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ORIGINAL RESEARCH

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

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Abstract

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

Introduction

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

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

Lodges are structures built above ground, usually made of plant material, offering protection for the nest which lays inside (Jackso et al., 2002). Beavers (*Castor spp.*) are famous for building extensive lodges inside ponds they create with beaver dams (Baker & Hill, 2003). North American pack rats (*Neotoma spp.*) use urine, plant and animal materials to build middens above ground, which are extremely sturdy and can last for thousands of years after being abandoned (Betancourt et al., 2021). Bush Karoo rats (*Otomys unisulcatus*) from South Africa and greater stick-nest rats (*Leporillus conditor*) from

Australia build extensive stick lodges which offer protection against the arid and hot climate (Copley, 1999; Moseby & Bice, 2004; Robinson, 1975; Vermeulen & Nel, 1988). For small rodents, lodges are energetically expensive to build but can offer protection for generations (Onley et al., 2022; Vermeulen & Nel, 1988).

Specific climate conditions can make the investment of lodge-building adaptive. For example, the temperature inside the lodges of bush Karoo rats from semi-deserts in South Africa varies less than ambient environment: The temperature inside is higher than outside in cold winter nights (ambient: 6.1–9.9°C; lodge: 10.5–12.1°C), and in general lower in hot summer days (ambient: 17.7–35.5°C; lodge: 19.7–21.5°C); water vapour pressure inside lodges is always higher and less variable than ambient environments in winter (ambient: mean = 5.8 mm Hg, CV = 19.7%; lodge: mean = 7.4 mm Hg, CV = 14.3%) and also in summer (ambient: mean = 10.9 mm Hg, CV = 19.2%; lodge: mean = 14.1 mm Hg, CV = 15.8%; Du Plessis et al., 1992). If lodges generally offer a favourable micro-climate, they may be especially adaptive in environments with extreme temperatures and aridity. Lodges built in arid and hot habitats may offer protection against the harsh ambient conditions, but the high temperatures and low rainfall can create low fuel moisture in such habitats. The dry plant material used to build these lodges is highly flammable and vulnerable to wildfires (Jackson et al., 2004; Kerley & Erasmus, 1992). In the event of a wildfire, the lodges that are meant to offer protection against the harsh environmental conditions might present a deadly trap. Thus, lodge building is likely an adaptation for arid environments with low fire risk.

Ecological factors and natural history shape evolution, but how they influence and interplay with the evolution of lodge-building behaviour is less clear. Ecological factors that can influence the evolution of lodge building include fire risk, aridity and habitat heterogeneity. As sheltering habit may evolve as an adaptation to specific habitats, species that occur in multiple types of habitats may develop either a consistent sheltering habit that is universally adaptive to all the habitats they live in or the ability to show multiple sheltering habits depending on the local environment. Regarding natural history factors, the protective nature of lodges could be especially important for animals with small body sizes, as they are more sensitive to thermal stress (Blanckenhorn, 2000; Klockmann et al., 2017), or alternatively, a larger body size may bring advantages in carrying building materials and in defending their precious lodges against competitors. Considering the overlap of food sources and building materials, plant-based diet can be expected to facilitate lodge building and maintenance, animals feeding on green plant materials may be more efficient in collecting sticks, and the food remains can contribute as building materials (Betancourt et al., 2021). Lodges may offer protection against the heat during the day for nocturnal species, or offer protection against predators for diurnal species (Betancourt et al., 2021). In sum, the natural history factors of body size, diet and activity pattern might influence the evolution of lodge building. Despite these potential influences, how this distinct trait in sheltering habit may differentiate these lodge-building species from their relatives in ecological and natural history remains unknown.

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

Materials and methods

Database on shelter use

We searched for information on shelter use of the 1655 species of Myomorpha (classified by IUCN, 2022) in the 'Handbook of the Mammals of the World. Vol. 7. Rodents II' (Wilson et al., 2017). Our search yielded sheltering information for 532 species (seven families, 201 genera). However, the type of sheltering was not clear for 11 species (e.g. the book only stated that the species use shelters without stating the type of shelter, or whether the species constructed shelters or used shelters that had been constructed by other species). For these species, we searched for additional information from online sources (i.e. publications and photos of shelters), which resulted in sheltering information for seven more species (included in the 532 species, see Appendix S1). Shelter type was categorized as natural shelter (nests inside dense vegetation, rock crevices, tree holes or shelters build by other species), burrows and lodges (shelters above ground constructed by sticks and other materials). Because some species can use more than one types of shelter, we classified shelter use into seven categories: lodge, burrow, natural, lodge + burrow, lodge + natural, burrow + natural, and lodge + burrow + natural.

Natural history variables

As important natural history variables that may affect preferred sheltering types and the ability of shelter construction (see introduction), we recorded body mass and body length, diet and activity patterns from the 'Handbook of the Mammals of the World. Vol. 7. Rodents II' (Wilson et al., 2017). Habitat type was obtained from the species description in the IUCN Red List of Threatened Species. Habitat heterogeneity was then calculated as the total number of habitats occupied per species (Olivier et al., 2022; Qiu et al., 2022). Table 1 summarizes the categories of these variables.

Aridity

Aridity was estimated based on the Koppen-Geiger climate classification map (Beck et al., 2018), which presents global climate classification maps from 1980 to 2016. Based on threshold values and seasonality of monthly air temperature

Table 1 Variables considered in this study on myomorph shelter use

	Variables	Category/Quantification
Shelter	Shelter type	Natural shelter, burrow and lodge
Body size	Body length	Average head–body length (mm)
	Body mass	Average body mass of both sexes (g)
Diet	Diet	Insectivorous, Omnivorous and Herbivorous
Behaviour	Activity pattern	Diurnal, nocturnal, both and others (crepuscular, polyphasic and activity pattern unclear)
Habitat	Habitat type	Forest, savanna, shrubland, grassland, wetlands, rocky areas, cave and subterranean habitats, desert and artificial
	Habitat heterogeneity	The number of habitats types occupied per species
	Fire risk	Total burnt area during 20 years (2001–2020) within the species distribution range/species distribution range
	Aridity	Percentage of arid habitat within the species' distribution range (category B according to Koppen-Geiger climate classification)

and precipitation, the Koppen-Geiger system classifies global climate into five main classes: tropical, arid, temperate, cold and polar (Beck et al., 2018). To focus on aridity, we coded the arid areas as one and non-arid areas as zero. By comparing this map with species distribution polygons, we could determine how much of the species distribution area falls into the arid climate classification. The levels of aridity for each species was then calculated by the percentage of arid area in each species distribution polygon, ranging from 0 (no distribution in arid climate) to 1 (totally distributed in arid climate).

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

Fire risk

We were interested to know if species building lodges do not occur in areas that frequently burnt (high fire risk). Thus, we calculated fire risk by the proportion of historically burnt area in this study. The data were produced by a data mining process using MODIS burnt area product Collection 6 (MCD64A1, https://lpdaac.usgs.gov/products/mcd64a1v006/). The entire product is available under the umbrella of the Global Wildfire Information System (GWIS, Boschetti et al., 2022), which provides numerous data services to report and forecast the global activity of wildfire. With this global burnt area map, we used all data available from 2001 to 2020, the fire information was presented by "tile", the smallest special unit that sum up the fire event and burnt area within a standardized square, 0.25*0.25°). Burnt area was acquired daily with accuracy of 1 ha, and overlapping in space on different days were counted separately (see Artés et al., 2019 for more details).

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

Statistical analysis

Phylogenetic comparative analyses were conducted in R v.3.6.1, using the R packages brms (Bürkner, 2017, 2018), RStan (Stan Development Team., 2020) and Rethinking (McElreath, 2020). The modelling and R code were adapted from Jaeggi et al. (2020) and Qiu et al. (2022). Habitat heterogeneity, aridity and fire risk were included in the Bayesian phylogenetic mixed-effects model to estimate whether they have an influence on the evolution of shelter use. Aridity was weakly correlated with fire risk (Pearson's $r = -0.02$), we therefore included them as independent variables in the model. We conducted an alternative model to test for the potential interaction between aridity and fire risk, which did not give any significant differences; therefore, we excluded the interaction from the main model. The phylogenetic relationships and their uncertainty were represented by a sample of 100 phylogenetic trees, downloaded from the phylogeny subsets of online database VertLife (http://vertlife.org/phylosubsets/), which produce distributions of trees with subsets of taxa (Jetz et al., 2012). Phylogenetic signal (λ) was calculated as the proportion of

random factors variance captured by the phylogenetic random effects, representing the tendency of related species to resemble each other more than species drawn at random from the same tree. The model employs a categorical error distribution, fitted with two Markov Chain Monte Carlo (MCMC) chains, undergoing a total of 2000 iterations each, with the first 1000 iterations in each chain designated as burn-in to allow for parameter convergence. The shelter categories were combined to simplify the model and increase statistical power: For, the main analysis, we used three categories: natural shelter (natural), burrows (burrow and burrows + natural) and lodge (lodge, lodge + burrow and lodge + natural). As some lodge-building species also dig burrows, we ran an additional phylogenetic analysis with four categories: natural shelter (natural), burrows (burrow and burrows + natural), lodge (lodge and lodge + natural) and burrow + lodge.

Results

Shelter usage

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

Description of natural history and ecological factors

The majority species were herbivorous, and this was more pronounced in lodge-building species (Appendix S3: Fig. S1; lodge 89%, burrow 54%, natural 56%). Most species were nocturnal independent of shelter use (Appendix S3: Fig. S2). The most common habitat was forest (270 species), followed by shrubland (240 species), grassland (216 species) and artificial (191 species). Mean habitat heterogeneity was two and did not differ between the species with different sheltering habit (Appendix S3: Fig. S3). Lodge-building species had a lower body length/mass ratio than others (Appendix S3: Table S1; lodge: 1.2 ± 1.07; burrow: 2.4 ± 1.5; and natural: 2.2 ± 1.39).

The mean aridity of lodge-building species was higher than species that dig burrows or live in natural shelters (lodge: 0.566 ± 0.416; burrow: 0.426 ± 0.406; and natural: 0.158 ± 0.260; Fig. 2, Appendix S3: Table S1). Fire risk was lowest where lodge-builders occur (lodge: 0.210 ± 0.324, burrow: 0.725 ± 2.231; and natural: 0.720 ± 1.345; Fig. 2, Appendix S3: Table S1).

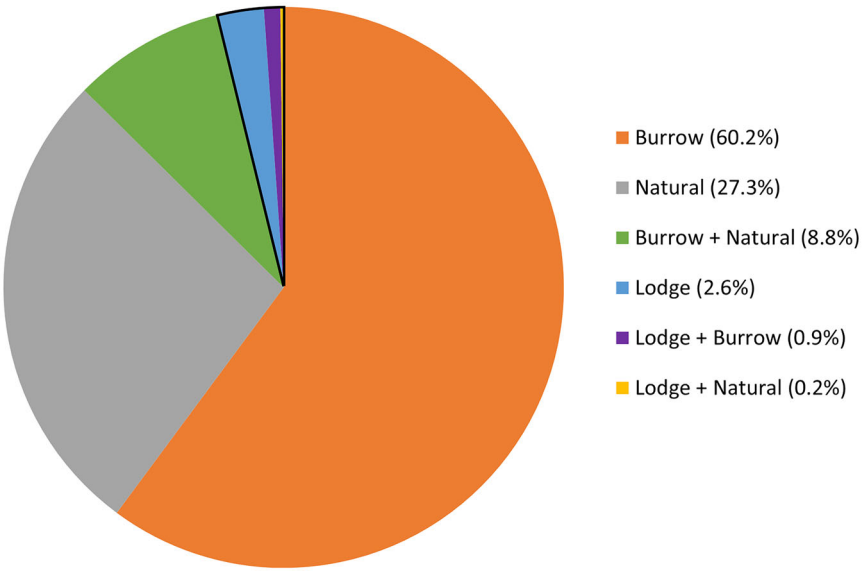

Figure 1 Five hundred and thirty-two Myomorpha species with available information on shelter use. Burrow: only construct burrows; Natural: only use natural shelters; Burrow + Natural: construct burrows and use natural shelters; Lodge: only construct lodges; Lodge + Burrow: construct lodges and burrows; Lodge + Natural: construct lodges and use natural shelters. The 20 species that build lodges are framed by black line.

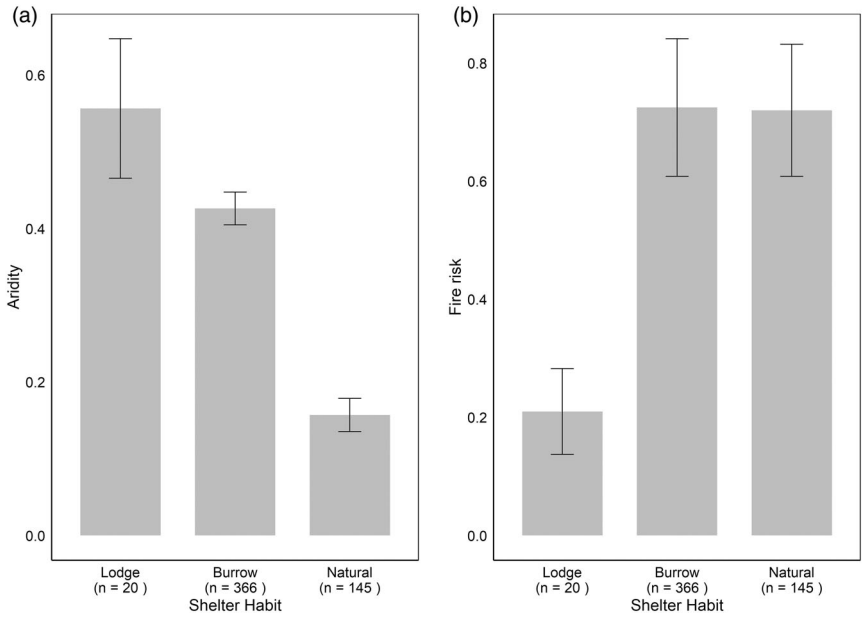

Figure 2 The association of sheltering habit with (a) aridity, ranging from 0 (no distribution in arid habitat) to 1(totally distributed in arid habitat) and (b) fire risk, i.e. total area burnt during 20 years within the species distribution range (km^2)/species distribution range (km^2), both as mean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

Phylogenetic comparative analyses

The phylogenetic signal ($\lambda = 0.43$) was moderate to high for the 515 Myomorpha species in the model. Phylogenetic distribution showed six independent evolutionary origins of lodge-building behaviour (Fig. 3). In the phylogenetically controlled analysis, the associations of lodge building with ecological factors (habitat heterogeneity, aridity and fire risk) were non-significant (Fig. 4). The additional model with four categories gave similar results (Appendix S3: Fig. S4).

Discussion

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

Wildfires directly threaten the survival of a variety of animals (Jolly et al., 2022). Small mammals cannot run away from wildfires but seek protection in shelters (Ford et al., 1999). Observations suggest that not many rodents can escape from wildfires unless protected by underground burrows (Howard et al., 1959). Wildfires can kill rodents directly and reduce their survival probability after fires. As fire destroy above ground shelters, they additionally increase predation risk (Pastro, 2013). Lodges are usually made of dry plant material in environment with low humidity and are thus vulnerable to fire. Fire vulnerability has been observed in pack rats (*Neotoma* spp.), which are reluctant to vacate their lodges and likely die under fire event (Howard et al., 1959; Simons, 1991). Although some lodge-building species can dig burrows underneath their lodges, this cannot protect their expensive and flammable lodges from being burnt down. A burning lodge would likely kill the rodent hiding in it, and even if it survives, it would loss its protecting shelter.

Our study points to two strategies for lodge-building species to avoid fire. Three semi-aquatic species build lodges near water, making fire unlikely to ignite their wet lodges. Similar tactics are observed in non-myomorph rodents such as the two species of beavers (*Castor spec.*), which construct lodges near waters with sticks and branches (Baker & Hill, 2003). Most lodge-building species (17 of 20) in Myomorpha habituated in arid environments, based on the hot weather with low humidity, they face a relatively high theoretical fire sensitivity. However, the actual fire risk was very low for lodge-building species, probably because their arid environments had little fuel available to support wildfires. Many arid environments are associated with low plant productivity (Miranda et al., 2009;

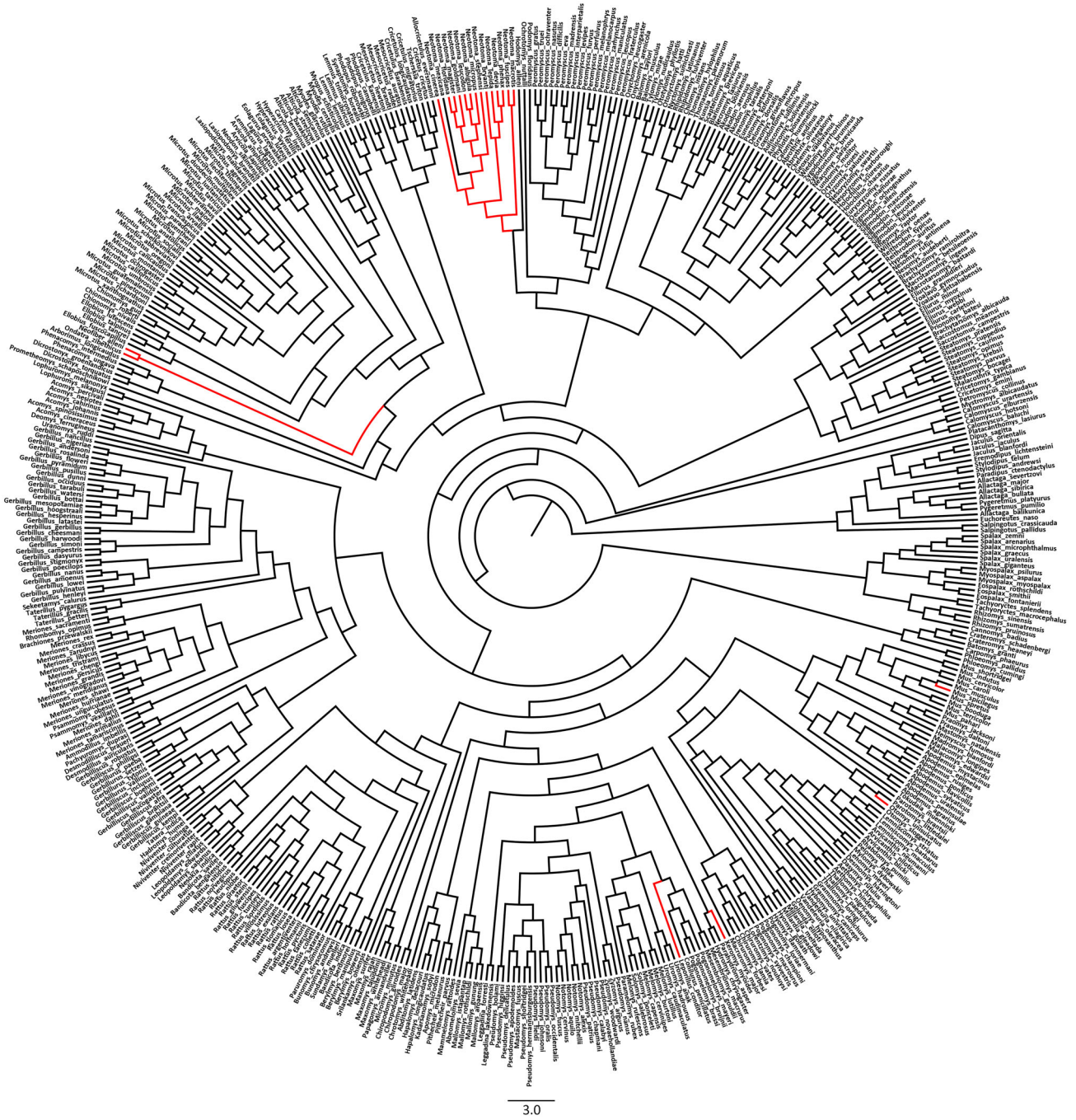

Figure 3 Phylogeny of 532 Myomorpha species and the occurrence of lodge building. Red branches represent the lodge-building species.

Turner & Randall, 1989; Yue et al., 2020), which does not only provide a lot of natural shelters but also makes fires unlikely to spread: If a fire starts, it simply runs out due to patches without any burnable material (McLaughlin & Bowers, 1982; Pausas & Keeley, 2021). For example, the bush Karoo rat (*Otomys unisulcatus*) occurs in the arid and hot Succulent Karoo of South Africa, where wildfires cannot spread as there is not sufficient plant material, but it does not occur in South African savannah habitat, where wildfires occur regularly (Kruger et al., 2006).

The dataset we used to calculate fire risk was based on daily observed fires with threshold 100 × 100 m (by hectare) for a period of 20 years, such that fires that occur in intervals longer than 20 years were not represented. The dataset does allow for

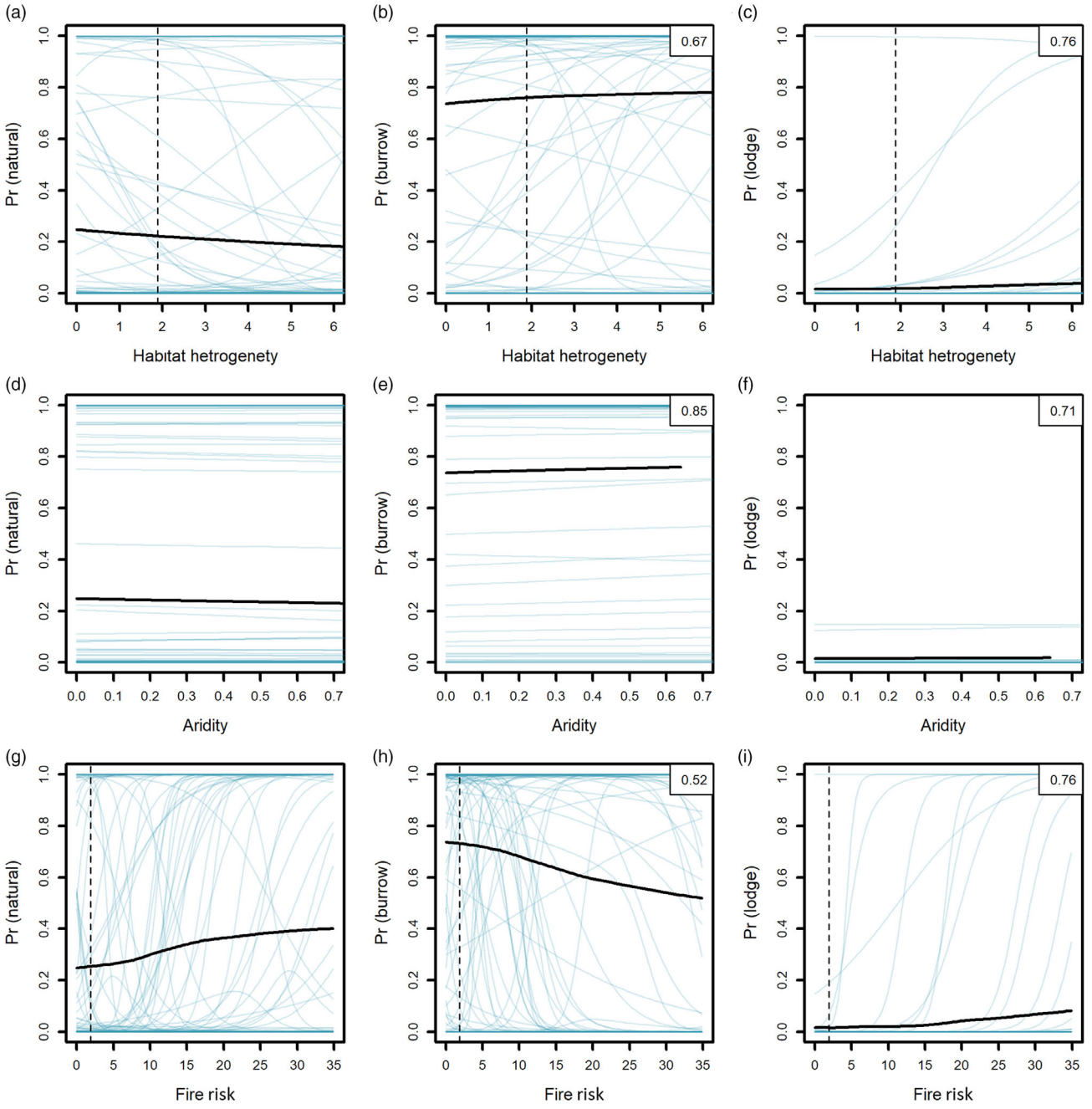

Figure 4 Illustration of evolutionary transitions in sheltering habit as a function of the predictors. Columns show (from left to right) the probability of natural shelter, burrows and lodge, while rows show (from top to bottom) predicted changes in those probabilities as a function of number of habitat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

the detection of relatively small fires, however, fires with burnt areas smaller than 1 ha were not represented. Even in areas with a high fire risk, there might be pocket areas that were less burnt, and in areas with low fire risk, small fires might occur in patches with sufficient fuel. Whether such local environmental characteristics influence species distribution would be interesting to study, especially to understand the variation in distribution of a species within its distribution range.

Our descriptive results agree with the hypothesis that lodge-building species are more likely distributed in arid environments with low fire risk, but these effects were not significant when controlled for phylogeny. Phylogenetically controlled models take the evolutionary relatedness of species into account (Hadfield & Nakagawa, 2010), and the 20 lodge-building species fall into seven genera (two of them closely related) of two (seven in total) myomorph families. Most (14 of 20) of the lodge-building species are pack rats (*Neotoma* spp.), such that their data are phylogenetically dependent, representing only one independent evolutionary transition. While only approximately one third of myomorph species had data on shelter usage, the use of lodges is very conspicuous and our data source has probably reported for most species that do build lodges. Thus, it is unlikely increase the statistical power of our analysis by including more species that build lodges. In summary, our result suggests lodge-building species often distribute in areas characterized by low fire risk, during evolutional processes, they may have persisted in areas with less incidence of large and intense fires, possibly due to low fuel loads.

Two evolutionary transitions to lodge building occurred in species living in wetlands and along waterways. These species (*Neofiber alleni, Ondatra zibethicus* and *Xeromys myoides*) live in regions with an overall three times higher fire risk compared to the other lodge-building species (0.63 vs. 0.21, see Appendix S1, column 'fire risk'). However, within these habitats they choose aquatic niches for lodge building which significantly reduces the likelihood of their lodges being burnt down. Therefore, these species suggest another possibility for the evolution of lodge building. The vulnerability of lodges to fire could be reduced by either (1) the environment being too wet to allow lodges to ignite, or (2) the environment has low primary productivity and does not produce sufficient fuel to maintain fires.

Based on the result of this study, we suggest future studies on lodge-building rodents should focus on specific species to test whether aridity combined with low fire risk is associated with the limitation of their distribution range, for example, this would predict that the range of lodge-building species ends where fire risk increases, or that in these areas, they use different shelters than lodges. In addition, studies on specific species also help capturing the effect of short and patched fires with smaller spatial and time scales, which are likely underestimated in studies conducted in global scale. Most lodge-building species are folivores (*Otomys, Leporillus*, many species of *Neotoma*), some eat seeds and fruits (*Mus spicilegus* and *Neotoma phenax*) and some even eat invertebrates (*Xeromys myoides*; see Appendix S1, column 'Diet'). The main folivores diet is consistent with their sheltering habit as lodges are mainly constructed with plant material and thus also offer a food source directly at the shelter. Our descriptive results suggested that lodge-building species have larger body size (body mass/length ratio) than those living in natural shelters or burrows, which may bring advantages for them to construct and defend their lodge against other rodents (Schradin, 2005; Schradin & Pillay, 2005). As these descriptive results are not controlled by phylogeny, we cannot determine to what extent the association is biased by their phylogenetic relatedness. It would be interesting to have further investigation on the natural history traits commonly shared by lodge builders and the potential interaction with ecological factors, for example, if lodge-builders becomes larger when faces high interspecific competition for their lodges. Therefore, studies comparing the body size between lodge-building species with sympatric non-lodge-building rodent species would be useful to test this potential association.

Conclusions

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

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Author contributions

J. Qiu collected and analysed the data, designed methodology and led the writing of the paper. C. Schradin conceived the ideas and designed methodology. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Dataset of sheltering habit and fire risk of Myomorph.

Appendix S2. Calculation of fire risk.

Appendix S3. Descriptive result of ecological and natural history factors.

Appendix S4. Phylogenetic models.