

Fitness consequences of chronic exposure to different light pollution wavelengths in nocturnal and diurnal rodents

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Article

Keywords: Light pollution, diurnal, nocturnal, Acomys, reproductive success, survival

Posted Date: April 14th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1538025/v1>

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Abstract

Use of artificial at night (ALAN) exposes the world to continuously increasing levels and distribution of light pollution. Our understanding of the adverse effects of ALAN is based on observational or laboratory studies, and its effects are probably underestimated. Demonstration of direct experimental fitness consequences of ALAN is missing. We studied the effects of chronic light pollution at different wavelengths on fitness and stress hormone levels under semi-natural conditions in two closely related species: the nocturnal common spiny mouse (*Acomys cahirinus*) and the diurnal golden spiny mouse (*Acomys russatus*). Our results clearly demonstrate the adverse effects of ALAN exposure on fitness of both nocturnal and diurnal species, manifested by changes in cortisol levels and reproductive timing, reduced reproductive output and reduced survival, which differed between species and wavelengths. In *A. russatus* exposure to blue ALAN had the strongest effect on fitness, followed by white and yellow ALAN exposure. In *A. cahirinus* results are more complex and suggest it suffered from combined effect of ALAN and competition. Our research shows that light pollution presents a real threat to both nocturnal and diurnal species, affecting the species fitness directly and through its interspecific interactions. Worryingly, these effects are probably not specific to spiny mice. The clear adverse effects we documented, as well as the differences between wave lengths, contribute to our ability present science-based recommendations to decision makers regarding the use of artificial light at night. Such information and guidelines are highly important nowadays when lighting systems are being replaced to promote energy efficiency.

Introduction

The extensive and increasing use of artificial at night (ALAN) exposes the world to continuously increasing levels and distribution of light pollution. The new world atlas of light pollution ¹ portrays an unsettling reality, in which 99% of US population and 80% of the world's population live under light polluted skies, and it is estimated that in areas where light pollution has not reached saturation, the increase in ALAN radiance and extent is 2–6% per year ^{2–4}.

Light pollution has attracted increasing scientific attention over the last two decades. Though it was considered to have a limited spatial extent compared to more familiar anthropogenic interferences such as climate change and plastic pollution, it is now accepted that ALAN effects are much more pervasive than previously considered, and that it is becoming a major threat to biodiversity^{2,5–8}. ALAN affects all living organisms at the molecular, physiological, behavioral and ecological level. For example, it was shown to disrupt foraging and feeding behavior, alter biological rhythms, cause mistimed reproductive behavior, and increase stress hormone levels (e.g., ^{9–20}), and it is clear that actions must be taken to mitigate its effects. However, to design effective mitigation measures, we must better understand the adverse effects of light pollution, which is currently based mostly on observational field studies or laboratory studies, mostly focusing on changes in species behavior and physiology ^{5,8,20,21}.

Length of photoperiod (day length) is a reliable indicator of time of year and serves as a cue for seasonal adaptation^{18,22}. However, the extensive use of artificial light disrupts the clear delineation day and night, and the reliability of photoperiod is compromised. As a result, seasonal acclimation and seasonal reproduction may be compromised, reducing both survival and reproductive success. However, to the best of our knowledge, direct experimental fitness consequences of ALAN exposure were never demonstrated. Moreover, to promote science-based policies regarding the outdoors use of light at night, the effects of different wavelengths of ALAN at relevant intensities should be compared. To close this knowledge gap, we chose to study the effects of chronic light pollution on fitness (survival and reproduction) under semi-natural conditions in two closely related, coexisting rodent species with opposite activity patterns: the nocturnal common spiny mouse (*Acomys cahirinus*) and the diurnal golden spiny mouse (*Acomys russatus*), which were chronically exposed to ALAN at different wavelengths at relevant intensity.

Materials And Methods

Experimental design

Experiments took place at the Zoological Research Garden at Tel Aviv University, where we used 8 enclosures (each 3X3 meters, 3 meters high) to test the long-term effect of ALAN under semi-natural condition on two species of spiny mice; the diurnal *Acomys russatus* and the nocturnal *A. cahirinus*. Experiments were conducted for 6–8 months in two consecutive years: the first repetition started on November 2018 and ended in July 2019. The second repetition started on November 2019 and ended in June 2020.

All experiments were carried out in accordance with the Israeli Ministry of Health guide for the care and use of laboratory animals and all experimental protocols were approved by the Tel-Aviv University Institutional Animal Care and Use Committee (IACUC protocol approval number 04-18-056, 04-19-031).

Enclosures

We divided individuals of both species into four treatments, two experimental enclosures each. Six enclosures were exposed to ALAN in different wavelengths (two enclosures/wavelength) translated to different colors: blue (420–520 nm), yellow (430–740 nm), and white (420–740 nm, measured using C-700 Spectrometer by Sekonic, see supplement 1 for spectrum and intensity measures). The other two enclosures were not exposed to ALAN and served as control (half-moon light level ca 0.1 lux). Each enclosure contained 12 individuals (6/species) with equal number of males and females for each species. Lights turned on automatically 30 minutes before sunset, and turned off 30 minutes after sunrise, exposing the animals to continuous 10 lux light during the night. The LED lamps (Product Nos. G334BL, G334Y, and G334WW, Eurolux, South Africa) were hung from the center of the ceiling in each enclosure, 3 meters above the ground. Animals were supplied with hollow blocks as hiding places, nesting material, rodent pellets (Product No. 2018SC, Teklad Global, USA) and water *ad libitum*.

Animals

A total of 247 animals took part in the experiment ($n_{A. russatus} = 117$; $n_{A. cahirinus} = 130$). All mice were taken from the spiny mice colony of the Zoological Research Garden at Tel Aviv University. The animals were marked with RFID for individual recognition (Product No. 040999, MS Schippers, The Netherlands) and were free to roam their enclosure. For physiological measurements and population evaluation the mice were captured once every other week using Sherman traps. Sample size varied between tests, as detailed below.

Population size and reproductive output

During the experiments we had unexpected mortality. Mortality date was determined by the date the corpse was found or estimated by failure to trap the individual over time. In the latter cases, date of death was determined as the date of first trapping failure. Newborns were trapped and documented and in most cases were removed from the enclosure. In some cases, pups were tagged with RFID and left in the enclosure in order to maintain the population size and structure.

Cortisol extraction

To examine whether light pollution affects cortisol levels, cortisol metabolites were extracted from the fecal material. Mice were trapped and feces were collected from the trap up to 8 hours from capture to get the baseline cortisol concentration, avoiding the appearance of the stress response due to capture in the feces, as we demonstrated elsewhere²³. Feces were collected 2 hours after the beginning of activity time of each species, in three sessions as detailed in Table 1 (supplementary materials). Feces were kept in -20°C until further analysis. ELISA kit (ARBOR ASSAYS catalog number K003-H1W/H5W) was used for the analysis. Samples preparation and analysis was conducted according to the steroid Solid Extraction Protocol of the manufacturer. In cases that feces weight was low, we normalized the data using the following equation $[Assay\ Concentration\ (i.e.,\ pg/mL) \div (Evaporation\ Vol\ (mL) \div 0.5)] / [Feces\ weigh\ (g) / Evaporated\ ethanol\ (mL)] = Analyte\ unit\ (i.e.,\ pg/gm)\ fecal\ solid$.

Statistical analysis

Statistical analysis was done using RStudio software (version 4.0.2) and Excel software (Office 2016), as detailed below.

Survival probability

We tested the effect of light pollution on the survival probability using Kaplan-Meier analysis (as review by Bewick, Cheek, & Ball, 2004). Survival curve was calculated for each treatment, with time of exposure in days. Comparison of survival curves was done by Post Hoc-Tukey test, using the packages *survival* and *survminer* in RStudio. Survival rates differed between species ($p < 0.05$, Fig. 2 (B)); therefore, analysis was done for each species separately.

Newborns

Probability that ALAN effects the reproductive success of each species throughout the year, was assessed using Chi Square goodness of fit, under the assumption that reproductive success should be even across enclosures. Dividing the data to seasons was made to emphasize the mistiming of reproductive activity, and not for statistical analysis due to small sample size. Winter- includes all pups born from November to February; Summer- all pups born from March to July.

Cortisol

Cortisol concentration in the feces can be affected by species, sex, and season among many other factors. Feces collected in summer (March and June) were combined to increase sample size, after making sure that cortisol concentration is not significantly different between these months (Wilcoxon rank sum test). Cortisol concentration data were highly skewed and did not distribute normally; therefore, analysis was done using *lme4* package in RStudio, with Generalized Linear Model (GLM) using gamma distribution, and AIC test to choose the best random structure.

The study is reported in accordance with ARRIVE guidelines.

Results

Survival probability

In general, *A. cahirinus* survival probability was lower compared to *A. russatus* even when not exposed to ALAN (Fig. 1 (B), $P=0.002$). Survival of the diurnal *A. russatus* was significantly lower when exposed to blue light compared to control (Fig. 2 (C), $P=0.029$). *A. cahirinus* exposed to blue ALAN had a significantly higher survival probability compared to *A. cahirinus* exposed to white ALAN (Fig. 1 (D), $P=0.049$). Populations of both species from enclosures exposed to white light collapsed in a manner of days on 2 different enclosures and at different times. The gap in physical location and time, eliminates the possibility that sudden death is related to the enclosure itself or that it was caused by the same reason. These incidents influenced overall mortality rates.

Despite mortality incidences, mortality rates did not differ significantly between years in both species and therefore were combined ($P_{cahirinus}=0.27$, $P_{russatus}=0.17$)

Reproduction

Reproductive behavior was significantly influenced by exposure to ALAN in both species. Equal distribution of reproductive success ($f_e=0.25$) was refuted for both species ($df=3$, $P<0.001$, Supplementary table 2). Total number of pups over the experiments was highest in *A. russatus* controls, and in *A. cahirinus* exposed to blue light. Controls of both species were reproductively active only during summer (Fig. 1. A). When exposed to ALAN, *A. cahirinus* were reproductively active all year including winter months. Reproduction during winter was also evident in *A. russatus* exposed to white and blue ALAN, although to a lower extent.

Cortisol

Fecal cortisol concentration of female *A. russatus* were significantly higher than males (Fig. 2, $P < 0.001$). Therefore, results were analyzed separately for each sex. Males exposed to blue light at night had higher level of cortisol compared to control (Fig. 2, $P = 0.057$). In summer, *A. russatus* females exposed to blue and white light at night, had higher level of fecal cortisol compared to control (Fig. 2, $P_{\text{blue}}=0.02$, $P_{\text{white}}=0.055$). In winter, cortisol levels of *A. russatus* males exposed to white light were significantly lower compared to controls (Fig. 2, $P = 0.02$). In *A. cahirinus* there were no differences in fecal cortisol level between groups.

Figure 2. Fecal cortisol concentration in *A. russatus* exposed to ALAN in different wavelength. (A) Cortisol concentration in females and males in both collection season (winter and summer); (B) Cortisol difference between sex in all mice (control and light treatment) (** $P < 0.001$); (C) Cortisol concentration in females in summer and winter (* $P < 0.05$); (D) cortisol concentration in males in summer and winter.

Discussion

Our experiments resulted in a clear demonstration of the adverse effects of ALAN exposure on fitness of both nocturnal and diurnal species, manifested by reduced survival rates and reproductive success. Mortality rates of diurnal *A. russatus* were significantly higher when exposed to blue ALAN, compared to the control groups (Fig. 1.C). While the controls did not reach the median of survival until the end of the experiment, *A. russatus* exposed to white and blue ALAN reached the median at similar time (after 160 days of exposure), and yellow light exposed *A. russatus* reached the median 2 months later (Fig. 1. C). These results suggest that the blue, short wavelength light (420–520 nm), which is also included in the white light but almost absent in the yellow light, had an adverse effect on the mice. Blue light is known to have the largest effect on the eye's intrinsically photosensitive, melanopsin containing, retinal ganglion cells (ipRGCs) which result in the direct suppression of melatonin and influences biological rhythms²⁴. Light intensities as low as 0.028 lux (monochromatic blue light) and 0.3 lux (white light) are capable of suppressing melatonin in rodents and birds, respectively²¹. Therefore, we suggest that our results indicate an involvement of biological rhythms in the effect.

The results of nocturnal *A. cahirinus* are more complex and suggest it suffered from competition in addition to the ALAN effect. Mortality rates in the control groups were significantly higher in *A. cahirinus* compared to *A. russatus* (Fig. 1. B $P = 0.002$). However, when *A. russatus* survival rates decreased significantly (under blue ALAN exposure) and as a result competition pressure reduced, survival rates of *A. cahirinus* were significantly higher compared to white ALAN exposure, where competition was presumably more intense. We suggest that the combined effects of competition and ALAN exposure affected all the other results we obtained for *A. cahirinus*, including reproductive success and fecal cortisol metabolites levels (see below).

This effect of competition may seem surprising at first, as it seems to contradict the observation that *A. cahirinus* competitively excludes *A. russatus* to diurnal activity²⁵. However, the mechanism of exclusion is resource (food) mediated²⁶, and in direct confrontations *A. russatus* is more aggressive than *A. cahirinus*²⁷. Under the current experimental conditions, where food was *ad libitum* available, there was no competition on food, and we suggest that the more aggressive *A. russatus* outcompeted, increased stress levels and reduced survival rates and reproductive success of *A. cahirinus*.

In the second year of the experiment, we had two high mortality incidents in two physically distant enclosures exposed to white ALAN, one enclosure in January 2019, and the other in March 2019. All individuals of both species from these two enclosures died within days. The dead animals were not wounded or underweight and the cause of death was undetermined in pathological examination. We hypothesize that disruption of biological rhythms (daily and/or seasonal) caused a mismatch between the internal clock and environmental challenges, possibly including a misalignment of the immune system, which resulted in higher susceptibility to pathogens¹⁵, as reported in hamsters²⁸, birds^{29–32} and aphids³³. Energy invested in immune function is often balanced against energy invested in reproduction, to optimize fitness²⁰. Since exposure to ALAN resulted in reproduction year-round, especially in *A. cahirinus*, it is possible that it compromised immune function during winter. Moreover, chronic activation of the HPA axis, manifested as high cortisol levels (see below) could have caused dysregulation of the immune system³⁴ leading to poor defense against pathogens, and as suggested in birds^{30–32}, inhibition of melatonin secretion by exposure to ALAN may be the underlying mechanism. However, this hypothesis and the role of melatonin in our system remains to be studied.

The effect of ALAN on reproductive success was striking (Fig. 2, Supplementary table 2). In their natural habitat, both species breed during summer: young individuals of *A. cahirinus* are observed from February until September, and young *A. russatus* are observed from April to July³⁵. While the reproductive activity in both species was affected by ALAN, the nature of response was different. *A. russatus* reproductive success was strongly affected by ALAN: the total number of pups of *A. russatus* exposed to all tested wavelengths significantly decreased by at least half compared to the control group (Supplementary table 2). Yet, in all treatments, reproduction appeared almost only during summer, which is the reproductive season of both species³⁵.

In *A. cahirinus* we again see a combined effect of ALAN exposure and interspecific competition, and a different effect of ALAN: The total number of pups of *A. cahirinus* seems to be affected mostly by competition. It had high number of newborns in the enclosures where *A. russatus* had low survival rates and fewer pups (blue treatment), and low number of pups in the control group, where *A. russatus* thrived most. Moreover, ALAN resulted in loss of seasonality of reproduction in *A. cahirinus*, which was reproductively active year-round under all ALAN exposed enclosures, as opposed to the control group, whose reproductive seasonality corresponded to their natural reproductive timing. In long day breeders like *Acomys*, seasonal reproduction is timed by day length, so we conclude that for *A. cahirinus* and somewhat for *A. russatus*, exposure to light pollution at all tested wavelengths led to a false perception of

summer day length and resulted the loss of seasonality and continuous reproduction. Yet, overall reproduction (total number of offspring) was negatively affected by exposure to ALAN.

An effect of light pollution on reproductive timing was previously described³⁶⁻³⁸, but these studies mostly focused on physiological reproductive state and did not measure reproductive output. Our experimental enclosures allowed us to continuously measure reproductive output and demonstrate the negative effect of ALAN on reproduction. However, our result may underestimate the actual effect under natural conditions: unlike natural conditions, the mice in our enclosures had *ad libitum* access to food and water. It is possible that in the wild, pups born during the winter, when temperatures and arthropods (*Acomys* preferred food) availability are lowest^{26,39}, and when spiny mice use torpor to reduce energy expenditure⁴⁰⁻⁴³, would have low survival rates, further decreasing fitness.

The effect of ALAN on all measured parameters may be mediated by two hormones – melatonin and glucocorticoids (GC). Daily and seasonal timing cues rely on melatonin secretion which plays a key role in the biological regulation of daily and seasonal rhythms. Melatonin secretion is confined to the night by the circadian clock and is inhibited by light in both diurnal and nocturnal mammals^{44,45}. Therefore, light at night can reduce or stop melatonin secretion, and hence disrupt the natural cycle of all downstream biochemical and physiological processes influenced by melatonin. In the current study we did not measure melatonin secretion, and its role in the observed effects of ALAN in this setup remain to be studied.

We did measure the effect of ALAN on *Acomys* main glucocorticoid - cortisol²³. We found that exposure to blue and white light at night increased the baseline GC levels of diurnal *A. russatus* (Fig. 2. A, C, D). GC are involved in various processes, acting as neurotransmitters and neuromodulators, activating, and regulating numerous processes related to stress response and homeostasis, and synchronization of peripheral clocks^{46,47}. Consistent with our data (Fig. 2. B), cortisol normally exhibits a dimorphic difference with higher concentration of GC among females⁴⁸. Cortisol follows a circadian rhythm with tendency to reach high concentration in the blood at or just before waking time, and decrease during the active hours⁴⁹. *Acomys* cortisol daily pattern in fecal material is 12 hours delayed compared to blood concentration, with high concentration of fecal cortisol at 21:00 for *A. russatus* and 16:00 for *A. cahirinus*²³. Setting the traps and feces collection was done in the beginning of activity time of each species, representing 12 hours earlier, meaning the trough of the daily pattern. Therefore, elevated cortisol level may indicate chronic stress of the individual or a shift in the circadian pattern of GC.

Cortisol displays a seasonal pattern in some mammals, which is associated with reproductive activity^{50,51} and with metabolic adjustment to changes in energy demand and thermoregulation^{52,53}. To distinguish between seasonality in cortisol and the reaction to light pollution, we compared cortisol level of each group (species and sex) at each season. We found that in summer, cortisol level of *A. russatus* females exposed to blue and white ALAN were significantly higher ($P < 0.05$) and marginally significant in females exposed to yellow light ($P = 0.55$) compared to control (Fig. 2. C). Male *A. russatus* exposed to

white light in winter had significantly lower level of cortisol compared to control (Fig. 2. D). Under free-living and semi-natural conditions, spiny mice of both species have lunar cycle in fecal cortisol metabolites levels, with increased levels during moon lit nights²³ as well as in response to artificially increasing light levels at night to moon levels⁵⁴. Full moon light levels (natural or artificial) also resulted in reduction of activity levels, foraging and food consumption in both species^{23,54,55}, and increased inter-specific aggressive interactions in *A. cahirinus*⁵⁴. However, these high cortisol levels were temporary and showed lunar cycle, while in the current experiment the exposure to ALAN and its effect on cortisol levels are chronic. High or low levels of cortisol may indicate that exposure to ALAN leads to an unbalanced activation of HPA axis with regards to season. Chronic dysregulation of the HPA axis is known to have many adverse physiological consequences and may result with a weakened immunity response³⁴ which leaves the individual more susceptible to infectious diseases and parasites⁵⁶, and may explain the higher mortality rates in the groups exposed to blue and white ALAN. In *A. cahirinus* we found no significant changes in fecal cortisol levels between males and females, treatments, or seasons. We suggest that cortisol levels of all *A. cahirinus* were constantly high in this experiment as a result of competition with *A. russatus*, which masked the effects of ALAN.

We hypothesize that in *A. russatus*, blue and white light which increased basal level of cortisol, activated the HPA axis and resulted in the inhibition of reproductive activity. The response to yellow ALAN was weaker in all parameters. The results for *A. cahirinus* are again more complex. Reproductive output of *A. cahirinus* is normally higher than that of *A. russatus*^{57,58}. Yet, in our experiment, the total number of *A. russatus* pups was almost double that of *A. cahirinus*. This result, together with the higher mortality rate of *A. cahirinus* supports our hypothesis that *A. cahirinus* suffered from a combined effect of competition and ALAN exposure. This hypothesis also suggests that cortisol levels were high in all *A. cahirinus* groups chronically, and therefore we did not find any effect of sex, season, or treatment as we did in *A. russatus*.

Exposure to blue and white, and to a lesser extent yellow ALAN, changed the inter-specific interactions between the species and resulted in population decline and reduced fitness in both species. Such conditions could promote the introduction or spread of alien species that are less sensitive to illumination, such as the house mouse⁵⁴.

Conclusions

Our research clearly shows that light pollution presents a real threat to both nocturnal and diurnal species, affecting species fitness directly as well as through interspecific interactions. Exposure to ALAN, which masks cyclic environmental light cues has severe consequences, influencing physiological and behavioral processes which are crucial for the survival and fitness of the species. Such effects on species fitness can compromise the health of the ecological system, eventually resulting in its collapse. Worryingly, there is no reason to assume the effects are specific to spiny mice.

We also found that the effects differ between wavelengths; Blue light had the worse effect, followed by white, and yellow light had the weakest effect, which was still significant. Such finding is highly important for planning mitigation actions. It supports our hypothesis that in mammals, blue and white light have the worst effect on fitness, and that yellow light is preferable when necessary.

Declarations

Acknowledgments:

This research was supported by THE ISRAEL SCIENCE FOUNDATION as part of the ISF-UGC joint program. The authors wish to thank Or mekuvan (<https://www.ormekuvan.co.il/>), a nonprofit organization promoting sustainable and responsible use of light, and especially Gilad Gozni, for their help in building the ALAN system.

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Figures

Figure 1

Population data: (A) newborns across all light treatments for 2 years, divided to season; (B) survival probability of the two species from the control group; (C) survival probability of *A. russatus* across treatments, and (D) survival probability of *A. cahirinus* across treatments. Dashed lines show the median survival probability of each group.

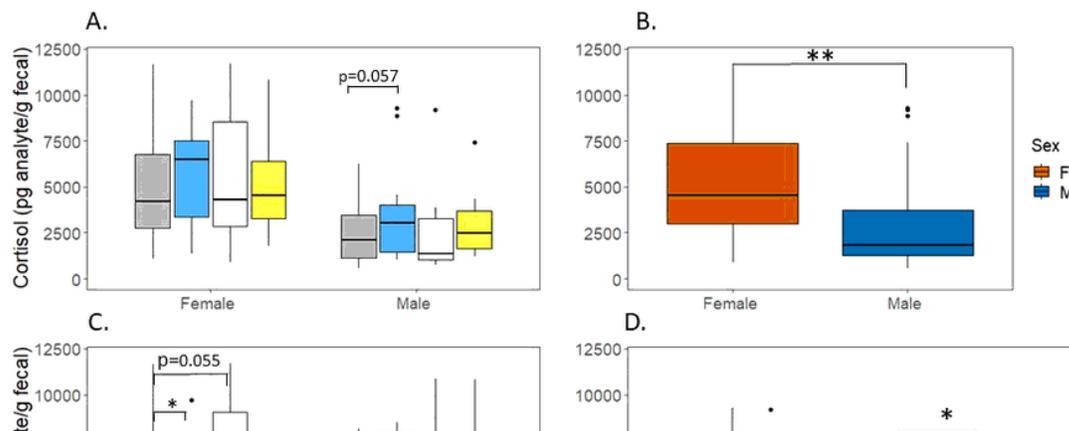


Figure 2

Fecal cortisol concentration in *A. russatus* exposed to ALAN in different wavelength. (A) Cortisol concentration in females and males in both collection season (winter and summer); (B) Cortisol difference between sex in all mice (control and light treatment) (** $P < 0.001$); (C) Cortisol concentration in females in summer and winter (* $P < 0.05$); (D) cortisol concentration in males in summer and winter.

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