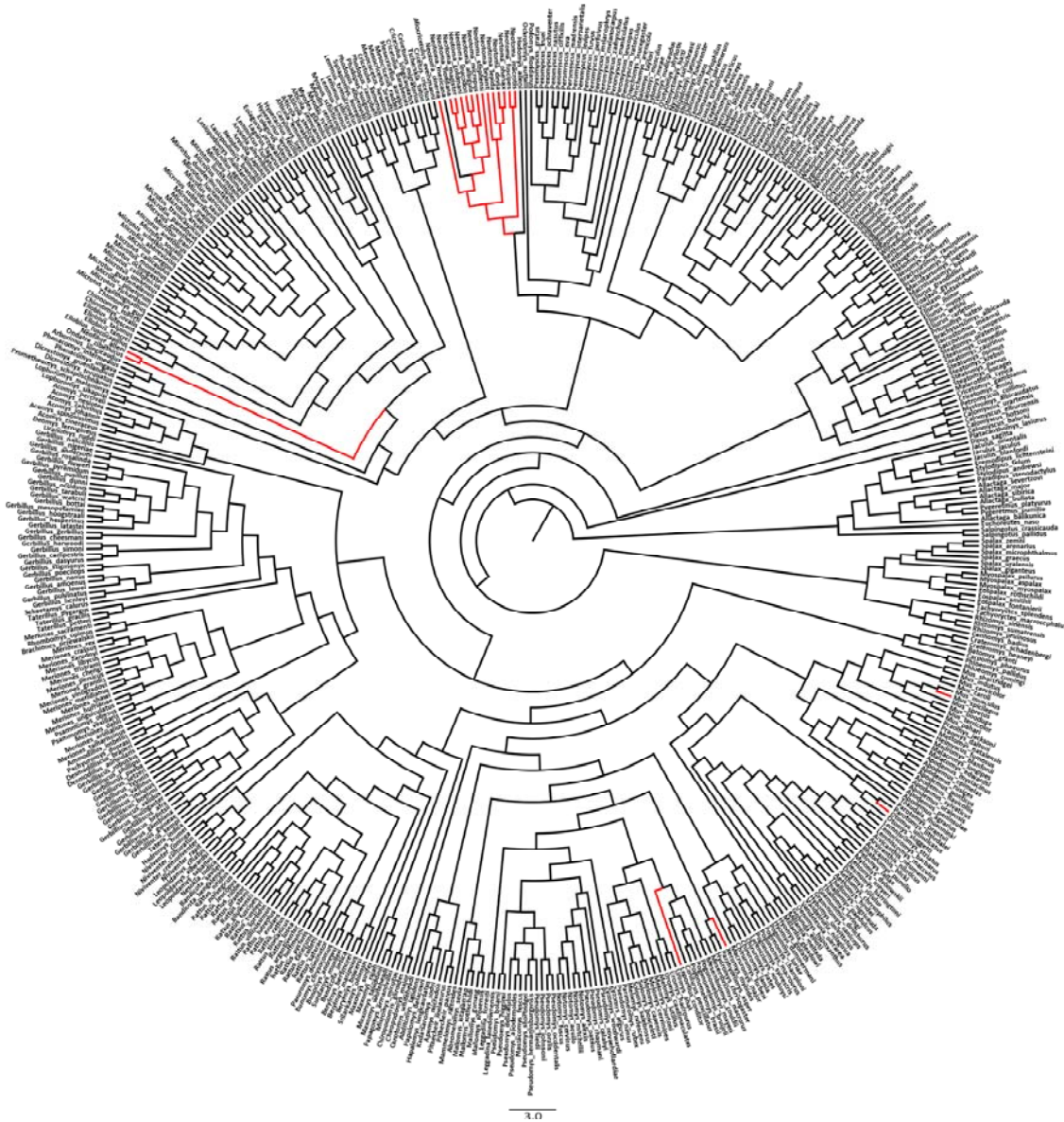
515 Figure 1: 532 Myomorpha species with available information on shelter use. Burrow: only  
 516 construct burrows; Natural: only use natural shelters; Burrow + Natural: construct burrows  
 517 and use natural shelters; Lodge: only construct lodges; Lodge + Burrow: construct lodges and  
 518 burrows; Lodge + Natural: construct lodges and use natural shelters. The 20 species that build  
 519 lodges are framed by black line.

520



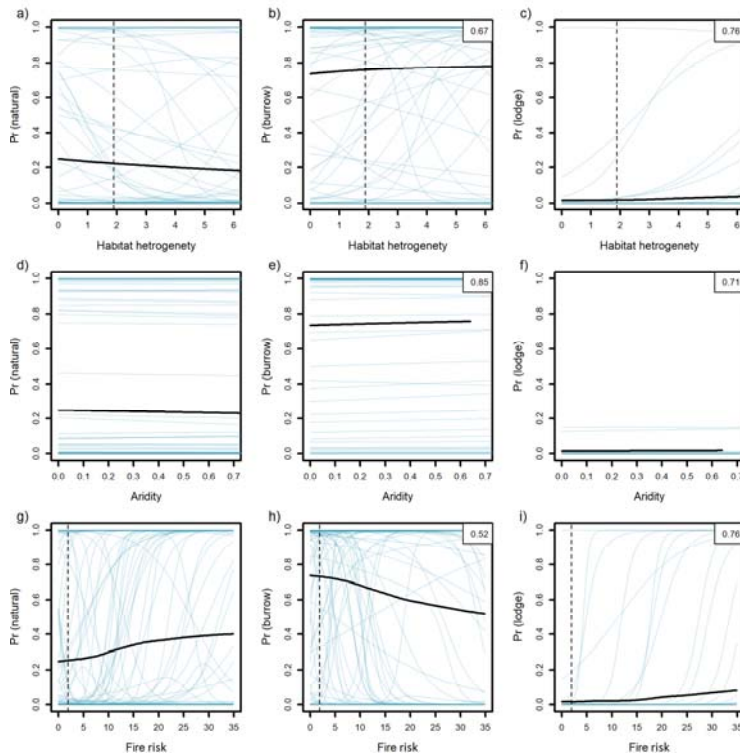
521

522 Figure 2: The association of sheltering habit with (a) aridity, range from 0 (no distribution in  
 523 arid habitat) to 1 (totally distributed in arid habitat) and (b) fire risk, total area burnt during 20  
 524 years within the species distribution range (km<sup>2</sup>)/species distribution range (km<sup>2</sup>), both as mean  
 525 ± SE. Data available for 531 Myomorpha species.



526

527 Figure 3. Phylogeny of 532 Myomorpha species and the occurrence of lodge building. Red  
 528 branches represent the lodge-building species.



529

530 Figure 4: Illustrating evolutionary transitions in sheltering habit as a function of the predictors.  
 531 Columns show (from left to right) the probability of natural shelter, burrows, lodge, while rows  
 532 show (from top to bottom) predicted changes in those probabilities as a function of number of  
 533 habitat (a–c), aridity (d–f) and fire risk (g–i). The numbers in the legends are the posterior  
 534 probabilities (PP), i.e. the proportion of the posterior distribution that supports a given  
 535 association; these were not available for natural shelter, as this was the reference category.  
 536 Within each row, all other predictors were held at their baseline value. Solid black lines are the  
 537 predicted means, thin coloured lines are 100 random samples drawn from the posterior to  
 538 illustrate uncertainty.