The nocturnal activity of a commonly housed rodent: How African pygmy dormice (*Graphiurus murinus*) respond to an enriched environment

Geminni P. S. A. Lang [1], Paul E. Rose [2], Steve M. Nash [3] and Lisa M. Riley [4*]

[1] University Centre Sparsholt, Sparsholt College Hampshire, Sparsholt, Hampshire, SO21 2NF, UK.

[2] Centre for Research in Animal Behavior, College of Life and Environmental Sciences, Washington Singer Labs, University of Exeter, Perry Road, Exeter, Devon, EX4 4QG, UK.

[3] Paignton Zoo Environmental Park, Totnes Road, Paignton, Devon TQ4 7EU, UK.

[4] Centre for Animal Welfare, University of Winchester, Sparkford Road, Winchester, Hampshire, SO22 4NR, UK.

* For correspondence: Lisa.Riley@winchester.ac.uk

ABSTRACT

Exotic rodents are becoming increasingly popular in industry, however, there is limited empirical evidence to guide husbandry practices. African pygmy dormice (Graphiurus murinus) are typical in this respect. This research aimed to determine the effect of environmental enrichment on the behavior (including stereotypical scratching at the glass walls of the enclosure) and space use of a group of eight African pygmy dormice at Sparsholt College Hampshire, UK. An apple-wood climbing grid and three raised (at various heights above the substrate) woven-wicker nest boxes were provided. Instantaneous scan sampling was used to record 150 hours of nocturnal behavior (19:00 – 07:00 daily) over five experimental phases (Phase 1 baseline; Phase 2 climbing grid provided; Phase 3 lower nest box provided; Phase 4 middle nest box provided; Phase 5 higher nest box provided). Space use was determined using the modified Spread of Participation Index. Nest box use was recorded continually. The provision of the climbing grid significantly increased the groups' time spent eating, digging, gnawing and climbing, and significantly decreased stereotypic scratching at glass. It also significantly changed the use of all enclosure zones, with mice utilizing the highest zones as soon as they were accessible. The addition of raised nesting opportunity saw the highest zones of the enclosure become those preferentially used. It also totally diminished stereotypic scratching at glass. The highest nest box was preferentially used and use of terrestrial nest boxes (those placed directly on top of the substrate) reduced significantly when raised alternatives were provided. This study suggests those working with African pygmy dormice should provide an enriched enclosure via 'arboreal' opportunity to increase active behaviors and reduce stereotypy.

Keywords: Welfare, *Graphiurus murinus*, nest box, behavioral repertoires, space use.

1. Introduction

African pygmy dormice (*Graphiurus murinus*) (henceforth "dormice") are now an established captive species and increasingly form part of zoo animal collections. As is typically for an exotic rodent species, husbandry guidance for dormice is rare and empirical research lacking. Determining optimal care guidelines is therefore essential; research on the effects of Environmental Enrichment (EE) on behavior and space use is particularly needed. Pedal grasping research suggests the potential EE provided to dormice is not always suitable; some branching provided in captivity fail to allow adequate grasping or associated postures to be performed by dormice mostly because climbing substrate diameter is too wide (Youlatos et al., 2015). It is understood that these types of restrictions lead to a static and overly predictable environment and may result in the expression of abnormal (including stereotypical) behaviors, or captive coping strategies. The performance of abnormal behavior may further diminish an individual's welfare; inability to exploit height variation within captivity may challenge dormice nesting behavioral repertoire forcing individuals to nest on the substrate of their enclosure rather than arboreally as was found with edible dormouse (*Glis glis*) (Marteau and Sara, 2015). Laboratory mice (*Mus musculus*) reared in a barren environment develop a wide spectrum of abnormal behavior (e.g. Gross et al., 2012) and access to EE throughout and after rearing can have long-term benefits including a reduction in the expression of abnormal behaviors (Garner and Mason, 2002).

For EE to be effective, the provisions given to any captive animal must afford individuals a chance to experience positive welfare states (Girbovan and Plamondon, 2013). Mason et al. (2007) suggest EE will have maximal positive effect when it is used in a targeted way (particular EE provisioned to solve a specific welfare issue) and when the EE has biological relevance to the species and individual (and see Rose, 2017; Rose and Riley, *in press*). In the wild, dormice are group living, widely distributed throughout Africa (Kingdon, 2015), and are classified as Least Concern by the IUCN (Cassola and Child, 2016). Their arboreal behavior has long been known (Shortridge, 1934; Kingdon, 1974). Dormice exploit many tree species including *Combretum caffrum*, an endemic species commonly found in moist montane forests and subtropical habitats (Birch, 2000; Salih et al., 2016). This tree species is favored as the trunk provides hollow spaces ideal for tiny dormice (15g to 200g weight range once adult, Striczky and Pazonyi, 2014) to nest in and avoid ground-dwelling predators (Beyer and Goldingay, 2006).

The behavior displayed by any captive species depends on the type of EE provided (e.g. Newberry, 1995), thus, it is logical to suggest, given the behavioral ecology of this species in the wild, that dormice should be kept in small groups, provided with climbing opportunity and arboreal nesting opportunities to mimic their wild ecological niche. In the interests of evidence-based husbandry (Melfi, 2009) rather than a reliance on anecdotal inference, this logic needs to be empirically tested. This research aimed to investigate the behavior and space use of a small group of dormice when living in an enriched enclosure that contained a climbing grid (allowing improved climbing opportunity and access to all enclosure zones) and sequentially available raised nesting opportunities (suspended from the climbing grid) compared with a typical exotic rodent enclosure design with limited climbing opportunity and only terrestrial nesting opportunity.

2. Materials and Methods

2.1. Study Population

Eight adult, captive-bred dormice (2:6:0) housed at the Animal Management Centre, Sparsholt College Hampshire, UK were studied. Throughout the study typical handling and husbandry routines were maintained, as was diet and feeding regime (commercial complete diet with supplementary nutritional enrichment that promoted variety and gnawing). Food was presented in the same location daily (directly on top of the substrate in an area later categorized as 'Zone A'). The group was housed in a single rectangular glass enclosure 60cm (h) x 45cm (w) x 60cm (d) with front opening doors, wood shaving substrate (approximately 4cm deep), furnished with three plastic domed nest boxes presented on the substrate, and a variety of horizontal and vertical sticks randomly presented in the lower vertical half of the enclosure. The group had been previously established in the enclosure for approximately three months before data collection commenced.

2.2. Apparatus and Environmental Enrichment

A three-dimensional climbing grid was constructed to create three height levels (‘higher’ tier at 55cm high, ‘middle’ tier at 30cm high, ‘lower’ tier at 15cm high) (Figure 1) and provide enhanced climbing opportunity to the eight dormice. The grid was made from aa lattice of apple twigs (non-toxic, collected from a local orchard) secured with twine. In addition, one, two and maximally three commercially available woven wicker bird nest boxes (Gardman Ltd, Huntingdon UK) were provisioned to provide raised (higher than substrate level) nesting opportunity, one at each of the three climbing levels (Figure 1) starting at the lower tier and ending with the higher tier. The enclosure, including existing and new EE, was divided into 10 three-dimensional zones of unequal area (Figure 2) to allow space use to be calculated using the Modified Spread of Participation Index (mSPI) formula (Plowman, 2003):

$$mSPI = \frac{\Sigma[fo - fe]}{2(N - fe\,\mathrm{min})}$$

f_o = observed frequency in each zone

f_e = expected frequency for each zone

f_e min = expected frequency in the smallest zone

A value of 0.0 is indicative of equal use of all zones whereas a value of 1.0 indicates unequal zone use. Only data for zones A-J were considered in the mSPI calculations.

Figure 1 GOES HERE

Figure 2 GOES HERE

2.3. Experimental Design and Data Collection

Behavior and space (zone) use were recorded between 19:00 – 07:00 from 17th January to 17th February 2017, via infra-red videography using a Sony night vision indoor HD CCTV™ camera system (Sony Europe B.V., Weybridge, Surrey). Individuals were indistinguishable on the video recording therefore data were grouped for analysis. The entire enclosure was visible on the recording. A five-phase repeated measures experimental design was used with increasingly more enrichment provided in each phase (Table 1). The dormice were observed for 30 hours in each phase. Phase 1 allowed baseline behavior and space use to be observed when climbing opportunity was limited, the highest zones of the enclosure (I and J) were not accessible and nesting was only possible directly on top of the substrate. Phase 2 allowed the effects of improved climbing opportunity to be assessed as the provision of the climbing grid allowed all zones of the enclosure to be accessed. Phases 3, 4, and 5 allowed the effects of adding one, two or three raised nesting opportunities respectively to be observed.

Table 1 GOES HERE

State behaviors (see ethogram - Table 2) were recorded using instantaneous scan sampling with one-minute intervals. Interactions with nest boxes were recorded continuously, using ad libitum sampling. The enclosure zone each mouse was observed in was recorded every minute.

Table 2 GOES HERE

2.4 Data Analysis

Data were analyzed using MiniTab^{R} 17 Statistical Software. Differences in the total time the dormice spent (minutes) nesting (rest), and performing each observed active behavior (groom, aggression, climb, walk, gnaw, nest-building, running, eating, scratching at glass, scratching, sit, dig) between all of the experimental phases was analyzed using Chi-Square Goodness of Fit test. The same test was applied to analyze significant differences in nest box use (total count) and significant difference in the use of a zone between the experimental phases.

An alpha level of 0.05 was used for all analysis. As multiple tests were performed on the same data set for some comparisons, both the Bonferroni Correction Factor and the Benjamini and Hochberg (1995) correction factor were applied to determine corrected alpha levels.

2.5. Ethical Statement

This study was approved by the Ethics Committee, University Centre Sparsholt, UK. The authors confirm that this research complies with the Elsevier Animal Ethics Policy.

3. Results

3.1. Nesting (Rest)

Nesting decreased significantly from Phase 1 to Phase 2 and decreased further in Phase 5 (χ^2=1697.46, df=4, P<0.001). During Phase 1 the dormice collectively nested for 84% of the observed time (Figure 3). Nesting reduced by over 20% when the climbing grid was introduced in Phase 2. As each raised nesting opportunity was added, nesting time reduced slightly and was least when climbing and raised nesting opportunity were maximal in the final experimental phase, 36% less compared to nesting in Phase 1.

Figure 3 GOES HERE

3.2. Active Behavior

The behavioral repertoire of the dormice showed a high degree of consistency across the five experimental phases. In each phase several locomotor patterns (walk, run, climb) and a range of behaviors (sit, eating, gnaw, nest building and dig) were observed. The total time the group spent performing each locomotor pattern and behavior increased significantly (all at P<0.001, see Table 3) from Phase 1 to Phase 2 when the climbing grid was introduced and, except for grooming, remained high compared to baseline when raised nesting opportunity was increased in subsequent phases. In Phase 5 when raised nesting opportunity and climbing opportunity were maximal, time spent by the group in walk, gnaw, running, eating, scratching and dig significantly increased further compared to Phase 1. During Phase 1 scratching at glass and aggression, were observed. In Phase 2 aggression ceased, while time spent scratching at glass significantly decreased from Phase 1 to Phase 2 (Table 3) and was not observed after the first raised nesting opportunity was provided in Phase 3. While the total time spent performing each observed behavior changed significantly once the dormice were living in an enriched enclosure, the percentage of active time spent performing each behavior did not change significantly for 11 of the 12 observed behaviors (Figure 4). Sit and eating remained proportionately the most frequently performed behaviors in each experimental phase. However, a significant reduction in the percentage of time the group spent scratching at glass was observed between Phase 1 and Phase 2 (χ^2=14.4252, df=1, P = 0.00015) (Bonferroni corrected alpha q*=0.0045; Benjamini and Hochberg (1995) corrected alpha q* = 0.0045).

Table 3 GOES HERE

Figure 4 GOES HERE

3.3. Nest Box Use

In each phase of the study, the dormice used all available nest boxes. In Phases 1 and 2 terrestrial nest boxes K, L and M were provided, K was used preferentially (Figure 5). Use of terrestrial nest box K differed significantly across experimental phases (χ^2=49378.2, df=4, P<0.001) as did nest box L use (χ^2=21424.6, df=4, P<0.001) and nest box M use (χ^2=23410.9, df=4, P<0.001) (Bonferroni corrected alpha q*=0.017; Benjamini and Hochberg (1995) corrected alpha q* = 0.05). Use of all terrestrial nest boxes increased when the climbing grid was added and use of nest box K increased further when raised nesting opportunity was provided in Phase 3 however nest box N (the raised nest box) was preferentially used in Phase 3. When multiple raised nest boxes were provided in Phases 4 and 5, the new, highest nest box was preferentially used while use of all terrestrial nest boxes reduced significantly.

Figure 5 GOES HERE

3.4. Space Use

Space use varied throughout the study; in Phase 1 unequal space use was observed with the dormice disproportionality using zones A and B, while in all other phases (when additional enrichment was added) the dormice spread their space use fairly equally across all zones (Table 4). During Phase 1 ten of sixteen zones were used by the mice; uppermost arboreal zones were not used (zones I and J could not be accessed as they were empty space). In all other conditions (except baseline), the mice used every zone. Use of the uppermost arboreal zones first occurred once the climbing grid was provided; once the highest nesting opportunity was added (experimental Phase 5) zones J, I and H were used extremely often. The middle zones, though the largest in area, were used less often throughout even when nest boxes were presented in the middle zones. The use of each zone differed significantly across the experimental phases (Table 4) though this is presumably because total activity increased across the phases. Zones A, I, J and P were used maximally in Phase 5, while zones C, D, E, F, G, H and L were used maximally in Phase 2, hence when the dormice could utilize the climbing grid to access middle zones they did, and once there was nesting opportunity in the highest zones the mice used the highest zones. The dormice continued to use zone A as this is where food was consistently presented.

Table 4 GOES HERE

4. Discussion

This study showed that provision of a climbing grid and raised nesting opportunity is enriching for captive dormice. Provision of the climbing grid caused a significant decrease in nesting behavior, a significant increase in the time spent performing natural behaviors (dig, eat, gnaw, climb, nest build), while the percentage expression of natural behaviors were maintained. The climbing grid also significantly reduced the time the group spent in stereotypic behavior (scratching at glass) and the percentage of time spent scratching at glass. The addition of raised nesting opportunity amplified these effects and stereotypy was no longer observed. All nest boxes were used but the dormice used the highest and newest nest box most frequently.

The enriched enclosure was designed with the behavioral ecology of the dormice in mind and to encourage natural behavioral expression. Small rodents are typically agile runners and climbers of vertical and horizontal branches (Delany, 1972; Gardner et al., 2007; Madikiza, 2010), and in the wild this dormouse species is known to be arboreal (e.g. Birch, 2000; Juškaitis, 2000; Avgar et al., 2013; Hoelzl et al., 2016; Salih et al., 2016). Youlatos et al., (2015) outlined how important it is for this species to express climbing behavior as it allows for expression of a natural physiological repertoire, otherwise individuals may develop morphological deformities that prevent behavioral expression and ultimately impact welfare. This study demonstrates that, in captivity, dormice will utilize enrichment with biological relevance and use of a climbing grid causes a significant reduction in the performance of stereotypy. The provision of climbing opportunity in captivity therefore seems important for good welfare and vital for suitable husbandry practices. Similarly, the provision of raised nesting opportunity in this study indicates how even small changes in husbandry and enclosure design, adding a commercially available nest box just above the substrate rather than on the substrate, can provide relevant opportunity in captivity. Madikiza et al. (2010) provisioned wild-living dormice with nest boxes, the mice used both the lower nest box placed 1.1m above ground and the higher nest box placed 2.32m above ground. Thus, captive provisions should provide similar opportunities to the wild but do not have to directly emulate the wild to beneficially change behavior.

Modified SPI analysis in this study revealed that enrichment provision can promote 'fairly equal' enclosure use where previously unequal zone use was observed. If there is a route provided either with or without a specific resource associated with it, dormice will explore and utilize that route, providing greater opportunity for active behaviors to be performed.

Throughout the baseline condition, the dormice utilized 'terrestrial' zone A and B more than all other zones and preferentially used zone A. It is thought that the preference of zone A could be a direct result of all food resources being presented here, showing how radically a husbandry practice can influence the space use of a species, even in a species who in the wild is known to feed arboreally and store abundant food in arboreal nests (Hoelzl et al., 2016; Avgar et al., 2013; Trout et al., 2015). Before the introduction of the enrichment grid, subjects were unable to access all zones (I and J were inaccessible). Zones G and H, the uppermost accessible zones during baseline testing were rarely used, possibly because they were difficult to get to as the branching provided was not securely fixed and was highly randomized, whereas the climbing grid was sturdy and secure. Inability to exploit height variation within captivity challenges *G.murinus* entire nesting behavioral repertoire forcing the individuals to conflict with their own evolutionary adaptations (Marteau and Sara, 2015) and nest on the substrate. When the enrichment grid was added, the subjects had the ability to access all zones and took advantage of this, preferring both the most arboreal zones and the terrestrial zones. The use of I and J zones were relatively static throughout the introduction of the enrichment grid and the first and second nest box whereas when the third nest box was introduced at the highest level there was a significant increase in use of zones J and I. The middle zones were used less frequently, these zones were used to travel to the highest zones demonstrating how important it is to provide multiple vertical pathways that lead to nest opportunity. Such complex enclosures with a large proportion of usable space allow for a range of behaviors to be expressed (Sargis, 2001; Youlatos, 2008) and the dormice in this study did not change the overall proportion of natural, active behaviors but they did perform more of all behaviors when provided with the EE.

Providing nesting opportunity and food provision at substrate level continued to provide opportunity for the captive dormice in this study who used the resources provided in ‘terrestrial’ zones. Resource distribution is a known and well-understood influencer on animal behavior, particularly food distribution. Food was consistently presented in zone A throughout this study and zone A was consistently one of the most frequently used zones. Here we identify the potential for further study – the provision of food on the lower, middle and higher tiers of the climbing grid. This may encourage greater zone use in the mid-enclosure – changing what was observed to be a travel route to a site of feeding and social interaction and therefore further choice and opportunity.

The importance of choice and control to promote animal welfare cannot be understated (Meehan and Mench, 2007) and the results of this study suggest a secure, rigid climbing grid made from inexpensive and widely available material provides biologically relevant opportunity and choice to captive dormice. Husbandry guidance should require the provision of such opportunity for arboreal dormice in captivity.

5. Conclusion

Our research indicates the provision of a climbing grid and raised nesting opportunity is enriching for dormice. When provided with an enriched enclosure, dormice utilize all available space, preferentially using the highest spaces provided. They nest most frequently in the newest and highest nest provided. When enriched, dormice decrease nesting (inactivity) and reduce the percentage of and total time spent performing stereotypic scratching at glass, while maintaining the proportionate expression of a range of natural behaviors. African pygmy dormice are an active, arboreal species. In typical enclosures with limited climbing and terrestrial nesting they can develop stereotypic behavior. Husbandry guidelines should recommend those who care for dormice ensure each group has climbing opportunity allowing access to high enclosure zones with nesting opportunity raised off the substrate, even if the nest is presented directly above the substrate.

Acknowledgements

We thank the keepers at the Animal Management Centre at Sparsholt College Hampshire for their support with this project, especially those who directly cared for the dormice in this study who were extremely accommodating.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Ethical Statement

This research was given ethical approval by the Ethics Committee, University Centre Sparsholt. Approval was not required under EU Directive 2010/63/EU for animal experiments as this was non-invasive research.

Conflicts of Interest Statement

The authors declare no conflict of interest.

Authorship Statement

The idea for the paper was conceived by Lang, Nash and Rose.

The experiments were designed by all authors.

The experiments were performed by Lang.

The data were analyzed by Lang and Riley.

The paper was written by all authors, led by Riley and Lang.

References

Avgar, T., Deardon, R., Fryxell, J. M. 2013. An empirically parameterized individual based model of animal movement, perception, and memory. Ecological Modelling. 251, 158-172.

Avgar, T., Street, G., Fryxell, J. M. 2013. On the adaptive benefits of mammal migration. Can. J. Zoo. 92(6), 481-490.

Benjamini, Y., Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J Royal Stat. Soc. Series B (Methodological). 57(1), 289-300.

Beyer, G. L., Goldingay, R. L. 2006. The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. Wild. Res. 33(3), 161-174.

Birch, N. V. E. 2000. The vegetation potential of natural rangelands in the Mid-Fish River Valley, Eastern Cape, South Africa: towards a sustainable and acceptable management system (Doctoral dissertation, Rhodes University).

Bright, P. W., Morris, P. A. 1991. Ranging and nesting behavior of the dormouse, Muscardinus avellanarius, in diverse low-growing woodland. J. Zool. 224(2), 177-190.

Büchner, S. 2008. Dispersal of common dormice (Muscardinus avellanarius) in a habitat mosaic. Acta Theriologica. 53(3), 259-262.

Cassola, F., Child, M.F. 2016. Graphiurus murinus (errata version published in 2017). *The IUCN Red List of Threatened Species* 2016: e.T9487A115093727. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T9487A22221270.en. Downloaded on 09 June 2019.

Delany, M. J. 1972. The ecology of small rodents in tropical Africa. Mammal Rev. 2(1), 1-42.

Gardner, T. A., Caro, T. I. M., Fitzherbert, E. B., Banda, T., Lalbhai, P. 2007. Conservation value of multiple-use areas in East Africa. Conserv. Bio. 21(6), 1516-1525.

Garner, J. P., Mason, G. J. 2002. Evidence for a relationship between cage stereotypies and behavioral disinhibition in laboratory rodents. Behav. Brain Res. 136(1), 83-92.

Girbovan, C., Plamondon, H. 2013. Environmental enrichment in female rodents: considerations in the effects on behavior and biochemical markers. Behav. Brain Res. 253, 178-190.

Gross, A. N., Richter, S. H., Engel, A. K. J., Würbel, H. 2012. Cage-induced stereotypies, perseveration and the effects of environmental enrichment in laboratory mice. Behav. Brain Res. 234(1), 61-68.

Hoelzl, F., Cornils, J. S., Smith, S., Moodley, Y., Ruf, T. 2016. Telomere dynamics in free-living edible dormice (Glis glis): the impact of hibernation and food supply. J. Exp. Biol. 219(16), 2469-2474.

Juškaitis, R. 2000. Abundance dynamics of common dormouse (Muscardinus avellanarius), fat dormouse (Glis glis) and yellow-necked mouse (Apodemus flavicollis) derived from nest box occupation. Folia Therio. Estonica 5, 42-50.

Kingdon, J. 1974. East African mammals. An atlas of evolution in Africa. Vol. I1 Part B (hares and rodents). Academic Press, London.

Kingdon, J. 2015. The Kingdon field guide to African mammals. Bloomsbury Publishing. London: UK.

Madikiza, Z. J. K. 2010. Population biology and aspects of the socio-spatial organiation of the Woodland dormouse Graphiurus murinus (Desmaret, 1822) in the Great fish river Reserve, South Africa (Doctoral dissertation, University of Fort Hare).

Madikiza, Z. J., Bertolino, S., Baxter, R. M., San, E. D. L. 2010. Nest box use by woodland dormice (Graphiurus murinus): the influence of life cycle and nest box placement. Eur. J. Wildlife Res. 56(5), 735-743.

Marteau, M., Sarà, M. 2015. Habitat preferences of edible dormouse, Glis: implications for the management of arboreal mammals in Mediterranean forests. Folia Zool. 64(2), 136-150.

Mason, G., Clubb, R., Latham, N., Vickery, S. 2007. Why and how should we use environmental enrichment to tackle stereotypic behavior? Appl. Anim. Behav. Sci. 102(3-4), 163-188.

Meehan, C.L., Mench, J.A. 2007. The challenge of challenge: can problem solving opportunities enhance animal welfare? Appl. Anim. Behav. Sci. 102(3-4), 246-261.

Melfi, V.A. 2009. There are big gaps in our knowledge, and thus approach, to zoo animal welfare: a case for evidence-based zoo animal management. Zoo Biol. 28(6), 574-588.

Newberry, R. C. 1995. Environmental enrichment: increasing the biological relevance of captive environments. Appl. Anim. Behav. Sci. 44(2-4), 229-243.

Plowman, A.B. 2003. A note on a modification of the spread of participation index allowing for unequal zones. Appl. Anim. Beh. Sci. 83(4), pp.331-336.

Salih, E. Y. A., Kanninen, M., Sipi, M., Luukkanen, O., Hiltunen, R., Vuorela, H., Julkunen-Titto, R., Fyhrquist, P. 2017. Tannins, flavonoids and stilbenes in extracts of African savanna woodland trees Terminalia brownii, Terminalia laxiflora and Anogeissus leiocarpus showing promising antibacterial potential. S. Afr. J. Bot. 108, 370-386.

Sargis, E. J. 2001. The grasping behavior, locomotion and substrate use of the tree shrews Tupaia minor and T. tana (Mammalia, Scandentia). J. Zool. 253(4), 485-490.

Shortridge, C.G. 1934. Mammals of South West Africa Vol I. William Heinemann Ltd. London, UK.

Striczky, L., Pazonyi, P. 2014. Taxonomic study of the dormice (Gliridae, Mammalia) fauna from the late Early Pleistocene Somssich Hill 2 locality (Villány Hills, South Hungary) and its palaeoecological implications. Fragmenta Palaeontologica Hungarica 31, 51-81.

Trout, R. C., Brooks, S., Morris, P. 2015. Nest box usage by old edible dormice (Glis glis) in breeding and non-breeding years. Folia Zool. 64(4), 320-324.

Youlatos, D. 2008. Hallucal grasping behavior in Caluromys (Didelphimorphia: Didelphidae): implications for primate pedal grasping. J. Hum. Evol. 55(6), 1096-1101.

Youlatos, D., Karantanis, N. E., Byron, C. D., Panyutina, A. 2015. Pedal grasping in an arboreal rodent relates to above-branch behavior on slender substrates. J. Zool. 296(4), 239-248.

Table 1. Experimental design. Five experimental phases were implemented, totaling 150 hours of behavioral recording (30 hours/phase).

Phase 1	Phase 2	Phase 3	Phase 4	Phase 5
Baseline. Original enclosure design. (Zones A-H and nest boxes K-M in Figure 2).	Climbing grid provided. (Zones A – J and nest boxes K-M in Figure 2).	Climbing grid and lower-level woven nest box provided. (Zones A-J and nest	Climbing grid and lower-level plus middle-level woven nest boxes provided. (Zones A-J and nest	Climbing grid and lower-level plus middle-level and higher-level woven nest boxes provided. (Zones

		boxes K-N in Figure 2).	boxes K-O in Figure 2).	A-J and nest boxes K-P in Figure 2).

Table 2. African pygmy dormice state behavior ethogram.

Category	Behavior	Description
Social	Aggressive interaction	Interaction involves more than one individual directing energy towards another in a confrontational manner. It may be presented with one running at another but will always result in physical interaction in the form of a bite, scratch or wrestle.
Immobile	Sit	The subject will have a small proportion of its hind quarters in contact with a surface within the accommodation. There will be no

		movement during the expression and often it is presented as a resting behavior.
	Dig	The subject will use its front peripheral limbs to repeatedly manipulate an area of substrate within the enclosure.
	Lying	A large proportion of the subject's body will be in contact with a surface within the enclosure, it is possible that the head will be elevated but the majority of the body will be in a relaxed state.
Grooming	Groom	The behavior can be carried out by one or multiple subjects during the investigation. It will involve the subject using their peripheral limbs to manipulate the fur of another individual, the behavior can be directed towards itself and it is common for the mouth components to be used during this exercise.
	Scratching	This behavior will allow for the subject to engage with an area of its own body by using their hind limbs in a repetitive motion to make contact with an area of particular interest.
Locomotive Behaviors	Climb	The subject will be observed to travel in a vertical motion at a point within the enclosure, this will allow for them to reach a higher surface and exercise various muscles.
	Walk	This behavior is carried out by the subject moving their front and hind limbs in a motion that allows for movement from one area to another. It is not carried out at a fast gait and will be expressed in an attempt of the individual moving from one place to another.
	Run	The subject will travel with speed from one place to another, this is carried out much like the walk but expressed using a faster and wider gait.
Abnormal Behaviors	Scratching at the glass	The subject will be identified using their back legs as an anchor point and using their front limbs to repetitively focus on an area of the glass surrounding the accommodation. This behavior will not serve any obvious function.
Consumption	Eating	The subject will be identified to collect a piece of food item and manipulate it with their front periphery limbs before placing it into the mouth or using their teeth to rapidly gnaw away at the food piece.
Other behaviors	Nest building	The subject will be observed moving from one location to another collecting small materials that are suitable for creating an idealistic nesting environment. The materials will be carried in the incisors of the subject and will often be placed in situated nest boxes.
	Gnaw	The subject will be identified to use their front incisors to repetitively chew at a fixture or fitting within the accommodation.
Nesting	Nesting	Subject is inside a nest and is not visible.

Table 3. Chi-Squared results for changes in state behavior (total time in minutes) between the five experimental phases. Aggression was only shown in Phase 1. In each comparison df=4 except scratching at glass when df=1. All comparisons were significant at P<0.0000000001. Bonferroni

corrected alpha q* = 0.0045, Benjamini and Hochberg (1995) corrected alpha q* = 0.05. Significant Yes denotes significant at all corrected alpha levels.

Behavior	**Phase 1**	**Phase 2**	**Phase 3**	**Phase 4**	**Phase 5**	**X^2**	**Significant**
Groom	86	294	129	76	53	295.056	Yes
Aggression	2	0	0	0	0	--	Yes
Climb	141	737	530	445	496	392.573	Yes
Walk	95	660	775	807	925	649.901	Yes
Gnaw	71	522	518	493	545	377.577	Yes
Nest-Building	230	607	582	523	613	203.065	Yes
Running	117	772	514	523	637	460.541	Yes
Eating	496	1010	1010	1370	1652	684.662	Yes
Scratching at Glass	327	12	0	0	0	292.699	Yes
Scratching	29	436	364	393	552	431.710	Yes
Sit	552	986	915	1016	999	169.849	Yes
Dig	39	518	409	492	638	495.207	Yes

Table 4. Space use across the five experimental phases (total count in minutes). mSPI value and meaning shown, as is Chi-square value for each zone. df=4 in each comparison. Use of each zone was significantly different across experimental phases at P<0.001 for every zone.

Zone Reference	**Zone size (%)**	**Experimental Phase**					**X^2**
		Phase 1: Baseline	**Phase 2: Climbing Grid**	**Phase 3: Nest Box Lower**	**Phase 4: Nest Box Middle**	**Phase 5: Nest Box Higher**	
J	3	0	833	789	820	1030	919.863
I	3	0	969	853	1039	1315	1182.38
H	16	1	835	691	952	888	894.293
G	16	0	793	495	536	603	714.283
F	16	24	388	314	211	267	313.965
E	16	2	402	251	231	263	361.614
D	9	50	560	347	278	292	434.549
C	9	96	580	579	489	470	362.509
B	6	936	489	502	520	517	249.411
A	6	1076	978	925	1062	1465	164.136
mSPI value		**0.83**	**0.31**	**0.38**	**0.39**	**0.44**	
mSPI meaning		**Unequal zone use**	**Fairly equal zone use**	**Fairly equal zone use**	**Fairly equal zone use**	**Fairly equal zone use**	

Figure 1. Climbing Grid enrichment and Woven-wicker bird nests added to enrich existing African pygmy dormouse enclosure. Bird nests were added sequentially over several days, one-at-a-time starting at the lower tier, ending at the higher tier.

Figure 2. Enclosure zones to facilitate modified Spread of Participation Index calculations. The enclosure was divided into 10 zones (A – I). The six nest boxes provided are also shown (K, L, M existing terrestrial nest boxes, N, O, P woven enrichment nest boxes). Enclosure size 60cm (h) x 45cm (w) x 60cm (d).

Figure 3. Collective time spent nesting (percentage total observation time) of the mouse group (eight adults) across each of the five experimental phases.

Figure 4. Activity budgets of the African pygmy dormice group during each experimental phase. Time is expressed as a percentage of the time spent (minutes) active (not nesting). *** significant difference $P<0.001$.

Figure 5. Changes in nest box use (total count) across the five experimental phases. Nest box use was recorded continuously (every mouse, every nest box use counted). Different nest boxes are represented by different colored/patterned bars. The letter of each nest box relates to the space use zone it was attributed (see Figure 2). Nest boxes K, L and M were the original terrestrial nest boxes (available in all experimental phases), nest boxes N, O, P were the novel raised nest boxes (available in experimental phases 3, 4, or 5).