

## Light sensitivity and diel activity rhythms in the Angoni vlei rat (*Otomys angoniensis*) under natural and artificial conditions

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### ABSTRACT

Artificial light at night (ALAN) can disrupt daily rhythms of wildlife, yet little is known about its effects on African rodents. We investigated the diel activity rhythms of the Angoni vlei rat (*Otomys angoniensis*), a species with an inconclusive temporal niche. We exposed wild-caught vlei rats to three treatments: (1) standard laboratory light–dark cycle; (2) laboratory light–dark cycle with low-intensity ALAN (2 Lux); and (3) natural ambient light and temperature fluctuations. Activity was recorded via infrared sensors, and the activity rhythm was quantified using Cosinor analysis. Activity was predominantly nocturnal across all treatments. However, rhythm amplitude, MESOR and robustness were nearly three-times higher under natural conditions than in both laboratory treatments. ALAN did not significantly suppress activity, suggesting minimal masking effects (unlike strictly nocturnal animals) and possible flexibility in the temporal niche. In nature, *O. angoniensis* occupies dense grass habitats, and therefore, its predominantly nocturnal activity in captivity could be due to the lack of adequate cover during experiments. Moreover, the greater activity under natural conditions could be a consequence of brighter daytime light and natural temperature cycles. We suggest that although *O. angoniensis* displays nocturnal activity in the laboratory, it may be more diurnal in its natural habitat. Our findings demonstrate that the temporal activity of *O. angoniensis* is shaped by environmental context, with implications for contextualising circadian flexibility in species inhabiting human-altered landscapes.

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### Introduction


Circadian rhythms are fundamental biological processes that synchronise physiological and behavioural functions with the external environment. These endogenous rhythms are entrained primarily by the daily light – dark cycle and are crucial for regulating activity patterns in most animals (Aschoff 1960; Hut et al. 2012). The temporal niche (i.e. the time of day when an animal is active) represents a key component of ecological specialisation, shaped by physiological circadian characteristics and external ecological triggers, such as competition and predation, and abiotic factors, such as weather (Refinetti 2008; Gao et al. 2020). The temporal niche is a critical component of a species' ecology, yet it is poorly studied in free-living rodents, particularly under realistic environmental conditions.

Animals have evolved within their specific environments and are usually well adapted to their particular temporal niche. Active times are commonly categorised as nocturnal (night active), diurnal (day active),

crepuscular (active around dusk and dawn) or cathemeral (active during both the day and night) (Refinetti 2008). Animals can show specific morphological and physiological adaptations to their niches (Hut et al. 2012). While diurnal animals rely on vision to forage and avoid predation, nocturnal animals are more dependent on olfaction, auditory and tactile cues (Prugh and Golden 2014). The photoreceptor proportions in the retina can provide insight to the primary temporal niche of animals. Diurnal animals typically have higher proportions of cones compared to nocturnal animals (Peichl 2005). Cone photoreceptors have a high acuity but are relatively insensitive to light and are therefore well adapted to daylight vision, whereas rods have a lower acuity but are sensitive to light and are better suited for night vision (Peichl 2005).

Most mammals, and in particular rodents, are nocturnal (Roll et al. 2006; Kay and Hoekstra 2008) and are typically exposed to very low levels of environmental light at night. On moonless nights, the ambient light can be as low as 0.001 Lux and as high as 2 Lux on a full

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moon night (Emmer et al. 2018; Alaasam et al. 2021). Nocturnal rodents reduce their activity during full moon (Griffin et al. 2005), concentrate their activity to the darkest times of the night (Daly et al. 1992; Pratas-Santiago et al. 2017), and remain under dense cover during the brightest times (Mandelik et al. 2003). The behavioural changes in response to increased ambient light at night have energetic consequences, such as decreased food consumption and increased competition for refugia (Perea et al. 2011; Navarro-Castilla and Barja 2014; Finch et al. 2020). There is thus a trade-off between safety and meeting energetic requirements by foraging (Kotler et al. 2010; Viljoen and Oosthuizen 2023).

Artificial light at night (ALAN) is a pervasive by-product of urbanisation, alters the natural light – dark cycle and can disrupt circadian regulation in both diurnal and nocturnal animals (Raap et al. 2015). Even very dim (naturalistic) light at night, equivalent to that of the moon and stars, can affect circadian responses in ways similar to that of brighter intensities (Walbeek et al. 2021), presumably as a result of its persistence throughout the night. ALAN can exert effects via masking by suppressing or enhancing activity independent of entrainment or through shifts in circadian phase and amplitude (Bedrosian et al. 2013; Spoelstra et al. 2015). In the laboratory, several rodent species showed a reduction in activity in response to artificial light at night under intensities varying from 0.5 Lux to 3 Lux (Kramer and Birney 2001; Bedrosian et al. 2013; Viljoen and Oosthuizen 2023; Oosthuizen et al. 2024a, 2024b). However, most of these studies were conducted under controlled laboratory conditions, often neglecting natural environmental cues such as ambient temperature, acoustic environments and natural twilight gradients (Calisi and Bentley 2009; Bedrosian et al. 2013). Consequently, laboratory findings may not accurately reflect activity patterns or flexibility under natural conditions. Moreover, temporal activity patterns can sometimes differ completely between the laboratory and natural environments (Calisi and Bentley 2009). Several studies reported temporal niche switches, mostly from diurnal to nocturnal, when animals are brought into the laboratory (Blanchong et al. 1999; Begall et al. 2002; Tomotani et al. 2012). This prompts consideration of the biological significance of laboratory studies and the extent to which their findings can be applied to natural environments.

Southern African rodents are appropriate models for examining circadian flexibility due to their diversity in temporal niche occupation and exposure to environmental heterogeneity. The genus *Otomys* comprises medium-sized, herbivorous rodents that inhabit dense vegetation in mesic grasslands (Skinner and Chimimba 2005; Kingdon 2013). Reports of its diel activity patterns

are inconsistent, with species variously described as diurnal, nocturnal, or crepuscular (Davis 1972; Packer 1980; Skinner and Chimimba 2005; Webber and Oosthuizen 2025). This variation is also evident in species that predate on them, including nocturnal and diurnal species such as herons, owl species, raptors, felids, and jackals (Skinner and Chimimba 2005; Kingdon 2013). One species, the Angoni vlei rat (*O. angoniensis*), remains particularly understudied in terms of its circadian biology. This species can be found alone, in pairs or in small groups, and breeds during the wet summer months (Skinner and Chimimba 2005; Kingdon 2013). It is also known to leave distinct runways (tunnels in the long grass), which is often utilised by sympatric rodents (Skinner and Chimimba 2005).

The temporal organisation of *O. angoniensis* is currently poorly defined; therefore, our aim was to characterise the temporal activity in *O. angoniensis* under contrasting environmental contexts and to assess its circadian flexibility in relation to ALAN. Specifically, we investigated the diel activity rhythms of wild-caught *O. angoniensis* under three light regimes: a standard laboratory 12h light:12h dark cycle, the same cycle with dim ALAN (2 Lux); and a semi-natural enclosure with ambient light, temperature and sound fluctuations. We used motion sensors and Cosinor analysis to quantify activity rhythm parameters, including amplitude, acrophase, MESOR and robustness. Our approach was not to assume that the species is strictly nocturnal and instead tested whether its activity rhythm was fixed or modulated environmentally. We hypothesised that if *O. angoniensis* is truly nocturnal, ALAN would suppress activity via negative masking. However, if it displays flexible temporal niche changes, we expected minimal suppression under ALAN and under natural conditions.

## Materials and Methods

### Animal Capture and Maintenance

During the summer of 2023, 19 Angoni vlei rats (10 females and 9 males, Figure 1) were collected at an urban study site at the Cradle Nature Reserve, Gauteng, South Africa (−25.9214, 27.8503). We baited 45 PVC live traps with a combination of sunflower seeds, oil, oats, granola, salt and peanut butter. Traps were strategically placed within high-use rodent highways. After capture, the rats were weighed with a spring balance (Pescola® hanging scale, Switzerland, 1 g precision), and sexed (using anogenital distance) and females were examined for signs of pregnancy (swollen abdomen). Pregnant females were released at the location where they were caught and excluded from the experiments.



**Figure 1.** The Angoni vlei rat, *Otomys angoniensis*. Photo: MK Oosthuizen.

The rats were introduced into individual transparent, plastic containers (60 × 40 × 36 cm), filled with 2 cm of sand (Kiddies play sand, EDCO Trading cc, RSA). The individual cages were stationed at a field laboratory on the Cradle Nature Reserve property and the rats remained in the same cage for the duration of the experimental treatments. The lids of the cages were replaced with mesh and an infrared detector was mounted over each cage to detect animal movement (BMT Digital PIR Motion Sensor, Communica, RSA). The location of the detectors remained constant during all treatments. Cardboard dividers were placed between cages to prevent the IR sensors from capturing the activity of neighbouring rats and to avoid interactions between neighbouring individuals.

Each individual was provided with an empty plastic 1 L container, tissue paper and hay for nesting material. Enrichment materials included a rock and stick in each cage (Figure S1). However, there was no vegetation cover to ensure consistent exposure to light stimuli and activity detection with the IR sensors. The rats had *ad libitum* access to water and were fed a combination of dry food (sunflower seeds, yellow maize, and Burgess Excel Guinea Pig Nuggets, Burgess Group Inc., United Kingdom) and fresh food (carrot, apple, and sweet potato). They were also provided with fresh grass and hay (Tiny Friends Farm Russel Rabbit Tasty Hay, Marltons Pets and Products, United Kingdom) on alternate days. The rats were acclimated to the laboratory for a minimum of 5 days before the experiments commenced. The experiments were approved by the University of the Witwatersrand Animal Research Ethics Committee (2021/08/09/B) and the animals were trapped under a trapping permit from the Gauteng Department of Agriculture and Rural Development (CPF6-0231).

## Experimental Design

We assessed the activity of *O. angoniensis* in three consecutive experimental treatments during the austral summer. These included (1) standard laboratory conditions (LAB), (2) standard laboratory conditions with distantly placed light at night (ALAN – a light positioned on the opposite side of the room, providing indirect light), and (3) natural environmental conditions (NAT). Each treatment was preceded by three acclimation days, followed by 10 experimental days. The LAB treatment consisted of a room without external cues and the temperature was kept constant at 24°C ± 1°C, with the lighting set to 12 h light and 12 h dark (overhead lights used during the light phase measured ±40 Lux). After 13 days of the LAB treatment, a light (Light: LightWorx, 9W 3000K LED, LightWorx LED & Electric Supply LLC, New Jersey; Dimmer: 500W rotary dimmer, Shuttle, Cape Town), dimmed to 2 Lux, was introduced in the corner of the room for the ALAN treatment, to provide light at night. After the ALAN treatment, the rats were moved to an ambient laboratory, which consisted of an outdoor enclosure that was fenced off and roofed over. The fence prevented other animals (e.g. predators) from entering the space while allowing test rats to be exposed to natural temperature and light fluctuations. The roof prevented rain from affecting the electronic equipment (see above). In the NAT treatment, daytime light levels reached between 500 and 700 Lux at midday, whereas the natural night light levels were too low to be measured by the available handheld device (Major Tech, RSA, to the nearest 0.01 Lux). During the NAT treatment, sunrise and sunset occurred at 06:19 and 17:59, respectively. To facilitate comparison between the different treatments, daytime was analysed from 06:00 to 18:00, and nighttime from 18:00 to 06:00 for the NAT treatment. The infrared motion detectors captured activity counts per minute per animal using VitalView software (VitalView™, Minimitter Co., Sunriver, USA). Rats were weighed between treatments, while their cages were cleaned to ensure that no weight loss occurred.

Two morphologically similar vlei rat species co-occur in part of their distributional ranges, including our wider study site; therefore, we confirmed the identity of *Otomys angoniensis* genetically; GenBank sequence reference number was AM408343.1.

## Data Analyses

To visually assess activity data, actograms were generated for each individual rat using ActiView software (ActiView™, Minimitter Co., Sunriver, United States).

Per minute data were summed per hour for each animal. Data were analysed using R (v4.2.1, Boston, United States). The data set was tested for normality using the Anderson–Darling normality test, and the distribution was found to be not normal ( $p < 0.05$ ). A generalized linear mixed model (GLMM) was run using the *lmer* function of the “lme4” package (Bates et al. 2015). The hourly counts were used as the response variable in the GLMM with a Gamma distribution and log link function. The predictor variables were the experimental treatments (i.e. LAB, ALAN, and NAT), the time of day (i.e. light or dark hours of the day), the sex (male or female), and all interactions. The identity of all rats was included in the model as a random variable. Post-hoc analysis was completed for all significant variables, using the Tukey HSD method.

The amplitude, acrophase (activity peak), midline estimating statistic of rhythm (MESOR) and the robustness (strength of the rhythm, calculated as percentage of variance) were calculated per individual per treatment using one-minute bins in Cosinor (<https://www.circadian.org/>). After establishing that all variables were non-parametric (Shapiro–Wilk test:  $p < 0.05$ ), a Kruskal–Wallis test was performed for each independent variable against the treatment variable. A pairwise Wilcoxon test with a Benjamini–Hochberg adjustment was conducted where significant differences were detected. Since sex did not affect activity levels in the GLMM, we did not consider sex with the amplitude, acrophase, MESOR and robustness analyses.

## Results

The experimental treatment affected the activity counts of *O. angoniensis* significantly ( $\chi^2 = 3431.72$ ,  $df = 2$ ,  $p <$

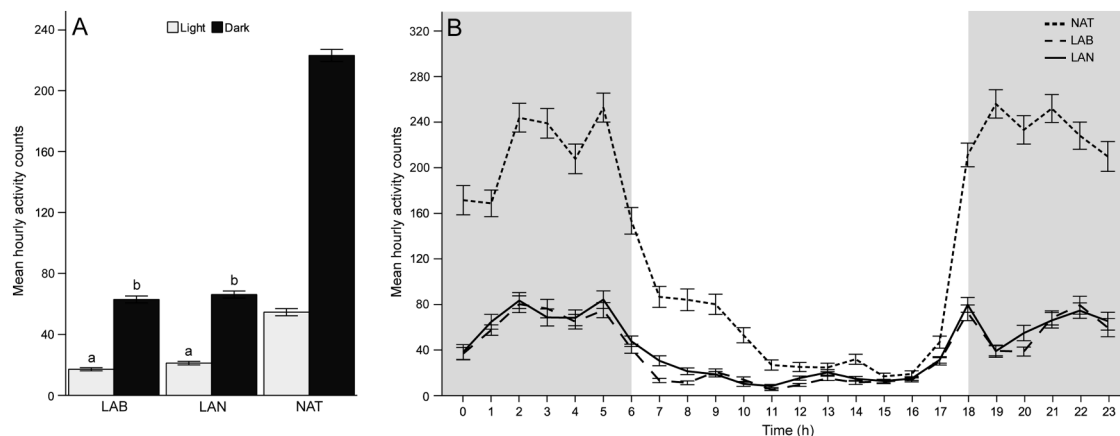
0.001, Figure 2). The activity levels in the NAT treatment were significantly higher than the two laboratory treatments ( $p < 0.001$  for both, Figure 2). The activity levels did not differ between the LAB and ALAN treatments ( $p = 0.192$ , Figure 2). *Otomys angoniensis* displayed more nocturnal activity than diurnal activity ( $\chi^2 = 3411.63$ ,  $df = 1$ ,  $p < 0.001$ ) and sex did not affect activity levels ( $\chi^2 = 0.13$ ,  $df = 1$ ,  $p = 0.715$ ).

The activity counts were influenced by the interaction between the experimental treatment and the time of day ( $\chi^2 = 87.82$ ,  $df = 2$ ,  $p < 0.001$ , Figure 2). During both light and dark hours, activity was higher under the NAT treatment than the LAB and ALAN treatments ( $p < 0.001$  for all, Figure 2). There was no difference between the LAB and ALAN treatments and none of the other comparisons were significant ( $p \geq 0.054$ ).

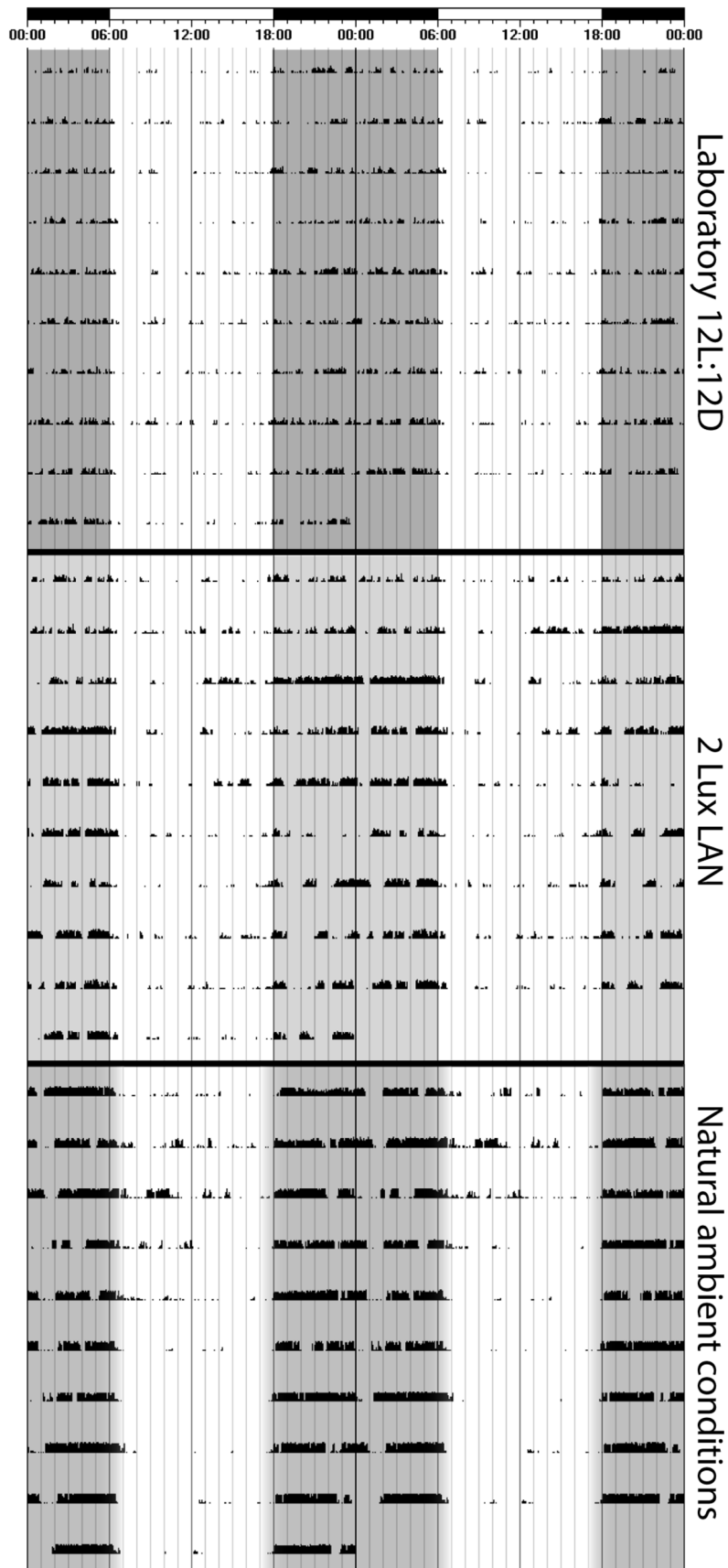
The interaction between experimental treatments and sex significantly affected activity counts ( $\chi^2 = 15.60$ ,  $df = 2$ ,  $p < 0.001$ ). Both males and females showed higher activity during the NAT treatment compared with both the LAB and ALAN treatments ( $p < 0.001$  for all). None of the remaining comparisons between sex and treatment were significant ( $p \geq 0.634$ ).

The activity of *O. angoniensis* was significantly affected by the interaction between time of day and sex ( $\chi^2 = 111.50$ ,  $df = 1$ ,  $p < 0.001$ ). Both males and females were more active during the dark hours than the light hours ( $p < 0.001$  for both). During the light hours, males were more active than females ( $p < 0.001$ ). No significant differences were seen between males and females during the dark hours ( $p \geq 0.086$ ).

The three-way interaction between experimental treatment, time of day and sex influenced the activity counts significantly ( $\chi^2 = 89.97$ ,  $df = 2$ ,  $p < 0.001$ ,



**Figure 2.** A – The mean hourly activity counts (mean  $\pm$  SE) recorded for *O. angoniensis* during the dark and light hours in three experimental treatments. The same letters on the plots indicate non-significant differences between treatments. B – The hourly activity counts (mean  $\pm$  SE) of *O. angoniensis* during each experimental treatment illustrated over the 24 h day. The activity counts of all individuals were averaged over the 10 experimental days per treatment. Shaded areas indicate the dark hours and unshaded areas indicate light hours.



**Figure 3.** A representative double-plotted actogram of an *O. angoniensis* female to illustrate activity during the different experimental treatments. LAB – laboratory 12h L:12h D, LAN – 2 Lux light at night and NAT – natural ambient conditions. The top bar indicates the light and dark hours of each day, with two days represented next to each other on each line. The black spikes illustrate activity counts per minute. The shaded areas indicate the dark hours and the unshaded areas indicate the light hours.

Figure 3). Both males and females exhibited higher activity counts during the dark hours in the NAT treatment compared to the LAB and ALAN treatments ( $p < 0.001$  for all). During the light hours, both males and females showed higher activity counts in the NAT treatment compared with both the LAB and ALAN treatments ( $p < 0.001$  for all). Both males and females were more active during the dark hours in all treatments ( $p < 0.001$  for all) compared with the light hours. None of the other comparisons for the three-way interaction were significant ( $p \geq 0.105$ ).

The amplitude of the activity differed significantly between treatments ( $\chi^2 = 23.97$ ,  $df = 2$ ,  $p < 0.001$ ,

Figure 4A) and was higher in the NAT treatment compared to both the LAB and ALAN treatments ( $p < 0.001$  for both; Table S1). The amplitude did not differ between the LAB and ALAN treatments ( $p = 0.640$ ). The acrophase was similar for all experimental treatments ( $\chi^2 = 5.27$ ,  $df = 2$ ,  $p = 0.072$ , Figure 4B, Table S1).

The activity MESOR differed significantly between experimental treatments ( $\chi^2 = 24.68$ ,  $df = 2$ ,  $p < 0.001$ , Figure 4C) and was significantly higher in the NAT treatment compared to the LAB and ALAN treatments ( $p < 0.001$ , for both; Table S1). There was no significant difference in the MESOR between the LAB and ALAN treatments ( $p = 0.82$ ). The robustness of the activity

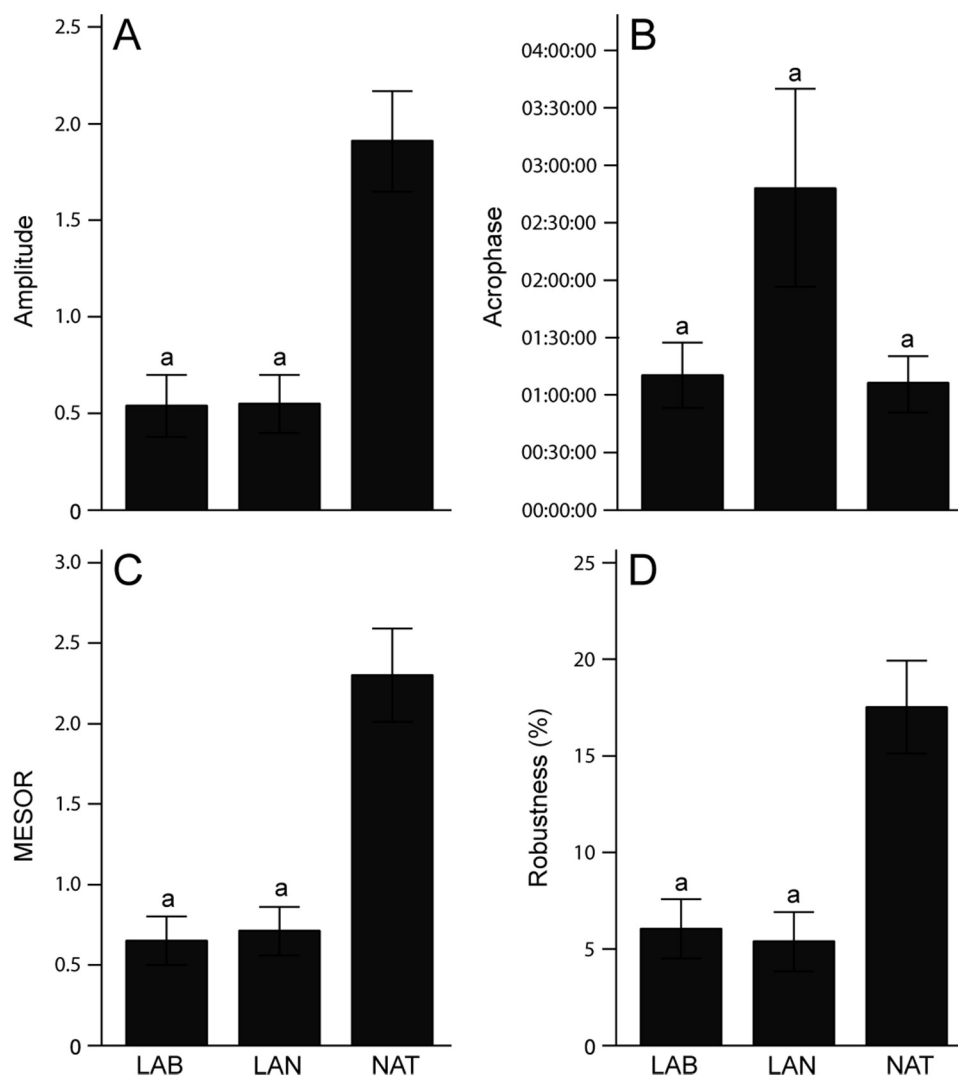


Figure 4. A – The mean amplitude of activity (mean  $\pm$  SE) recorded for *O. angoniensis* for each treatment. B – The mean acrophase of activity (mean  $\pm$  SE) for each experimental treatment. C – The mean MESOR of activity (mean  $\pm$  SE) for each treatment. D – The mean robustness of activity (mean  $\pm$  SE) for each experimental treatment. The same letters on the plots indicate non-significant differences between treatments.

patterns differed between the treatments ( $\chi^2 = 20.72$ ,  $df = 2$ ,  $p < 0.001$ , [Figure 4D](#)). The rhythms were more robust during the NAT treatment compared to both the LAB and ALAN treatments ( $p < 0.001$ , for both; [Table S1](#)). Yet, there was no difference in robustness between the LAB and ALAN treatments ( $p = 0.474$ ).

## Discussion

Our study provides new insights into the diel activity rhythms and light sensitivity of *Otomys angoniensis*, an indigenous African rodent inhabiting anthropogenically influenced grasslands. Although the species exhibited predominantly nocturnal activity across all treatments, its daily rhythm, including amplitude, MESOR and robustness, was enhanced under natural environmental conditions. This indicates that multiple natural cues, such as ambient temperature fluctuations, broader light intensity ranges, and natural twilight transitions, influence daily rhythms in this species.

The literature presents inconsistencies regarding the temporal niche of the Angoni vlei rat. Although it consistently increased nocturnal activity during all experimental treatments, 75% individuals were trapped at 06:00 during the first trap check, while the remainder were collected during the day. In contrast, under experimental conditions, *O. angoniensis* was most active during the night, with limited diurnal activity. Niche switches are not uncommon when diurnal animals are brought into the laboratory; both the tuco-tuco (*Ctenomys knighti*) and the golden spiny mouse (*Acomys russatus*) are diurnal in their natural environments but exhibit nocturnal activity in captivity (Cohen and Kronfeld-Schor 2006; Tomotani et al. 2012). However, the ice rat (*O. sloggetti*), a naturally diurnal *Otomys* species, retained its diurnal activity in the laboratory (Oosthuizen 2020). Additionally, the southern African vlei rat (*O. auratus*) is nocturnal under laboratory conditions despite being collected during both day and night (Webber and Oosthuizen 2025). Therefore, while *O. angoniensis* showed predominantly nocturnal activity in our experiments, its diurnal activity bouts during the experiment and trapping times suggest that it is not strictly nocturnal.

The absence of a significant reduction in activity under dim artificial light at night (ALAN) suggests that *O. angoniensis* is not highly light-sensitive, which is atypical for strictly nocturnal rodents. In laboratory studies, several nocturnal species, such as the African pygmy mouse (*Mus minotoides*; 0.5–2 Lux), southern multimammate mouse (*Mastomys coucha*; 2 Lux), Namaqua rock mouse (*Micaelamys namaquensis*; 3.2–4.8 Lux), and Siberian hamster (*Phodopus sungorus*; 5 Lux), exhibited significant reductions in locomotor

activity under ALAN (Bedrosian et al. 2013; Ackermann 2019; Viljoen and Oosthuizen 2023; Oosthuizen et al. 2024a). Similarly, field data showed that the nocturnal wood mouse (*Apodemus sylvaticus*) was observed less frequently on camera traps when 8.2 Lux ALAN was introduced at a forest edge (Spoelstra et al. 2015). The crepuscular single-striped grass mouse (*Lemniscomys rosalia*) also displayed reduced activity under 2 Lux indirect ALAN in the laboratory (Oosthuizen et al. 2024b). Diurnal species typically show minimal reductions in activity in response to ALAN but do not necessarily extend their activity into the night due to increased visibility. Examples include the mesic four-striped grass mouse (*Rhabdomys dilectus*; 3.2–4.8 Lux) and the golden spiny mouse (*A. russatus*; 2 Lux) (Rotics et al. 2011; Ackermann 2019). In comparison, *O. angoniensis* behaved more like a diurnal species because of its weak response to ALAN, indicating only minor masking effects and suggesting a degree of temporal niche flexibility. This response pattern aligns with that of crepuscular or facultatively diurnal rodents (Ackermann et al. 2020; Oosthuizen et al. 2024b).

When *O. angoniensis* was exposed to natural ambient conditions, it maintained the temporal organisation seen under laboratory conditions but displayed an almost three-fold increase in activity amplitude. Several environmental factors likely contributed to this increase. First, the natural light – dark cycle includes gradual transitions at dawn and dusk, which are absent in the square-wave light regimes typical of laboratory experiments. Some studies suggest that twilight enhances the light's role as a zeitgeber (Boulos et al. 1996b; Bromundt et al. 2019), although others found no such effect (Boulos et al. 1996a). Strictly nocturnal rodents typically delay activity until it is completely dark and become inactive before first light (van der Merwe et al. 2014; Viljoen and Oosthuizen 2023; Oosthuizen et al. 2024a). In the laboratory, both the diurnal *R. dilectus* and nocturnal *M. namaquensis* reduced activity when exposed to simulated twilight rather than square-wave lighting (Ackermann et al. 2020).

Second, natural diurnal illumination far exceeds laboratory lighting in brightness, and brighter daytime light can enhance circadian amplitude and rhythm robustness (Bano-Otalora et al. 2021). For example, the diurnal four-striped mouse (*R. pumilio*) showed increased circadian robustness under higher daytime irradiance (18–1900 Lux; Bano-Otalora et al. 2021). Another study using light intensities from 1 to 330 Lux reported higher activity with brighter lighting in both the diurnal *R. pumilio* and the nocturnal *M. namaquensis* (van der Merwe et al. 2017).

Third, fluctuating ambient conditions, especially temperature, can interact with the circadian system to reinforce behavioural rhythms. The nocturnal Mahali mole-rat (*Cryptomys h. mahali*) displayed greater locomotor activity with higher amplitude under simulated ambient temperature cycles compared to constant conditions (van Jaarsveld et al. 2019). When exposed to temperature fluctuations, *R. dilectus* showed reduced activity, whereas *M. namaquensis* showed increased activity (Ackermann et al. 2020).

Finally, natural soundscapes, characterised by low-frequency ambient noise, may be less stressful than high-frequency mechanical noise typical of laboratory equipment (Sales et al. 1988), potentially reducing anxiety. Rodents can detect ultrasonic frequencies (Heffner and Heffner 2007) and may be less sensitive to lower-frequency sounds (Reynolds et al. 2010). Therefore, the unfamiliar acoustic profile of laboratory environments may heighten alertness or stress in wild-caught animals.

The presence of both nocturnal and diurnal predators in the ecological landscape of *O. angoniensis* may also influence its temporal activity. Its predominantly nocturnal activity in captivity, contrasted with its diurnal activity in nature together with our trapping records, suggests a flexible temporal niche shaped by varying ecological pressures. Such flexibility may buffer the species against circadian disruptions linked to urbanisation and ALAN, although it remains vulnerable to other anthropogenic stressors such as habitat loss. All of the factors likely contributed to the observed changes in locomotor activity. We propose that a combination of environmental cues (light intensity, temperature, twilight, and soundscape) may underlie the increase in amplitude under natural conditions. Nevertheless, these effects appear to be species-specific and influenced by the primary temporal niche. For example, the crepuscular *L. rosalia* showed a similar, though less pronounced, increase in activity under the same experimental setup (Oosthuizen et al. 2024b), whereas the nocturnal *M. coucha* decreased activity under natural conditions (Oosthuizen et al. 2024a). However, both species retained their overall temporal pattern.

Sex-specific analyses in our study revealed only limited differences in activity patterns. Males showed slightly higher diurnal activity under natural conditions, but overall rhythm strength and structure were consistent between the sexes. This suggests that both sexes experience similar environmental responsiveness in captivity. However, sex-specific ecological roles, especially during the breeding season when reproductive priorities differ, may modulate behaviour in natural contexts (Bronson 1989).

In conclusion, *O. angoniensis* displays a flexible circadian system and can maintain its rhythms under diverse lighting conditions. Overall, our results highlight the importance of assessing circadian behaviour under both controlled and ecologically realistic conditions. The flexibility shown by *O. angoniensis* highlights the limitations of relying solely on laboratory assessments when defining a species' temporal niche. Moreover, its relatively weak masking response to ALAN, despite its nocturnal activity, demonstrates that light sensitivity cannot be inferred solely from the timing of activity. This species occupies areas with dense vegetation (Skinner and Chimimba 2005). We did not add vegetation to the cages to attempt to mimic its natural habitat. This would have obscured its locomotor activity during motion detection, enhancing the perceived impact of ALAN, and even with the more exposed environment, the animal did not show a marked response to ALAN. The temporal niche represents an important ecological resource for animals (Kronfeld-Schor and Dayan 2003). Although ALAN does not appear to suppress its behaviour directly, indirect consequences of urbanisation, such as vegetation loss and habitat fragmentation, are serious conservation concerns. With the continued expansion of urban environments and degradation of grasslands (Bardgett et al. 2021; Mahtta et al. 2022), evaluating the resilience of grassland specialists such as vlei rats is essential. Our findings contribute to insights of circadian flexibility in wild rodents and emphasise the importance of an integrative approach in chronobiological research.

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

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## Data Availability Statement

The data used for this study will be made publicly available upon publication.

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