

https://dspace.org/

A mouse in the spotlight Response capacity to artificial light at night in a rodent pest species the southern multimammate mouse Mastomys coucha

Tasha Oosthuizen; Neville Pillay; Maria Oosthuisen

ACADEMIC PRESS LTD- ELSEVIER SCIENCE LTD
https://hdl.handle.net/10539/43135
WOS

Downloaded from a DSpace repository. https://dspace.org/

Journal of Environmental Management 372 (2024) 123373



Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman



Research article

A mouse in the spotlight: Response capacity to artificial light at night in a rodent pest species, the southern multimammate mouse (*Mastomys coucha*)

Tasha Oosthuizen [a,*], Neville Pillay [a], Maria K. Oosthuizen [a,b,c]

[a] School of Animal, Plant and Environmental Sciences, University of Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050, South Africa
[b] Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028, South Africa
[c] Mammal Research Institute, University of Pretoria, Hatfield, 0028, South Africa

ARTICLE INFO

Keywords:
Activity profile
Artificial light at night
Circadian rhythms
Mastomys
Nocturnal rodent
Urbanisation

ABSTRACT

Multimammate mice are prolific breeders, can cause significant agricultural damage, and are reservoir hosts for a number of pathogens. They are nocturnal and given their success in urbanised rural environments, we were interested in how they would respond to increasingly bright anthropogenic spaces. We evaluated the locomotor activity of southern multimammate mice (*Mastomys coucha*), under four treatments: in an outdoor enclosure with natural light and temperature fluctuations, in a laboratory under a standard light regime, and two artificial light at night (ALAN) regimes (2 Lux) of varying proximity. The study animals remained nocturnal for the duration of the experiments. They were more active under the laboratory conditions with lower day-time light levels compared to the outdoor treatment but reduced their activity under ALAN. When the night light originated remotely, activity levels decreased by more than 50%, whereas under direct ALAN from above the cages, there was a 75% decrease in activity. The onset of activity was later during the two LAN treatments. We concluded that *Mastomys coucha* is strongly averse to light and show severe behavioural and circadian responses to light at night. We predict that it is unlikely that *Mastomys* will flourish in cities, but that they could thrive in and around dark urbanised refugia.

1. Introduction

Rodents are essential components of ecosystems; they perform several critical ecosystem services and can have both positive and negative effects on the environment (Fischer et al., 2018). Generally, rodents have a high adaptive capacity to new and changing environments, although not all species acclimatise successfully to the fast anthropogenic changes or the close proximity to humans (Auffray et al., 2009). Urbanisation leads to habitat loss and fragmentation and is associated with several other anthropogenic disturbances such as air and water pollution, noise and artificial light at night (Liu et al., 2016; Raap et al., 2015).

The natural light-dark cycle is the most predictable environmental cue and provides crucial signals for wildlife to regulate their circadian and seasonal rhythms (Benstaali et al., 2001; Griffiths, 1986; Ikeno et al., 2014). Wildlife have evolved with the natural light cycle over many years and are adapted to occupy specific temporal niches so that they are active at the times of the day that provide them with the greatest fitness benefits (Kronfeld-Schor and Dayan, 2008). Light affects nocturnal and diurnal animals in different ways (Bourgin and Hubbard, 2016). Artificial light at night (ALAN) can disturb the temporal niches of animals by suppressing activity in nocturnal animals while diurnal animals can potentially expand their active time (Mendoza, 2021; Shuboni et al., 2015). Most rodents are nocturnal and therefore have the potential to be negatively affected by light at night to a greater extent than diurnal species (Gerkema et al., 2013).

Locomotor activity is frequently used as a proxy for circadian phase and overall disposition of animals, as it coincides with many other physiological and behavioural rhythms (Ackermann et al., 2020; Benstaali et al., 2001). ALAN can disrupt circadian rhythms of activity, other behaviours and physiological processes, as well as annual rhythms such as reproduction, communication, feeding patterns, and competition (Navara and Nelson, 2007). Such changes in natural behaviours can result in extensive disruptions to ecosystems and have fitness and survival implications for wildlife (Navara and Nelson, 2007).

The multimammate mouse (*Mastomys* spp.) is the most widespread rodent complex in Africa (Colangelo et al., 2013). Two *Mastomys* species occur in South Africa, *M. coucha* and *natalensis* (Monadjem et al., 2015).

* Corresponding author.
E-mail addresses: 2579791@students.wits.ac.za (T. Oosthuizen), Neville.Pillay@wits.ac.za (N. Pillay), moosthuizen@zoology.up.ac.za (M.K. Oosthuizen).

https://doi.org/10.1016/j.jenvman.2024.123373
Received 8 August 2024; Received in revised form 12 November 2024; Accepted 13 November 2024
0301-4797/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

They are indistinguishable from one another morphologically, but their chromosomal numbers differ and there is no evidence of interbreeding (Green et al., 1980). *Mastomys coucha* is associated with higher altitude habitats than *M. natalensis*, although they overlap somewhat in their ranges (Kneidinger et al., 2014). The species have similar habits (Skinner and Chimimba, 2005) and both species are frequently associated with urbanised landscapes (Avenant, 2011). Because of its proclivity for human habitations, *Mastomys* is of interest for several reasons.

The multimammate mouse is an opportunistic, granivorous omnivore (De Graaff, 1981), and assists with seed dispersal, pollination and is prey for a diverse group of predators (Jones and Safi, 2011). However, *Mastomys* is prone to population explosions in favourable conditions and at high densities, it can cause devastation to crops such as maize and sorghum (Mulungu et al., 2011; Mwanjabe et al., 2002). Thus, it is regarded as a pest species of major economic importance in sub-Saharan Africa (Van Hooft et al., 2008).

Mastomys species are pioneer species, because they colonise recently disturbed areas, for example, post-fire landscapes and become quickly established and exploit these areas (Manyonyi et al., 2020). They are abundant in human-disturbed habitats and therefore act as indicators of poor ecosystem integrity (Avenant, 2011). Multimammate mice are also of medical importance, because they can act as disease reservoirs and transmission of disease vectors such as Bubonic plague (Davis, 1964) and Lassa virus (Monath et al., 1974).

Given the widespread distribution, economic and medical significance, and tendency to gravitate towards human settlements, we found it pertinent to investigate the responses of the southern multimammate mouse (*M. coucha*) to urbanisation, and specifically to increased artificial light at night. This mouse is nocturnal in nature and remains strictly nocturnal in captivity (Makundi et al., 2009; Perrin, 1981). Nevertheless, it is very successful in urbanised environments. Although many wildlife populations tend to avoid urban areas, the multimammate mouse exploits a variety of urbanised environments to the extent that it is regarded as a pest. Therefore, we were interested in whether the multimammate mouse, a strictly nocturnal rodent, will be able to adapt and thrive in the increasingly illuminated urban environment.

We assessed the response capacity to anthropogenic-driven artificial light at night by performing controlled experiments on multimammate mice under different ambient conditions. Activity is a useful proxy for the internal circadian environment of organisms and provides an accurate representation of their temporal inclinations. It also coincides with a large number of physiological rhythms (Koubi et al., 1991). We evaluated the locomotor activity of the mice housed in an outdoor enclosure where they were exposed to natural light and temperatures, to obtain a close representation of the natural behaviour of the mice. We expected the mice to be nocturnal with their locomotor activity distributed relatively evenly over the night. The activity of the mice was also assessed in a standard laboratory environment that resembles darker human dwellings in rural areas. We anticipated that the mice would remain nocturnal and that the onsets of activity would be more robust since the distinction between light and dark is more abrupt. Animals were exposed to two different ALAN treatments in the laboratory, first from a remote corner in the experimental room with 2 Lux at cage level (rLAN), then from directly above the animal cages with 2 Lux at the cage floor (dLAN). We predicted that the activity of the mice would show a reduction with rLAN and that the onset of activity may be delayed. A further reduction in activity was anticipated under dLAN because the light is more direct and intense. Since the sample contained equal numbers of male and female animals, we also compared the sexes under each treatment. We did not specifically expect differences between the sexes.

2. Materials and methods

2.1. Study animals

We trapped 19 southern multimammate mice in the Cradle Nature Reserve, Gauteng, South Africa (−25.9214, 27.8503) during the austral summer of 2023. The trapping site is located close to the largest metropolitan area in southern Africa. The study site is characterised by a dry winter and wet summer and falls within the Magaliesberg Biosphere Reserve South Africa, which is primarily part of the Savanna biome (Mucina and Rutherford, 2006). The mice were captured using PVC live small mammal traps baited with a mixture of oats, peanut butter, salt, sunflower oil, and sunflower seeds. Since *M. coucha* is nocturnal, traps remained open during the night only and were checked before sunrise each morning. We obtained permission to trap small mammals from the Gauteng Department of Agriculture and Rural Development (permit CPF6-0231).

Species identity was confirmed through DNA analysis against GenBank sequence reference number: KY754025.1. Trapped mice were taken to a field laboratory approximately 500m from the trapping site. They were then weighed (Pescola® hanging scale, Switzerland, to the nearest gram), sexed using the anogenital distance (larger distance present in males), and housed individually in transparent cages (60 x 40 × 36 cm) for the duration of the experiment. Each cage contained approximately 2 cm of sand (Kiddies play sand, EDCO Trading cc, RSA) and a shelter. A rock, stick and empty toilet roll served as enrichment. Mice had *ad libitum* access to water and were fed a combination of seeds and fresh food (millet and sunflower seeds with a piece of apple, carrot, or sweet potato) once per day. Each cage was equipped with an infrared motion sensor (BMT Digital PIR Motion Sensor, Communica, RSA) placed approximately three-quarters to the back of the cage lid to capture any movement of a mouse on VitalView software (VitalViewTM, Minimitter Co., Sunriver, USA). All cages were separated with cardboard dividers to prevent visual signals between neighbouring mice and IR motion sensors from capturing the activity of neighbouring individuals. Mice were weighed, and cages were cleaned after each experimental treatment (every 14 days).

2.2. Experimental design

Mice were subjected to four treatments in succession. The treatments were not counterbalanced, as we were trying to eliminate further confounding factors by exposing all mice to the same environmental factors (temperature and light) during the first treatment that took place outside under natural conditions. During this first treatment (designated as NAT), mice were housed in an open enclosure adjacent to the laboratory. The enclosure had a roof to prevent direct sunlight or rain from entering the cages and was fenced off to prevent direct contact with predators, such that they were protected but were exposed to natural light and temperature cycles. Mice were tested once in each treatment, for a period of 13 days. The mice were acclimated to the experimental conditions for three days, followed by 10 experimental days. Since no dramatic changes in activity were observed between the acclimation period and the experimental period, three days were deemed sufficient, and this protocol was repeated for each of the remaining treatments. For the second treatment (designated as LAB), the mice were transferred to an enclosed standard laboratory room with controlled environmental conditions at 24 °C ± 1 °C and a 12h light:12h dark light cycle. The overhead LAB lights measured at approximately 40 Lux and automatically switched on at 06:00 and switched off at 18:00. During the third treatment, (designated as rLAN; remote light at night), the original laboratory conditions were retained, while dim light was presented during the dark phase of the light cycle, with a LED lightbulb (LightWorx, 9W 3000K LED, LightWorx LED & Electric Supply LLC, USA) on the opposite side of the laboratory room. The light bulb was dimmed to 2 Lux at cage level with a rotary dimmer (500W rotary dimmer, Shuttle,

RSA). The night light penetrated the transparent cages, which resulted in a light intensity of 1.5 Lux inside the cage, as measured with a hand-held Lux meter (Major Tech, RSA, to the nearest 0.01 Lux). Following the rLAN treatment results, a reduced exploratory treatment was added. During this complementary treatment, the original laboratory conditions were retained, but the animals were exposed to direct light at night (designated as dLAN) consisting of warm white LED strip lights (12 V/DC 3528) fixed above the cages that were dimmed to 2 Lux at the level of the floor of the cages. The number of animals was reduced to 14 in this treatment as a result of limited available strip lights, and because a heightened negative response was anticipated, we reduced the number of experimental days to seven. For the rLAN and dLAN treatments, the night lights remained on during the night and day. Experimental procedures were approved by the University of Witwatersrand Animal Ethics Committee (2021/08/09/B).

2.3. Data analyses

Activity data, recorded using VitalView software, was visually assessed using ActiView (ActiView™, Minimitter Co., Sunriver, United States). We recorded data as counts per minute per mouse, and we summed the minute data to counts per hour per mouse for data analysis. The data set was tested for normality using the Anderson-Darling normality test and was not normally distributed ($P < 0.05$). We analysed the data using a generalized linear mixed model (GLMM) with a Gamma distribution and log link function in R software (R v4.2.1, Boston, United States). Activity counts per hour were used as the response variable and the mouse identity as the random variable. The fixed variables included experimental treatment (NAT, LAB, rLAN and dLAN), time of day (light or dark), sex and all interaction terms. For the analysis, the dawn and dusk period of NAT were not regarded as a separate light phase, all treatments were divided in 12 h light and 12 h dark to be able to compare activity between treatments. Tukey HSD post-hoc comparisons were performed for all significant variables. We determined the onset of activity of each mouse by recording the mean time the mouse became active during each treatment. A similar approach was followed to determine the offset of activity, i.e., the mean time the mouse stopped activity during each treatment. To analyse whether the onset and offset of activity differed between experimental treatments, we conducted a Kruskal-Wallis test, because the onset and offset were not normally distributed ($P < 0.05$). We then compared the treatments using the Dunn test with the Bonferroni method. The duration of the biological rhythm (tau) was computed in ClockLab (ClockLab™, Actimetrics, USA) and we ran a Kruskal Wallis test with the Dunn test and Bonferroni method to analyse whether the duration of activity differed between treatments. We also assessed the period the mice were active (alpha; time activity stopped – activity start time) for the LAB, rLAN and dLAN treatments using ClockLab and analysed this in the same way as the onset and offset data, because the active period of the mice was also not normally distributed ($P < 0.05$).

3. Results

The activity of the multimammate mice differed significantly during the four treatments ($\chi^2 = 470.13$, df = 3, $P < 0.001$, Fig. 1). Activity levels were significantly higher in the LAB treatment compared to all other treatments ($P < 0.001$ for all, Fig. 1). Compared to the LAB treatment, the activity was 11.1% lower during the NAT treatment, 55.7% lower under the rLAN, and decreased by 75.5% under the dLAN treatment The activity levels in the NAT treatment were higher than both the rLAN and dLAN treatments ($P < 0.001$ for both, Fig. 1), and mice were more active during the rLAN treatment compared to the dLAN treatment ($P < 0.001$, Fig. 1). Overall, mice were significantly more active during the dark phase compared to the light phase ($\chi^2 = 7219.07$, df = 1, $P < 0.001$); and males were significantly more active than females ($\chi^2 = 81.99$, df = 1, $P < 0.001$).

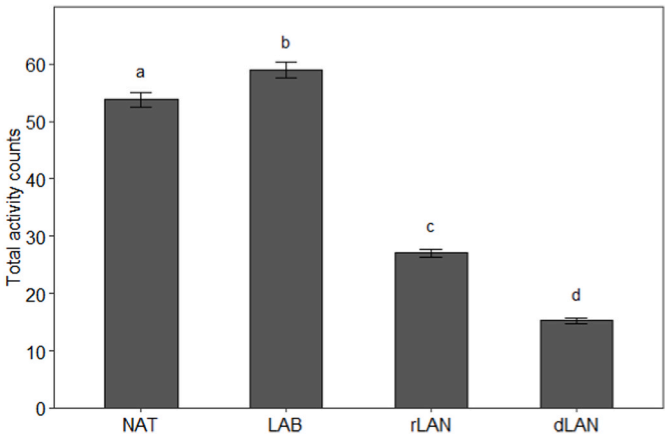


Fig. 1. The total activity counts (mean ± SE) of all *M. coucha* individuals in four experimental treatments. The same letters on the plots indicate non-significant differences between treatments. NAT – natural environmental conditions, LAB – laboratory conditions, rLAN – light at night on the opposite side of the room and dLAN – light at night suspended directly above the cages.

The activity levels of the mice were significantly influenced by the interaction between treatment and time of day ($\chi^2 = 515.78$, df = 3, $P < 0.001$, Fig. 2). Activity for all treatments was higher during the dark phase compared to the light phase ($P < 0.001$ for all, Fig. 2). Activity in the dark phase was the highest in the LAB treatment, followed by the NAT treatment and then the rLAN treatment, with the lowest nocturnal activity during the dLAN treatment ($P < 0.001$ for all, Fig. 2). None of the remaining comparisons were significant ($P \geq 0.620$, Fig. 2).

The interaction between treatment and sex influenced the activity levels of the mice ($\chi^2 = 7.27$, df = 3, $P < 0.001$, Fig. 3). Both males and females showed higher activity scores in the LAB treatment compared to all other treatments, followed by the NAT and rLAN treatments and they displayed the lowest activity under the dLAN treatment ($P < 0.001$ for all, Fig. 3). Males were significantly more active than females during the NAT, LAB and rLAN treatments ($P \leq 0.002$, Fig. 3), but the two sexes were equally active during the dLAN treatment ($P = 0.398$, Fig. 3).

The interaction between time of day and sex was a significant predictor of activity ($\chi^2 = 67.06$, df = 1, $P < 0.001$, Fig. 4). During the dark phase, males were more active than females ($P < 0.001$, Fig. 4), but the sexes did not differ in their activity during the light phase ($P = 0.922$, Fig. 4). Both males and females were more active during the dark phase compared to the light phase ($P < 0.001$, Fig. 4).

The onset of activity of *M. coucha* differed significantly between

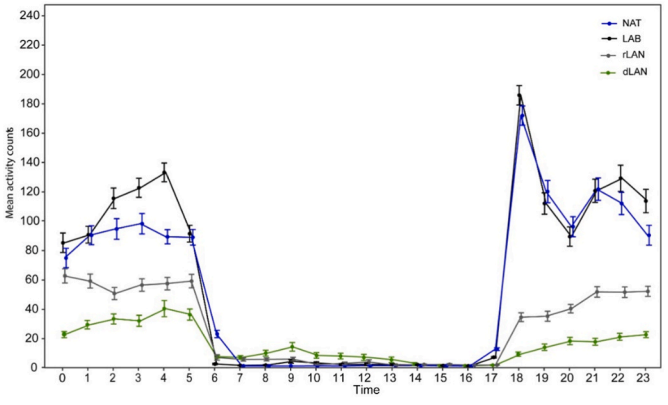


Fig. 2. The hourly activity counts (mean ± SE) for all individuals during the 24 h of the day in the different experimental treatments. NAT – natural environmental conditions, LAB – laboratory conditions, rLAN – light at night on the opposite side of the room and dLAN – light at night suspended directly above the cages.

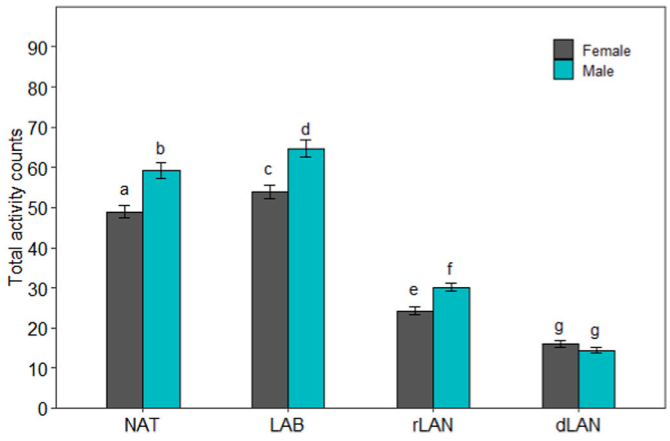


Fig. 3. The total activity counts (mean ± SE) of all the female and male *M. coucha* in four different experimental treatments. The same letters on the plots indicate non-significant differences between treatments. NAT – natural environmental conditions, LAB – laboratory conditions, rLAN – light at night on the opposite side of the room and dLAN – light at night suspended directly above the cages.

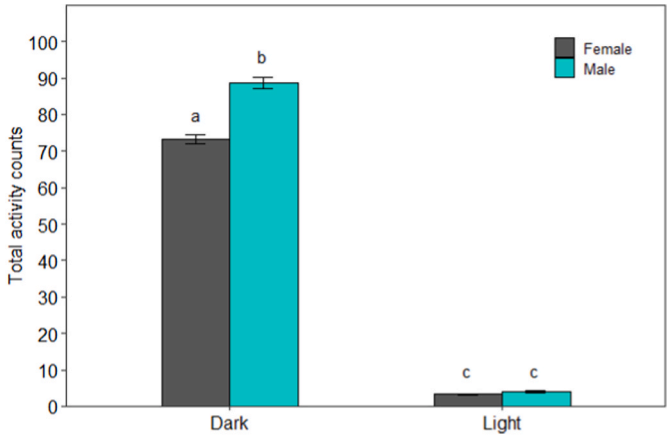


Fig. 4. The total activity counts (mean ± SE) of all the female and male *M. coucha* in the dark and light phases of the day. The same letters on the plots indicate non-significant differences between phases. NAT – natural environmental conditions, LAB – laboratory conditions, rLAN – light at night on the opposite side of the room and dLAN – light at night suspended directly above the cages.

treatments (Kruskal-Wallis test: $\chi^2 = 46.35$, df = 3, $P < 0.001$, Supplementary Table 1). It was delayed significantly for both of the LAN treatments compared to the NAT and LAB treatments. The mean onset of activity under the rLAN treatment was significantly later compared to both the NAT and LAB treatments ($P \leq 0.001$ for both, Supplementary Table 1), and activity under dLAN commenced later than NAT and LAN ($P \leq 0.001$ for both), but not rLAN ($P = 0.194$, Supplementary Table 1). The onset of activity was similar between the NAT and LAB treatments ($P = 0.998$, Fig. 5, Supplementary Table 1).

Similarly, there was a significant difference in the activity offset between treatments (Kruskal-Wallis test: $\chi^2 = 14.75$, df = 3, $P = 0.002$, Supplementary Table 1). During the dLAN treatment, the activity of the mice terminated significantly later compared to the NAT treatment ($P = 0.011$) and the LAB treatment ($P = 0.002$), but not the rLAN treatment ($P = 0.052$, Fig. 5). Activity terminated at the same time during the NAT, LAB and rLAN treatments ($P = 1.000$).

Treatment was not a significant predictor of the duration of activity (Kruskal-Wallis test: $\chi^2 = 4.92$, df = 3, $P = 0.178$, Supplementary Table 1). Although the mean period of the activity was slightly longer

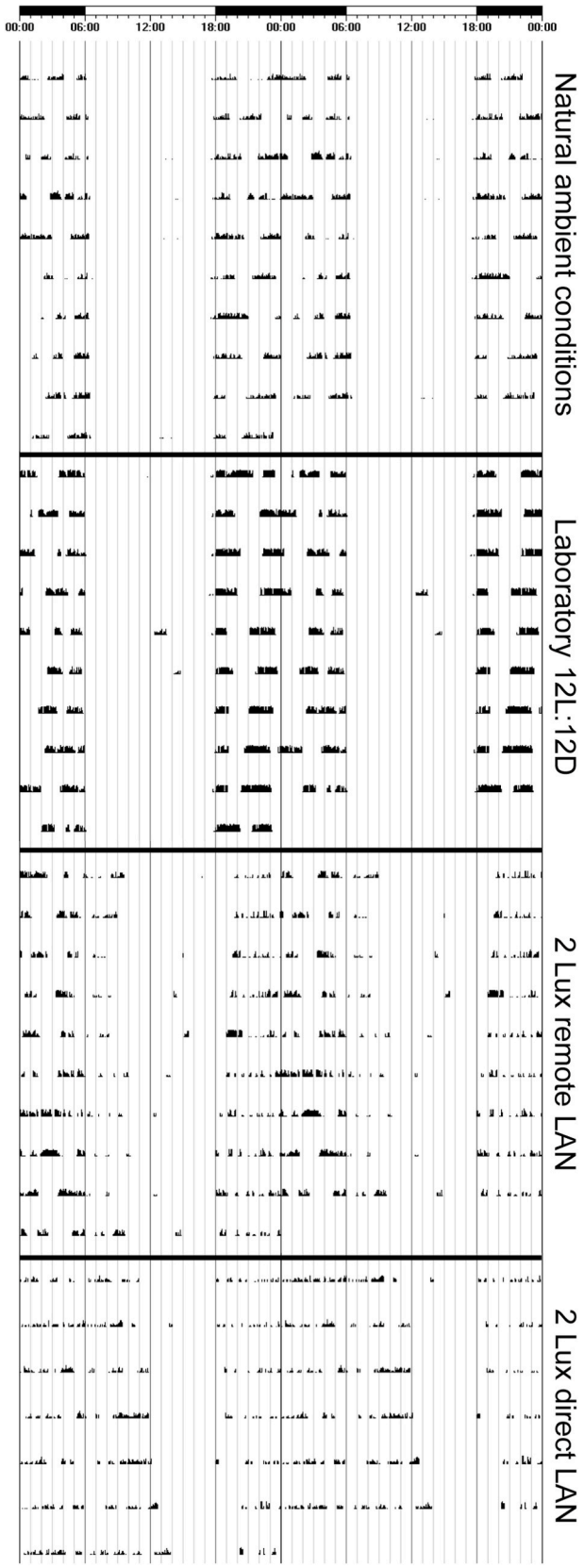


Fig. 5. A double-plotted actogram of a single *M. coucha* to illustrate the changes in onset (start of activity) and offset (end of activity) during the different experimental treatments. NAT – Natural ambient conditions, LAB – Laboratory 12L:12D, rLAN – 2 Lux remote LAN, dLAN – 2 Lux direct LAN. The top bar indicates the light and dark hours of each day, with two days represented next to each other. The black spikes illustrate activity counts per minute.

during dLAN compared to rLAN and LAB, this difference was not significant (τ: LAN – 23.98 ± 0.004; rLAN - 23.98 ± 0.04; dLAN – 24.26 ± 0.14; Kruskal-Wallis test: $\chi^2 = 3.86$, df = 2, P = 0.145).

4. Discussion

Mastomys species are remarkably successful in urbanised and cultivated areas. Because of their economic and medical importance, it is pertinent to investigate how *Mastomys* responds to anthropogenic disturbances that are associated with urbanisation, such as light at night. Here we investigated the locomotor activity of *Mastomys coucha* under natural environmental conditions while contained in cages and in the laboratory.

4.1. Natural vs laboratory activity

Under natural environmental conditions, *M. coucha* emerged from its nests shortly before complete darkness, terminated its activity soon after first light, and was inactive during the day. The activity occurred in intervals throughout the night. This is consistent with previous reports of *Mastomys* species (Isaacson, 1975; Monadjem et al., 2015).

In standard laboratory conditions, with immediate changes between light and dark, *M. coucha* remained strictly nocturnal, becoming active after the lights were switched off and activity was stopped immediately when lights were switched on again. This is typical for strictly nocturnal animals, several other rodent species show similar activity in the laboratory (Hoole et al., 2017; Robbers et al., 2015; Sharma and Daan, 2002; van der Merwe et al., 2014). The abrupt changes in lighting rendered the onset and offset of activity more precise than when the mice were exposed to natural light, which suggests that the activity is masked by light. Masking of activity by light was also observed in a laboratory setup with a reduction in activity in the nocturnal African pygmy mouse (*Mus minutoides*) (Viljoen and Oosthuizen, 2023) and the house mouse (*Mus musculus*), but only during specific times of the day (Shuboni et al., 2012).

The mice were more active in the laboratory compared to under natural light. The light intensity of the overhead lights in the laboratory was much lower than the natural light and is likely the driver of the increased activity levels observed. The highveld mole-rat, a subterranean rodent that is adapted for life in dark environments, showed a similar phenomenon of reduced activity under higher light intensities (Chanel et al., 2024). Nocturnal Namaqua rock mice (*Micaelamys namaquensis;* van der Merwe et al., 2017) and social voles (*Microtis socialis;* Zubidat et al., 2009) displayed lower activity counts and lower energetic expenditure (indicative of lower activity) when the daytime light intensity became reduced. The social voles also showed increased urinary cortisol metabolites under low daytime light levels which suggests that unnatural light conditions are stressful to the animals, and the increased activity could be an anxiety response. Captive-bred nocturnal Syrian hamsters (*Mesocricetus auratus*) reduced their activity when the photophase intensity was reduced in the laboratory (Labyak et al., 1998). In this case, higher light intensities provide stronger environmental signals for entrainment, and hence more robust activity patterns were observed. Interestingly, two syntopic rodent species (*Otomys angoniensis* and *Lemniscomys rosalia*) that were investigated under similar experimental conditions, but exhibited more diurnal activity, showed a decrease in activity in the laboratory compared to activity under natural conditions (Oosthuizen, 2024; Oosthuizen et al., 2024).

4.2. Artificial light at night

Artificial light at night is more persistent throughout the night and can be orders of magnitude brighter than natural levels of light at night created by celestial bodies (Stöckl and Foster, 2022). Typically, nocturnal animals are affected more severely than diurnal animals by unnatural changes during the night. When *M. coucha* was exposed to 2 Lux light at night from a remote light source, it decreased its activity by more than 50%, and when the light source was directly above the housing containers, activity was reduced by approximately 75%. Previous studies also showed a reduction in the activity of nocturnal rodents, such as *M. musculus* and *M. minutoides*, when they were presented with LAN in the laboratory (Shuboni et al., 2015; Viljoen and Oosthuizen, 2023). They can also show signs of depressive behaviours, reduced learning and memory (Fonken et al., 2012) and altered times of food consumption (Fonken et al., 2010).

Both the intensity and proximity of the light source appear to affect the response of the animals. Patagonian leaf-eared mice (*Phyllotis xanthopygus*) and African pygmy mice (*M. minutoides*) both showed significantly less activity under high levels of nocturnal illumination in the laboratory (Kramer and Birney, 2001; Viljoen and Oosthuizen, 2023), while the multimammate mouse was less active when presented with direct overhead LAN compared to when the light source was in a corner of the room (this study). When presented with LAN from a remote light source, mice in our study had the advantage of remaining behind features in their containers, and therefore could remain active while shielded from the light. Under a light source directly from above, the light may be perceived more intensely because they could not escape it unless they remained in their shelters.

The onsets and offsets of activity were less defined under the two LAN treatments compared to the standard laboratory treatment. During the remote light treatment, activity initially commenced later and then became earlier again. Offsets, however, extended past the time that the overhead lights were switched on again for the duration of this treatment. This may be driven by energetic requirements. When the LAN was presented directly above the housing containers, the activity of some animals appeared to drift, onsets started later each evening, and similarly, the offsets became later each consecutive day. This implies a disruption in the daily cycles of these animals such that they could not distinguish between day and night anymore, and they started displaying their internal circadian rhythm. Typically, under constant light, circadian rhythms are longer than 24 h (Benstaali et al., 2001), which appeared to be the case with some of the study animals. The extent of the response of *M. coucha* under direct lighting was surprising, compared to other syntopic nocturnal rodents. When the *M. minutoides* was exposed to artificial light at night, its activity never exceeded past the commencement of the simulated twilight periods, even with an 88% reduction in activity (Viljoen and Oosthuizen, 2023).

4.3. Potential ecological implications

We conclude that *M. coucha* is strongly averse to light, as evidenced by the increase in nocturnal activity in an overall darker environment. It also shows similar or more severe behavioural and circadian changes than other nocturnal rodents exposed to illuminated night conditions. Despite its activity being masked by light, multimammate mice naturally thrive in close proximity to humans (Dalecky et al., 2024). They are attracted to the abundance of food, and in turn can provide a challenge in terms of food security and public health (Dalecky et al., 2024). However, *Mastomys* species are unlikely to flourish in cities, in particular because of the extent of artificial light at night in and around these areas. Males showed to be more active than females in all treatments except during dLAN, indicating that bright environments were perceived as high risk for both sexes which could influence the success of finding a mate and breeding. In addition, it appears that *Mastomys* is absent where domesticated species such as house mice and rats are present (Davis, 1953; Isaacson, 1975), although this may be coincidental and result from the differing habits or competition between the different species. In African villages where multimammate mice are abundant, closed houses or houses without electricity provide dark environments for the mice and even enable them to be active during the day (Lalis and Wirth, 2018). The increased activity of the *M. coucha* in the darker laboratory conditions in our study also suggest that the mice are more comfortable

in environments with low illumination. Human-wildlife conflict, particularly with rodents, needs different approaches and perspectives. Our study suggests that artificial light at night might mitigate multimammate mice invasions in homesteads and agricultural areas but creates electricity costs and impacts on other wildlife. Homesteads without artificial light at night could benefit from better management of the environment by practicing cleanliness about food storage (e.g. no open food and storage in rodent-proof containers) to discourage rodents (Dalecky et al., 2024).

CRediT authorship contribution statement

Tasha Oosthuizen: Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation. **Neville Pillay:** Writing – review & editing, Supervision, Funding acquisition, Resources. **Maria K. Oosthuizen:** Writing – review & editing, Visualization, Supervision, Resources, Methodology, Conceptualization.

Funding sources

The financial support to conduct this study was provided by the University of Witwatersrand (Wits 7741) and the Lee Berger Foundation (#BSAL015).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We acknowledge Mr Tim Nash and the Nash Foundation for allowing us to use the Cradle Nature Reserve as a study site, collect animals and conduct expeirments on their property. We thank the staff at the Cradle Nature Reserve for their assistance and Prof Lee Berger for funding and technical support. We are grateful for the help of several volunteers throughout the study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.123373.

Data availability

The data is uploaded on Figshare and is available with the following link: https://doi.org/10.6084/m9.figshare.26363452.v1.

References

Ackermann, S., Bennett, N.C., Oosthuizen, M.K., 2020. The effect of varying laboratory conditions on the locomotor activity of the nocturnal Namaqua rock mouse (*Micaelamys namaquensis*) and the diurnal Four-striped grass mouse (*Rhabdomys dilectus*). Zoology 141, 125804. https://doi.org/10.1016/j.zool.2020.125804.

Auffray, J., Renaud, S., Claude, J., 2009. Rodent biodiversity in changing environments. Kasetsart J./Nat. Sci. 43, 83–93.

Avenant, N., 2011. The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of South African grasslands. Wildl. Res. 38, 626. https://doi.org/10.1071/WR10223.

Benstaali, C., Mailloux, A., Bogdan, A., Auzéby, A., Touitou, Y., 2001. Circadian rhythms of body temperature and motor activity in rodents. Life Sci. 68, 2645–2656. https://doi.org/10.1016/S0024-3205(01)01081-5.

Bourgin, P., Hubbard, J., 2016. Alerting or somnogenic light: pick your color. PLoS Biol. 14, e2000111. https://doi.org/10.1371/journal.pbio.2000111.

Chanel, P., Bennett, N.C., Oosthuizen, M.K., 2024. Light sensitivity of the circadian system in the social highveld mole-rat, Cryptomys hottentotus pretoriae. J. Exp. Biol. 227, jeb247793. https://doi.org/10.1242/JEB.247793.

Colangelo, P., Verheyen, E., Leirs, H., Tatard, C., Denys, C., Dobigny, G., Duplantier, J.-M., Brouat, C., Granjon, L., Lecompte, E., 2013. A mitochondrial phylogeographic scenario for the most widespread African rodent, *Mastomys natalensis*. Biol. J. Linn. Soc. 108, 901–916. https://doi.org/10.1111/bij.12013.

Dalecky, A., Sow, I., Ibrahim Danzabarma, A.A., Garba, M., Etougbétché, J., Badou, S., Dossou, H.-J., Niang, C.T., Diene, O., Diallo, I., Saghiri, M.S.A., Sidatt, M.E.H., van Steenbergen, F., Bal, A.B., Bosma, L., Houéménou, G., Ag Atteynine, S., Hima, K., Dobigny, G., Meheretu, Y., 2024. From problem to progress: rodent management in agricultural settings of sub-Saharan Africa and calling for an urban perspective. Crop Prot 181, 106673. https://doi.org/10.1016/j.cropro.2024.106673.

Davis, D.H., 1953. Plague in Africa from 1935 to 1949; a survey of wild rodents in African territories. Bull. World Health Organ. 9, 665–700.

Davis, D.H.S., 1964. Ecology of wild rodent plague. In: Ecological Studies in Southern Africa, pp. 301–314.

De Graaff, G., 1981. The rodents of southern Africa: Notes on their identification, distribution, ecology and taxonomy. Butterworths, Pretoria.

Fischer, C., Gayer, C., Kurucz, K., Riesch, F., Tscharntke, T., Batáry, P., 2018. Ecosystem services and disservices provided by small rodents in arable fields: effects of local and landscape management. J. Appl. Ecol. 55, 548–558. https://doi.org/10.1111/1365-2664.13016.

Fonken, L.K., Kitsmiller, E., Smale, L., Nelson, R.J., 2012. Dim nighttime light impairs cognition and provokes depressive-like responses in a diurnal rodent. J. Biol. Rhythms 27, 319–327. https://doi.org/10.1177/0748730412448324.

Fonken, L.K., Workman, J.L., Walton, J.C., Weil, Z.M., Morris, J.S., Haim, A., Nelson, R. J., 2010. Light at night increases body mass by shifting the time of food intake. Proc. Natl. Acad. Sci. 107, 18664–18669. https://doi.org/10.1073/pnas.1008734107.

Gerkema, M.P., Davies, W.I.L., Foster, R.G., Menaker, M., Hut, R.A., 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. Proc. R. Soc. B Biol. Sci. 280, 20130508. https://doi.org/10.1098/rspb.2013.0508.

Green, C.A., Keogh, H., Gordon, D.H., Pinto, M., Hartwig, E.K., 1980. The distribution, identification, and naming of the *Mastomys natalensis* species complex in southern Africa (Rodentia: muridae). J. Zool. 192, 17–23. https://doi.org/10.1111/J.1469-7998.1980.TB04215.X.

Griffiths, R.A., 1986. Natural environmental cues and circadian rhythms of behaviour - a perspective. Chronobiol. Int. 3, 247–253. https://doi.org/10.3109/07420528609079542.

Hoole, C., McKechnie, A.E., Parker, D.M., Bennett, N.C., 2017. The endogenous activity patterns of Africa's smallest terrestrial mammal, the pygmy mouse (*Mus minutoides*). Can. J. Zool. 95, 745–752. https://doi.org/10.1139/cjz-2016-0250.

Ikeno, T., Weil, Z.M., Nelson, R.J., 2014. Dim light at night disrupts the short-day response in Siberian hamsters. Gen. Comp. Endocrinol. 197, 56–64. https://doi.org/10.1016/j.ygcen.2013.12.005.

Isaacson, M., 1975. The ecology of *Praomys* (*Mastomys*) *natalensis* in southern Africa. Bull. World Health Organ. 52, 629–636.

Jones, K.E., Safi, K., 2011. Ecology and evolution of mammalian biodiversity. Philos. Trans. R. Soc. B Biol. Sci. 366, 2451–2461. https://doi.org/10.1098/rstb.2011.0090.

Kneidinger, C.M., van Heerden, H., MacFadyen, D., van der Merwe, M., Avenant, N.L., van der Bank, H., 2014. Species identification, habitat preferences and population genetics of *Mastomys natalensis* (A. Smith, 1834). Navors. van die Nas. museum Bloemfontein 30, 1–15. M. coucha (A. Smith, 1836) in an enclosed area, Kruger National Park, South Africa.

Koubi, H.E., Robin, J.P., Dewasmes, G., Le Maho, Y., Frutoso, J., Minaire, Y., 1991. Fasting-induced rise in locomotor activity in rats coincides with increased protein utilization. Physiol. Behav. 50, 337–343. https://doi.org/10.1016/0031-9384(91)90075-Y.

Kramer, K.M., Birney, E.C., 2001. Effect of light intensity on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. J. Mammal. 82, 535–544. https://doi.org/10.1644/1545-1542(2001)082<0535:EOLIOA>2.0.CO;2.

Kronfeld-Schor, N., Dayan, T., 2008. Activity patterns of rodents: the physiological ecology of biological rhythms. Biol. Rhythm. Res. 39, 193–211. https://doi.org/10.1080/09291010701683268.

Labyak, S.E., Turek, F.W., Wallen, E.P., Zee, P.C., 1998. Effects of bright light on age-related changes in the locomotor activity of Syrian hamsters. Am. J. Physiol. Integr. Comp. Physiol. 274, R830–R839. https://doi.org/10.1152/ajpregu.1998.274.3.R830.

Lalis, A., Wirth, T., 2018. Mice and men: an evolutionary history of Lassa fever. In: Biodiversity and Evolution. Elsevier, pp. 189–212. https://doi.org/10.1016/B978-1-78548-277-9.50011-5.

Liu, Z., He, C., Wu, J., 2016. The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. PLoS One 11, e0154613. https://doi.org/10.1371/journal.pone.0154613.

Makundi, R.H., Massawe, A.W., Mulungu, L.S., Katakweba, A., 2009. Species diversity and population dynamics of rodents in a farm-fallow field mosaic system in Central Tanzania. Afr. J. Ecol. 48, 313–320. https://doi.org/10.1111/j.1365-2028.2009.01109.x.

Manyonyi, A.M., Mariki, S.B., Mnyone, L.L., Belmain, S.R., Mulungu, L.S., 2020. Effects of prescribed burning on rodent community ecology in Serengeti National Park. J. Vertebr. Biol. 69, 1–13. https://doi.org/10.25225/jvb.20001.

Mendoza, J., 2021. Nighttime light hurts mammalian physiology: what diurnal rodent models are telling us. Clocks and Sleep 3, 236–250. https://doi.org/10.3390/clockssleep3020014.

Monadjem, A., Taylor, P.J., Denys, C., Cotterill, F.P.D., 2015. Rodents of Sub-saharan Africa, Rodents of Sub-saharan Africa. DE GRUYTER. https://doi.org/10.1515/9783110301915/HTML.

Monath, T.P., Newhouse, V.F., Kemp, G.E., Setzer, H.W., Cacciapuoti, A., 1974. Lassa virus isolation from *Mastomys natalensis* rodents during an epidemic in Sierra Leone. Science 185, 263–265. https://doi.org/10.1126/science.185.4147.263.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Mulungu, L.S., Massawe, A.W., Kennis, J., Crauwels, D., Eiseb, S., Mahlaba, T.A., Monadjem, A., Makundi, R.H., Katakweba, A.A.S., Leirs, H., Belmain, S.R., 2011. Differences in diet between two rodent species, *Mastomys natalensis* and *Gerbilliscus vicinus*, in fallow land habitats in central Tanzania. African Zool 46, 387–392. https://doi.org/10.1080/15627020.2011.11407512.

Mwanjabe, P.S., Sirima, F.B., Lusingu, J., 2002. Crop losses due to outbreaks of *Mastomys natalensis* (smith, 1834) muridae, rodentia, in the lindi region of Tanzania. Int. Biodeterior. Biodegradation 49, 133–137.

Navara, K.J., Nelson, R.J., 2007. The dark side of light at night: physiological, epidemiological, and ecological consequences. J. Pineal Res. 43, 215–224. https://doi.org/10.1111/j.1600-079X.2007.00473.x.

Oosthuizen, T., 2024. Effects and Consequences of Natural and Artificial Light at Night on Small Mammals in Peri-Urban Johannesburg, South Africa. University of Witwatersrand. PhD thesis.

Oosthuizen, T., Pillay, N., Oosthuizen, M.K., 2024. Wild mice in an urbanized world: effects of light at night under natural and laboratory conditions in the single-striped grass mouse (*Lemniscomys rosalia*). Chronobiol. Int. 41, 347–355. https://doi.org/10.1080/07420528.2024.2317284.

Perrin, M.R., 1981. Notes on the activity patterns of 12 species of southern African rodents and a new design of activity monitor. South African J. Zool. 16, 248–258. https://doi.org/10.1080/02541858.1981.11447763.

Raap, T., Pinxten, R., Eens, M., 2015. Light pollution disrupts sleep in free-living animals. Sci. Rep. 5, 13557. https://doi.org/10.1038/srep13557.

Robbers, Y., Koster, E.A.S., Krijbolder, D.I., Ruijs, A., van Berloo, S., Meijer, J.H., 2015. Temporal behaviour profiles of *Mus musculus* in nature are affected by population activity. Physiol. Behav. 139, 351–360. https://doi.org/10.1016/j.physbeh.2014.11.020.

Sharma, V.K., Daan, S., 2002. Circadian phase and period responses to light stimuli in two nocturnal rodents. Chronobiol. Int. 19, 659–670. https://doi.org/10.1081/CBI-120005389.

Shuboni, D.D., Cramm, S., Yan, L., Nunez, A.A., Smale, L., 2012. Acute behavioral responses to light and darkness in nocturnal *Mus musculus* and diurnal *Arvicanthis niloticus*. J. Biol. Rhythms 27, 299–307. https://doi.org/10.1177/0748730412449723.

Shuboni, D.D., Cramm, S.L., Yan, L., Ramanathan, C., Cavanaugh, B.L., Nunez, A.A., Smale, L., 2015. Acute effects of light on the brain and behavior of diurnal *Arvicanthis niloticus* and nocturnal *Mus musculus*. Physiol. Behav. 138, 75–86. https://doi.org/10.1016/j.physbeh.2014.09.006.

Skinner, J.D., Chimimba, C.T., 2005. The Mammals of the Southern African Sub-region, third. Cambridge University Press, Cape Town.

Stöckl, A.L., Foster, J.J., 2022. Night skies through animals' eyes - quantifying night-time visual scenes and light pollution as viewed by animals. Front. Cell. Neurosci. 16, 1–19. https://doi.org/10.3389/fncel.2022.984282.

van der Merwe, I., Bennett, N., Haim, A., Oosthuizen, M.K., 2014. Locomotor activity in the Namaqua rock mouse (*Micaelamys namaquensis*): entrainment by light manipulations. Can. J. Zool. 1091, 1083–1091.

van der Merwe, I., Oosthuizen, M.K., Ganswindt, A., Haim, A., Bennett, N.C., 2017. Effects of photophase illuminance on locomotor activity, urine production and urinary 6-sulfatoxymelatonin in nocturnal and diurnal South African rodents. J. Exp. Biol. 220, 1684–1692. https://doi.org/10.1242/jeb.146951.

Van Hooft, P., Cosson, J.F., Vibe-Petersen, S., Leirs, H., 2008. Dispersal in *Mastomys natalensis* mice: use of fine-scale genetic analyses for pest management. Hereditas 145, 262–273. https://doi.org/10.1111/j.1601-5223.2008.02089.x.

Viljoen, A., Oosthuizen, M.K., 2023. Dim light at night affects the locomotor activity of nocturnal African pygmy mice (*Mus minutoides*) in an intensity-dependent manner. Proc. R. Soc. B Biol. Sci. 290, 20230526. https://doi.org/10.1098/rspb.2023.0526.

Zubidat, A.E., Nelson, R.J., Haim, A., 2009. Photosensitivity to different light intensities in blind and sighted rodents. J. Exp. Biol. 212, 3857–3864. https://doi.org/10.1242/jeb.033969.