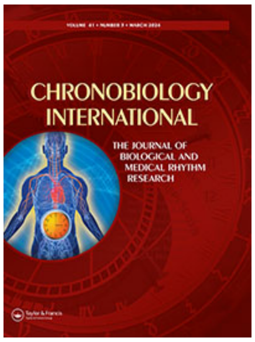

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ORIGINAL ARTICLE

Wild mice in an urbanized world: Effects of light at night under natural and laboratory conditions in the single-striped grass mouse (*Lemniscomys rosalia*)

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ABSTRACT

Urbanization, and the accompanying artificial light at night (ALAN), can disrupt the activity of animals. Such disruptions at the base of a food web can ripple through the ecosystem. Most studies of ALAN are performed in the laboratory. Thus, we lack basic information about the circadian responses of animals under natural environmental conditions to fully evaluate the impact of ALAN. We studied the behaviour and activity of wild-caught, peri-urban single-striped grass mice (*Lemniscomys rosalia*) under a natural treatment and in a standard laboratory treatment, including dim light at night to mimic conditions that they could experience. The species exhibited predominantly crepuscular activity under all experimental treatments. It showed the highest level of activity under the natural treatment, whereas ALAN significantly suppressed its activity. Males were more active than females under all experimental treatments. The marked changes in activity under ALAN is of particular concern since global change in combination with urbanization can lead to a change in vegetation density and composition that will decrease the number of suitable microhabitats and expose small mammals to novel habitat changes. We suggest that the single-striped mice could become vulnerable because of urbanization, leading to impacts on its ecosystem broadly.

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Activity; laboratory; rodent; natural environmental conditions; urbanization; artificial light at night

Introduction

Urbanization is increasing rapidly worldwide, and the accompanying environmental changes create new challenges for wildlife (Sanders et al. 2021). In addition to habitat loss, anthropogenic disturbances such as artificial light at night (ALAN) poses a significant threat to the natural behaviours of animals (Ikeno et al. 2014; Mazza et al. 2019). In their natural habitats, animals synchronise their physiology and behaviour to cyclic environmental cues, with the light-dark cycle being the most prominent and reliable cue (Aschoff 1960; Benstaali et al. 2001). ALAN can alter the perception of light levels, causing animals to shift or modify their temporal and/or spatial activity patterns (Dupke et al. 2017; Gaynor et al. 2018).

Temporal activity patterns of mammals evolved over millennia. Early mammals are believed to have been nocturnal, with diurnality emerging as a secondary evolutionary trait (Roll et al. 2006). Globally, about 70% of all mammals are nocturnal (Bennie et al. 2014), and many species show anatomical adaptations of their visual systems that match their temporal niches (Peichl 2005). Nocturnal animals usually have a larger proportion of rods in their retinae that have low acuity but are very sensitive to light, whereas diurnal animals have a higher proportion of cones adapted for colour vision, with a high acuity but a lower sensitivity (Peichl 2005; van der Merwe et al. 2018). Nevertheless, both nocturnal and diurnal species are affected by ALAN. Light can affect animals in two ways, the first is masking, a direct and immediate effect that does not alter entrainment of the circadian rhythms, and the second is the disruption in the circadian responses by altering the length and expression of the rhythm (Hoffmann et al. 2018; Mrosovsky 1999). In their natural habitat, diurnal and nocturnal animals experience light at different times of the temporal day, and also at different intensities, and can therefore have different responses to light at night. Diurnal animals can extend their active time into the night, thereby disrupting their sleep patterns (Aschoff 1960; Fonken et al. 2010; Russart and Nelson 2018). In contrast, the activity of nocturnal animals may be suppressed (Aschoff 1960; Viljoen and Oosthuizen 2023; Zhang et al. 2020).

Experiments to test the effect of ALAN are often conducted under controlled laboratory settings where

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environmental conditions such as ambient temperature and light are kept constant (Ackermann et al. 2020; Kronfeld-Schor et al. 2013). The laboratory environment eliminates variation in environmental variables, and results are more predictable and easier to interpret. However, it is not always clear whether laboratory outcomes are representative of behaviour in natural environments (Calisi and Bentley 2009). Several studies highlight differences in the circadian behaviour of animals in the laboratory and the field (Blanchong et al. 1999; Levy et al. 2007; Rotics et al. 2011a,2011b; Yan et al. 2020).

To investigate how animals would react in a natural environment, a more realistic approach should be adopted (Ackermann et al. 2020; Kronfeld-Schor et al. 2013). A blend between a laboratory and a natural treatment on the same individuals would be an ideal approach since this would provide an opportunity to assess the response capacity of animals to changing environmental conditions. A natural environment has fluctuating temperature and lighting conditions and a natural soundscape. For example, in response to a simulated dawn and dusk period in a laboratory setting, diurnal animals extended their activity into the increased light hours (Ackermann et al. 2020), such that these results could be more representative of animal behaviour in a natural environment. In another study, researchers compared the activity of four-striped mice (*Rhabdomys pumilio*) in a natural enclosure with that of the same species in the laboratory under a square wave light cycle (light switches on and off immediately without a dawn and dusk period). The results revealed similar activity patterns between the two groups, but the onsets and offsets of activity differed (Schumann et al. 2005).

The effect of anthropogenic disturbances on southern African small mammals is virtually unknown. The circadian biology of several rodents and other small mammalian species has been investigated in the laboratory (Ackermann et al. 2020; Hoole et al. 2012,2017; Perrin 1981; Ribble and Perrin 2005; Schumann et al. 2005; van der Merwe et al. 2011,2012,2014), some more detailed than others. Only a single, very recent study considered the effects of ALAN on the behaviour of a southern African rodent (Viljoen and Oosthuizen 2023). This illustrates a significant paucity in published literature on the effect of light at night on African small mammals.

We studied a small African rodent, the single-striped grass mouse (*Lemniscomys rosalia*), originating from a peri-urban area (Skinner and Chimimba 2005). This species is terrestrial, mostly herbivorous and is found within grasslands with long and dense grasses that provide good cover (Monadjem and Perrin 1997; Skinner and Chimimba 2005). Very little is known about the single-striped grass mouse, although it has been reported to be active during the day with possible crepuscular activity (Skinner and Chimimba 2005). Skinner and Chimimba (2005) also suggest that this species used burrows. However, several other sources indicate that they make untidy grass nests on the ground at the base of grass clumps (Chidumayo 1977; Kingdon 2013; Monadjem unpublished data; N Pillay personal observation). This species is solitary and have been observed to show aggressive interactions in the laboratory, yet males and females can share a nest in the presence of offspring (Kingdon 2013).

Our study is the first to empirically test the temporal activity of *Lemniscomys rosalia*. We assessed the locomotor activity of wild-caught single-striped grass mice under controlled light and temperatures in the laboratory and under natural ambient conditions in an outside enclosure. In the outside enclosure, animals were exposed to similar ambient conditions and other disturbances in their natural environment. Therefore, we expected their activity to closely resemble their natural behaviour. We compared the activity of single-striped grass mice under the natural environmental treatment with that under a standard laboratory treatment, and predicted more variable activity under natural conditions, whereas in the laboratory, we expected more activity during the day. We also evaluated the activity when animals were subjected to artificial light at night (ALAN) in the laboratory and compared this to activity under the standard laboratory treatment and the natural environmental treatment. We expected animals under ALAN to increase their activity compared to when they are exposed to dark nights in the laboratory, thus showing more activity compared to activity under natural conditions. We predicted that males would be more active than females since rodent males are normally the more explorative sex and more risk prone compared to females.

Materials and methods

Animal capture

Trapping took place during the austral spring of 2022 at the Cradle Nature Reserve (−25.9214, 27.8503), Gauteng, South Africa. The study site is located in a peri-urban area close to Johannesburg, the largest metropolitan area in Africa, and is therefore exposed to a high concentration of ALAN. We trapped mice using PVC small mammal live traps, baited with a mix of sunflower seeds, sunflower oil, oats, granola, salt and peanut butter. Traps were placed in areas with signs of rodent presence, such as rodent runways and beneath bushes. When a single-striped grass mouse was captured, it was transported to a field laboratory for further processing. At the laboratory, the mouse was weighed, sexed and checked for pregnancy. Pregnant animals were excluded from the study and released at the capture site. We used 19 adult single-striped grass mice (10 males (57.44 g ±3.45) and 9 females (45.38 g ±1.91)) in this study.

Animal maintenance

Study animals were housed individually in transparent, plastic experimental cages (60 × 40 x 36 cm). Mice were in their cages at least a month before the commencement of the experimentation. The cages had wire mesh lids and cage floors were layered with 2 cm of sand (Kiddies play sand, EDCO Trading cc, RSA) to cover the entire surface. Each cage had a plastic shelter, hay and tissue paper for nesting material, a rock and a stick for enrichment, and *ad libitum* water. Animals were fed daily at random times, and their diet consisted of fresh food (apples, carrots or sweet potato) and sunflower and millet seeds. To monitor body condition, the mice were weighed after each experimental treatment. The experimental procedures were approved by the University of Witwatersrand Animal Research Ethics Committee (2021/08/09/B) and we obtained a collection permit from the Gauteng Department of Agriculture and Rural Development (CPF6–0231).

Experimental design

The activity of the mice was detected using infrared motion detectors (BMT Digital PIR Motion Sensor, Communica, RSA). The sensors were mounted on top of the lids of each cage without blocking external light and positioned to cover movement of the whole floor. Cardboard dividers were inserted between cages to prevent neighbouring mice from influencing each other. Mice were allowed to acclimate to their surroundings for three days before experiments.

Mice were subjected to three experimental treatments in the following order: (1) laboratory (LAB), (2) artificial light at night (ALAN) and (3) natural ambient conditions (NAT). Each experimental treatment lasted 10 days during which locomotor activity counts were continuously recorded with VitalView software (VitalViewTM, Minimitter Co., Sunriver, OR, USA). The LAB treatment took place under standard laboratory conditions with 12 h dark and 12 h light (LED warm white light, Leroy Merlin, RSA; ±50 Lux at ground level) and constant temperature set to 24°C. During the ALAN treatment, environmental conditions remained the same as during LAB, but a LED light connected to a dimmer (Light: LightWorx, 9W 3000K LED, LightWorx LED & Electric Supply LLC, New Jersey; Dimmer: 500W rotary dimmer, Shuttle, Cape Town) was added to provide 2 Lux of indirect light at night at the level of the cages. The dim light remained on permanently for the duration of the ALAN experimental treatment; it was dim enough that it did not add additional light during the day. For the last treatment (NAT), mice were moved to an outside enclosure attached to the field laboratory (Figure S1). The enclosure had an opaque roof, and the sides were covered with wire mesh to expose mice to natural light and temperature, but not rain. The NAT treatment included the natural soundscape and anthropogenic disturbances such as noise, intermittent car traffic and lights, but the animals were trapped within close proximity of the laboratory, therefore the disturbances were not deemed novel. Cages were cleaned after every treatment.

Data analyses

Activity data were visually assessed using double-plotted actograms generated with ActiView (ActiView^{TM}, Minimitter Co., Sunriver, OR, United States). Activity counts were summed and recorded per minute and, were converted to per hour counts per animal and we analysed it using R (R v4.2.1, Boston, United States). The dataset was not normally distributed (Anderson-Darling normality test: $p < 0.05$), thus we analysed the data using a generalized linear mixed model (GLMM) with a Gamma distribution and log link function, using the lmer package (Bates et al. 2015). The response variable was activity counts, the fixed variables sex (male/female), experimental treatment (LAB, ALAN or NAT) and the time of day (light/dark), and we considered all interactions. To account for individual variation, we included the animal ID as the random variable. We used Tukey HSD for our post-hoc comparisons. Two males that displayed stereotypical behaviour (abnormally high activity and repetitive movements concentrated in one part of the cage), were excluded from the analyses, resulting in a final sample of 17 mice. A Spearman correlation ($p < 0.05$) was conducted to assess the relationship between the activity counts and temperature during the NAT treatment. The correlation was not performed on the laboratory conditions since the ambient temperature was constant during these treatments. We visually examined the actograms for each animal per experimental setting in order to determine the on and offsets of activity, however, the start and end of the activity were too variable over the days and between mice. This is also the reason the alpha (duration of activity) could not be determined accurately.

Results

The experimental treatment had a significant effect on the total activity counts ($\chi^2 = 104.395$, df = 2, $p < 0.001$, Figure 1). Mice were least active during ALAN and most active under the semi-natural environmental conditions (NAT) (NAT < LAB < ALAN, $p < 0.001$, Figure 1). Under NAT, the activity counts were weakly negatively correlated with the temperature ($r = -0.10$, $p > 0.001$, Figure 2).

Overall, sex did not influence the activity counts ($\chi^2 = 3.394$, df = 1, $p = 0.065$), but mice showed more activity during the night compared to the day ($\chi^2 = 365.569$, df = 1, $p < 0.001$, Figure 2).

The interaction between sex and experimental treatment significantly affected the activity ($\chi^2 = 77.872$, df = 2, $p < 0.001$, Figure 3a). Females showed significantly higher activity in NAT compared to both ALAN and LAB ($p < 0.001$ for both, Figure 3a). Males were significantly less active during ALAN compared to LAB and NAT ($p < 0.001$ for both, Figure 3a). Across all three settings, males were more active than the females ($p \leq 0.014$, Figure 3a). All other interactions between sex and experimental treatment were not significant ($p \geq 0.249$, Figure 3a).

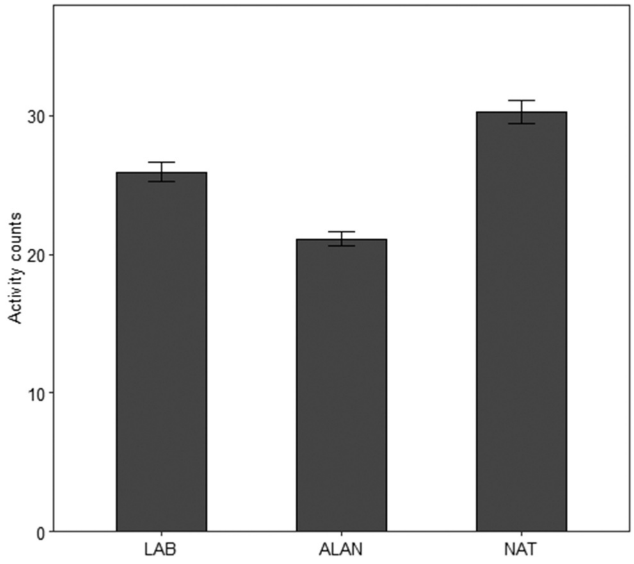

Figure 1. The total activity counts of all *Lemniscomys rosalia* (mean ± SE) during the three environmental treatments (LAB – laboratory treatment, ALAN – 2 lux light at night, NAT – semi-natural environmental treatment). Bars with the same letters indicate non-significant differences.

The interaction between sex and time of day significantly affected the level of activity ($\chi^2 = 52.823$, df = 1, $p < 0.001$, Figure 3b). Both males and females were significantly less active during the light phase compared to the dark phase ($p < 0.001$, Figure 3b) and females were significantly less active during the dark period compared to males ($p < 0.001$, Figure 3b). None of the remaining comparisons involving sex and time of day affected the activity ($p \geq 0.5081$, Figure 3b).

Activity was significantly influenced by the interaction between the experimental treatment and time of day ($\chi^2 = 140.3561$, df = 2, $p < 0.001$, Figure 3c). During the dark phase, mice displayed reduced activity under ALAN compared to LAB and NAT and lower activity during LAB than NAT (NAT < LAB < ALAN; $p < 0.001$ for all interactions, Figure 3c). Under ALAN, the activity counts were lower during the light compared to the dark phase ($p = 0.004$, Figure 3c), and the same was observed for LAB and NAT ($p < 0.001$ for both, Figure 3c). No other comparisons between the experimental treatment and time of day were significant ($p \geq 0.160$, Figure 3c).

The three-way interaction between sex, experimental treatment and time of day did not affect the activity counts ($\chi^2 = 1.434$, df = 2, $p = 0.488$).

Discussion

Urbanization and the accompanying anthropogenic changes transform both the spatial and temporal landscapes of wildlife. Large areas of natural habitat are being transformed and, in addition to habitat loss, wildlife faces other disruptions, such as ALAN and anthropogenic noise (Willems et al. 2021). Rodents are an important component of ecosystems. However, the biology of most of southern Africa's rodents are poorly studied (Viljoen and Oosthuizen 2023). To predict the responses of rodents to anthropogenic changes and the broader implications for the ecosystem, it is important to investigate the effects of urbanization and its repercussions on wildlife. We investigated the locomotor activity of the single-striped grass mouse (*L. rosalia*) under standard and ALAN laboratory treatments and a natural environmental treatment to assess how they might be affected by anthropogenic pressures.

Single-striped mice displayed predominantly crepuscular activity with distinct peaks at dawn and dusk, but also some diurnal and nocturnal activity. The species was previously described as crepuscular (Monadjem et al. 2015), diurnal (Monadjem and Perrin 1997), or diurnal with some crepuscular activity (Skinner and Chimimba 2005). Nevertheless, our results showed that they were more active during dark hours compared

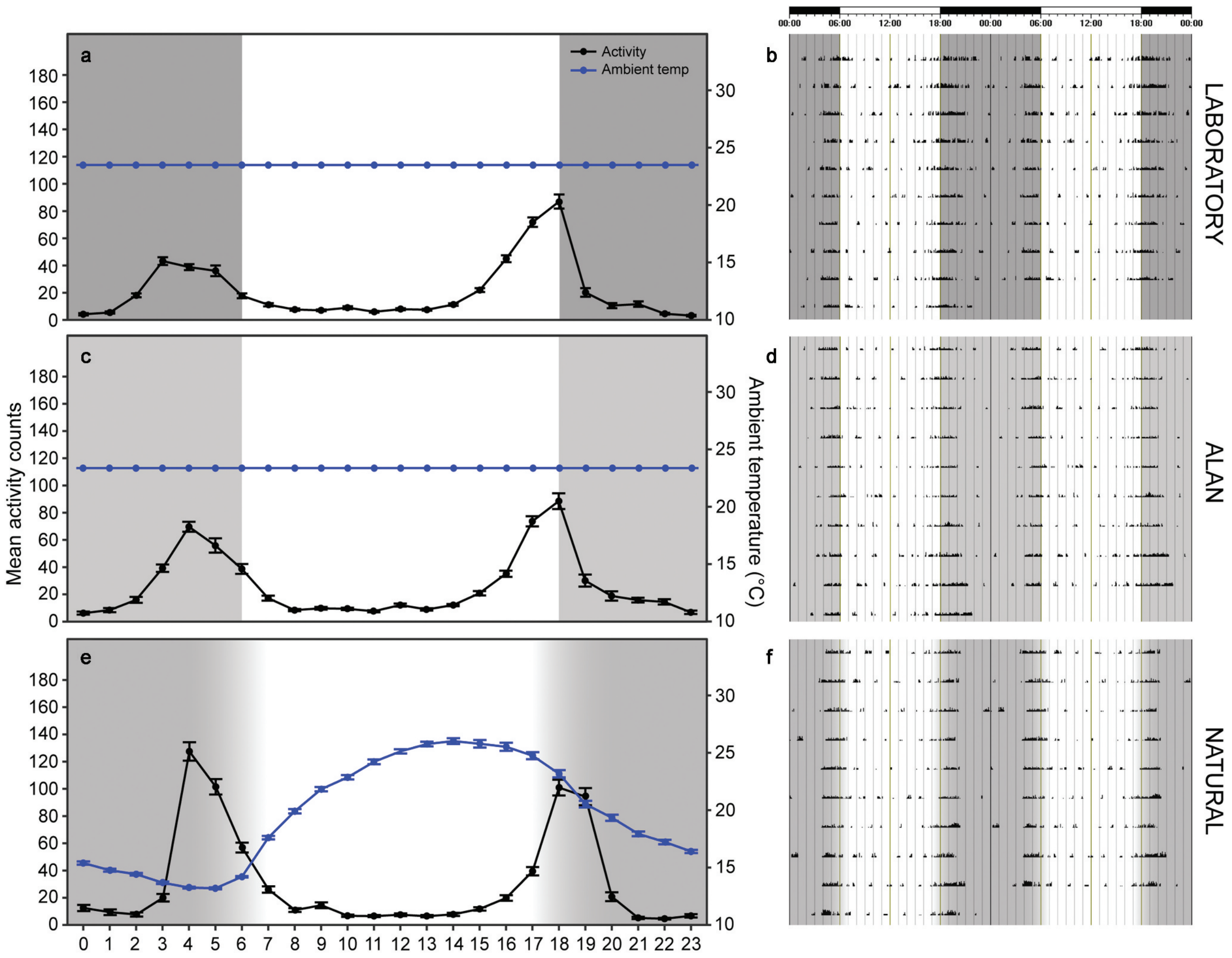

Figure 2. The activity of *Lemniscomys rosalia* over the 24-hour day for the three experimental treatments. A, C, E – hourly activity counts (mean ± SE) of all individuals (black line) and the ambient temperatures (blue line) during the three different treatments. B, D, F – Actograms of a single representative individual corresponding to the treatment in the figure to the left of it. The LAB (a and b) and ALAN (c and d) experimental treatments were on a square wave regime and a constant temperature, whereas NAT (e and f) mice were exposed to the natural dawn and dusk (approximately 05:00–07:00 and 17:00–19:00) and naturally fluctuating temperatures. Shaded areas show periods of darkness, and the faded periods between 05h00 and 07h00, and 17h00 and 19h00 indicate dawn and dusk.

to light hours during all three experimental treatments, although the level of recorded activity differed between treatments. We suggest that the transition period between light and dark was the significant driver behind their locomotor activity.

We assumed that the activity of the mice under the natural environmental treatment would be similar to the activity of the mice in their natural habitat. During the natural treatment, mice were exposed to both natural and anthropogenic sounds as well as natural light and indirect ALAN. Therefore, our setup is representative of an anthropogenic environment. As predicted, the mice displayed the highest level of activity under natural ambient conditions with the additional disturbances. The higher activity could be as a result of the natural temperature cycle. Ambient temperature cycles support and enhance locomotor activity rhythms, with animals displaying higher and more robust activity rhythms under ambient temperature cycles compared to constant ambient temperatures (van Jaarsveld et al. 2019). The decreased activity during daylight hours could be a result of competition with the diurnal four-striped grass mouse (*Rhabdomys* spp.) that occurs syntopically with *L. rosalia* where they were caught. Two *Acomys* species were found to display nocturnal activity when they occur separately, but when they occur together in the same space, temporal segregation was observed (Gutman et al. 2011).

In the laboratory, the single-striped mice were less active compared to the natural environmental

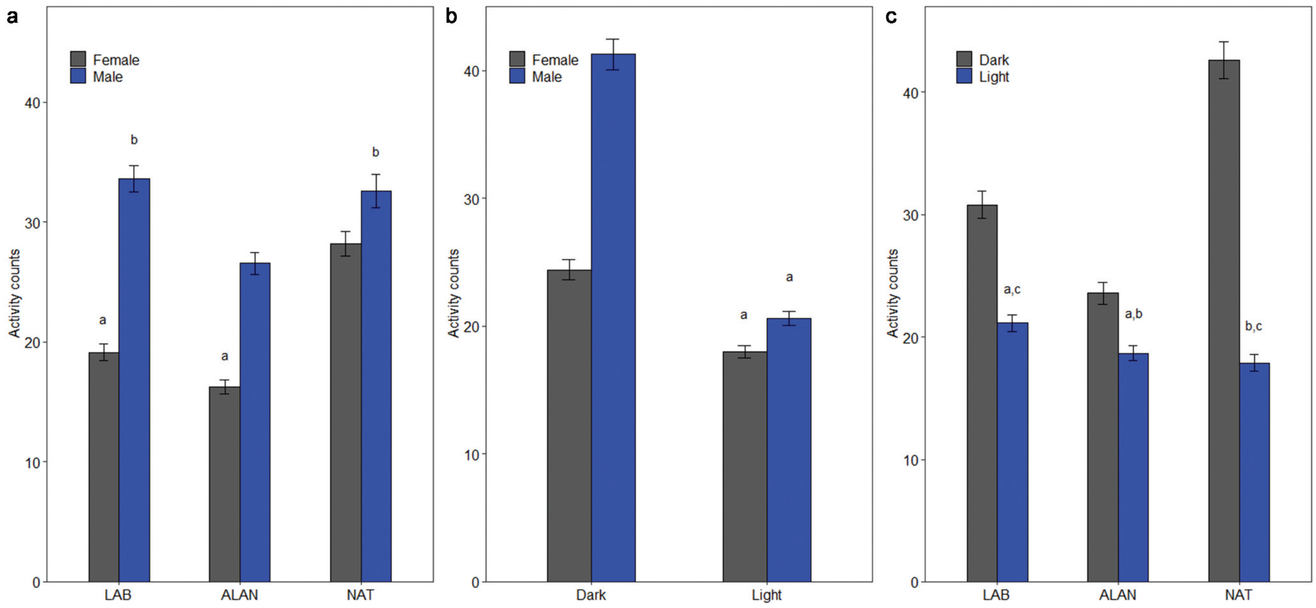

Figure 3. a – The total activity counts (mean ± SE) of male and female *Lemniscomys rosalia* during the three different experimental treatments. Bars with the same letters indicate insignificant differences. b – The total activity counts (mean ± SE) of male and female *Lemniscomys rosalia* during the light phase and dark phase during the three experimental treatments. Bars with the same letters indicate insignificant differences. c – The total activity counts (mean ± SE) of *Lemniscomys rosalia* during the dark and light phases of the three different experimental treatments. Bars with the same letters indicate insignificant differences.

conditions. They displayed a similar temporal activity profile but with a reduced activity peak at dawn. The reduced activity in the laboratory could result from wild-caught animals being housed in the laboratory. Laboratory conditions were darker and quieter, and can lead to stress in experimental animals. The overall activity decreased further when ALAN was added under the standard laboratory treatment. The mice were indirectly exposed to continuous ALAN in the laboratory for the duration of the night, which could have increased their anxious response over a longer period.

ALAN has variable effects on the behaviour and physiology of diurnal rodents, but little is known about its influence on crepuscular animals. Some species extend their active times into the night (reviewed in Gaynor et al. 2018), whereas others perceive the high illumination as high risk in terms of predation (Ditmer et al. 2021). In the diurnal Nile grass rat (*Arvicanthis niloticus*), ALAN has been linked to adverse behaviours such as depressive-like behaviours and reduced cognitive abilities (Fonken et al. 2009). Diurnal spiny mice (*A. russatus*), studied in a natural experimental setup under ALAN, showed increased stress levels that led to decreased reproductive output and survival (Vardi-Naim et al. 2022). Single-striped mice appear to fall in the latter group, showing more adverse effects under ALAN, acting more similar to nocturnal animals in response to ALAN by decreasing nocturnal activity. Caged animals are usually provided with reduced cover compared to animals in their natural environment, and ALAN in the laboratory is presented more continuously. Although mice in the outside enclosure in our study were also exposed to ALAN, the light was much further away and animals were not exposed to it continuously for the duration of the night. The ALAN treatment in our study represented a more intense scenario of light at night that would likely not be experienced naturally in peri-urban populations of single-striped grass mice.

Several previous studies raised concern regarding the extrapolation of laboratory results to natural environments since laboratory experiments are highly controlled and the ambient conditions are quite different from natural conditions (Ackermann et al. 2020; Kronfeld-Schor et al. 2013). However, our results illustrate that single-striped grass mice behave similarly in the laboratory and under natural conditions, although the magnitude of activity is greater under natural conditions. The effect of ALAN appears to be amplified under controlled conditions, probably because the light source was placed closer to the animals and for a more continuous period without a real escape for the mice. Therefore, we believe that the temporal activity that this species displayed in the laboratory can be extrapolated to field scenarios with relative confidence, although at a lower amplitude, and it obviously would not reflect the natural general behaviours of the animals.

Our study animals were wild-caught from a peri-urban study site and were therefore already exposed to some level of ALAN in their natural habitat. However, these mice are mainly found in areas with tall grasses and good vegetation cover (Skinner and Chimimba 2005) that provide shelter from both predators and ALAN, especially during the summer growing season. Densely vegetated areas are a critical resource for small mammals seeking refuge from predators and other unfavourable environmental conditions (Teckentrup et al. 2018). However, future climate change predictions forecast dryer and warmer climates in our study area that could drastically change the vegetation composition and density (Idris et al. 2022). The remaining dense vegetation could become highly attractive to a variety of species seeking refuge, resulting in competition that could ultimately affect individual fitness and the community structure. Single-striped mice are one of two grassland species (the other being *Rhabdomys dilectus*) that show some diurnal activity at our study site. They have similar life history traits and will likely share the same fate in response to habitat changes. Both species, serve as prey for a variety of predators, and should they disappear because of changes in their habitat, there will be knock-on effects for predators that are dependent on them as a food source.

Finally, we investigated the influence sex had on the activity. Males were more active during the laboratory treatment and the females more active during the natural treatment. This could be as a result of males being more explorative of a novel environment and risk prone compared to the more risk-averse females (Jolles et al. 2015). Both males and females showed the lowest activity during ALAN, possibly suggesting an increased predation risk for both males and females over the experimental period.

Conclusions

Our study provides the first comparisons of activity between traditional laboratory and natural environmental treatments in a wild-caught peri-urban South African rodent. We confirmed that the single-striped grass mouse is primarily crepuscular, with varying levels of diurnal activity and even more varied nocturnal activity. They were adversely affected by ALAN in the laboratory, as indicated by the reduction in activity, responding similarly to nocturnal species under the influence of ALAN. They were most active in the natural environmental treatment when exposed to naturally fluctuating light and temperature cues. We propose that activity under the natural treatment corresponds to the natural activity of the species, and they were not adversely affected by the presence of anthropogenic factors in our experimental setup, perhaps because the disturbances were not experienced directly. In their natural habitat, dense vegetation would buffer the effects of ALAN. Our study contributes to the conservation of biodiversity by assessing the response capacity of a species occupying a basal trophic level and how changes in its behaviour and survival could impact the ecosystem it occupies. Changes in the activity and behaviour in our study and in other studies in response to ALAN appears to be exaggerated in the laboratory but could be used to predict the future pressures and the response of rodents to expanding urbanization and the accompanying ALAN.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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