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Long-term dim light during nighttime changes activity patterns and space use in experimental small mammal populations☆

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ABSTRACT

Artificial light at night (ALAN) is spreading worldwide and thereby is increasingly interfering with natural dark-light cycles. Meanwhile, effects of very low intensities of light pollution on animals have rarely been investigated. We explored the effects of low intensity ALAN over seven months in eight experimental bank vole (*Myodes glareolus*) populations in large grassland enclosures over winter and early breeding season, using LED garden lamps. Initial populations consisted of eight individuals (32 animals per hectare) in enclosures with or without ALAN. We found that bank voles under ALAN experienced changes in daily activity patterns and space use behavior, measured by automated radio-telemetry. There were no differences in survival and body mass, measured with live trapping, and none in levels of fecal glucocorticoid metabolites. Voles in the ALAN treatment showed higher activity at night during half moon, and had larger day ranges during new moon. Thus, even low levels of light pollution as experienced in remote areas or by sky glow can lead to changes in animal behavior and could have consequences for species interactions.

1. Introduction

Life on earth is strongly influenced by natural rhythms, with day length used as a *zeitgeber* for diurnal and seasonal patterns in many biological systems (Thomas and Vince-Prue, 1996; Bradshaw and Holzapfel, 2007). Under natural light conditions, the change of the dark-light cycle is transduced into a biochemical signal. In mammals, melatonin is secreted into the blood during the night while secretion is inhibited by light (Reiter, 1993). Thereby, the photoperiod is used by many animals to synchronize their circadian rhythm through endogenous biological clocks (Challet, 2015). Many prey species, especially small nocturnal mammals, use the photoperiod and moonlight as cues to adjust their foraging behavior to avoid increased risks of predation in illuminated time periods (Clarke, 1983; Daly et al., 1992; Mougeot and Bretagnolle, 2000; Perea et al., 2011; Navarro-Castilla and Barja, 2014).

However, in recent decades the spread and intensity of artificial light at night (ALAN) has increased steadily on a global scale (Hölker et al., 2010b; Bennie et al., 2014). ALAN can act as an environmental pollutant on many taxa and rhythms such as on activity in mammals (Rotics et al., 2011), foraging in amphibians (Buchanan, 1993), dispersal in fish (Riley et al., 2015), melatonin pattern in birds (Dominoni et al., 2013), mating in insects (van Geffen et al., 2015) and flowering in plants (Bennie et al., 2015).

In consequence of the extensive spread of ALAN, its negative effects on different aspects of the environment in general and on animal behavior and physiology in particular increase rapidly. In rodents, a distinct change in activity in response to differing intensities of ALAN has been demonstrated (Blair, 1943; Clarke, 1983; Kotler et al., 1991). Subsequently, masking of the natural dark-light regime by ALAN can cause the circadian cycle to drift out of phase (Redlin, 2001). This is often a result of the suppression of the hormone melatonin (Brainard et al., 1984; Falchi et al., 2011).

There is accumulating evidence through laboratory experiments that under ALAN the proportion of food intake in rodents increases during the day, which leads to an increase in body mass although total food intake remains the same (Fonken et al., 2010, 2013). Fonken et al. (2012) also found elevated corticosterone levels in Nile grass rats subjected to dim artificial light in the laboratory. In contrast, Bedrosian et al. (2013) found that Siberian hamsters did not show a typical diurnal pattern of cortisol concentrations under

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similar night light conditions.

Meanwhile, the majority of studies, especially regarding the physiological changes induced by ALAN, have been conducted under laboratory conditions. It is unknown how these findings translate into natural environments and natural populations. Further, in many studies the exposure to light is rather short so that long-term effects and adaptations to light cannot be investigated. Additionally, most experiments concentrate on rather high levels of direct light exposure, while light pollution often consists of low light intensities on a wide spatial scale, e.g. sky glow around a city.

The aim of this study was to investigate how chronic dim ALAN influences behavior and body condition of mammals. We used experimental bank vole populations (*Myodes glareolus*) in semi-natural grassland in a replicated design of illuminated and non-illuminated enclosures. The bank vole is a common and widespread microtine rodent in Eurasia. It is short-lived and iteroparous, usually surviving only one reproductive season (Tkadlec and Zejda, 1998). Bank voles show an ultradian rhythm with a polyphasic activity pattern throughout the year (Ylönen et al., 1988; Halle, 2006). This ultradian rhythm is controlled by the circadian clock so that short activity bouts keep their position in relation to sunrise and sunset during a seasonally changing photoperiod (Halle, 2006). So far, there is no knowledge on the effects of ALAN on animals that display an ultradian rhythm. As bank voles partially forage on insects (Hansson and Larsson, 1978), they might increase their activity during night under ALAN to exploit those insects that are drawn to the light sources. Thus, they potentially can be influenced by ALAN through several direct and indirect ways.

During the seven-month study, we subjected animals to artificial illumination with light intensities lower than full moon using single-LED garden lights. Since voles are short lived, they were subjected to this dim ALAN over the longest part of their life span, during winter into the breeding season, to investigate the long-term effects of light pollution. We measured body mass, glucocorticoid metabolite levels, survival, day range and activity of individuals.

We hypothesize that dim ALAN has a negative influence on the physical condition of individuals. Circadian disruption can cause an increased concentration of glucocorticoids (Abílio et al., 1999). An elevated glucocorticoid level in turn can lead to a lowered body mass (Harris et al., 1998) which will, together with an increased visibility by predators, result in a lowered survival rate. Furthermore, we predict that ALAN leads to a change in activity patterns, potentially by masking of natural *zeitgebers*. We predict that prey animals have a higher perceived predation risk at illuminated nights as the perceived visibility to predators increases (e.g. Clarke, 1983). Since vigilant prey individuals may deplete their food patches less thoroughly, they may need to cover a larger area to forage sufficiently (Lagos et al., 1995). In consequence, we expect an enlargement of individual day ranges.

2. Materials and methods

2.1. Study subjects and experimental site

The study was conducted over a seven-month period from November 2012 to June 2013 in large (0.25 ha) grassland enclosures near Potsdam, Eastern Germany. Bank voles were the laboratory-born offspring of wild-captured individuals kept in standard rodent cages on a standard rodent diet until the experiment. For individual identification they were equipped with a passive integrated transponder tag (PIT; Trovan ID-100, 2.12 mm × 11.5 mm, 0.1 g). Each animal was tested repeatedly for its risk taking behavior as part of a project on animal personality, assuming that environments with ALAN would favor more risk prone behavioral types. However, the tests developed to phenotype a related vole species (Herde and Eccard, 2013) turned out to yield too little variation in this species, and needed further refinement, therefore results are not reported here.

The experiment was conducted under the permission of the 'Landesamt für Umwelt, Gesundheit und Verbraucherschutz' (LUGV; reference number V3-2347-44-2011) investigating effects of animal personality on risk taking (here: ALAN). Animals were housed under the permission and control of the LUGV (reference number 3854-1-132).

We conducted the experiment in eight large outdoor enclosures with a size of 0.25 ha (50 × 50 m) each. Every enclosure was surrounded by a galvanized metal wall extending 1 m below and 0.5 m above ground. Voles were protected against terrestrial predators through an electrical veterinary fence surrounding all enclosures. Multicapture live traps (Ugglan special No2, Grahnab, Sweden) were evenly distributed across each enclosure (N = 36, 6 × 6 grid). Traps were sheltered against wind and sun by metal boxes (30 × 20 × 20 cm) and a tile as cover.

2.2. Experimental design

For the ALAN treatment in half of the enclosures we used 85 small solar powered garden lamps with single-LEDs (light emitting diodes) per enclosure. Control enclosures were provided with the same amount of wooden dummies (same height and diameter) at the same locations to serve as controls for the potential effects of additional artificial structures on prey or predators of bank voles, which may affect their behavior. Lamps were 36 or 60 cm high and were above the grass layer in winter, but immersed in the grass layer later in spring. Each enclosure was illuminated by two similar lamp types that generated "white" light through one diode and contained a diffuser to scatter the light (Type A: Item-No. 57 21 29, Conrad Electronics, height = 60 cm, N = 60; Type B: Item-No. 1015021500/00158077, RTI, height = 36 cm, N = 35). Spectral measurements of lamp type A showed that the diode emits cold white light with a high proportion of blue light (color temperature = 7250 K). Diode and diffuser created a brighter zone surrounding the lamp (radius r = 25 cm, illuminance i = 0.8 lx) and a dimmer outer zone (r = 2.5 m, i < 0.1 lx, for details see Eccard et al., 2018 (in revision)). The integrated solar panel recharged a battery (1.2 V, 600 mAh) during daytime and an integrated sensor switched the diode on automatically at night. Duration of artificial illumination after sunset increased over the course of the season as daylight hours and temperatures increased to recharge and operate the batteries (Fig. 1) until in April the entire nighttime was

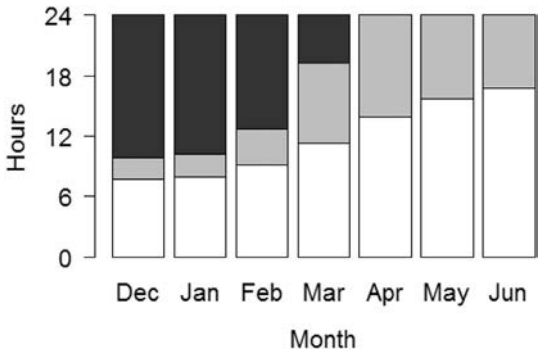

Fig. 1. Duration of daylight (white) and nighttime without (black) and with dim nighttime illumination (ALAN, grey) by solar garden lamps in 4 out of 8 enclosures. Duration of ALAN increased with progressing season due to increased solar charging during daytime.

artificially illuminated.

The experiment was conducted in two phases (Table 1). 48 bank voles were transferred to the enclosures from late November until early December. Each experimental vole population consisted of four females and four males. During the first phase of the experiment, animals were captured once a month at sunrise to obtain body mass, survival estimates and glucocorticoid measurements. Traps were closed 1 h before sunrise baited with rolled oats and apple and controlled twice after 2 h and 4 h. During these trapping sessions individual weight was measured (±0.1 g) and fecal samples were collected.

Vole survival over winter was 50%, which is high compared to natural populations (Andrzejewski, 1975). To conduct the second phase of the experiment with sufficient sample size and under balanced sex ratio in each population, we transferred additional animals into the enclosures in mid-March (24 animals, 2–3 per enclosure, Fig. 2). Using repeated live trapping we calculated the minimum number of days alive for each individual. End of May all voles and their offspring were captured from the enclosures to calculate survival, and voles were returned to the laboratory.

2.3. Analysis of fecal glucocorticoid metabolites

We measured fecal glucocorticoid metabolites (FGM), a non-invasive and non-terminal measurement of adrenocortical activity. Although bank voles show an ultradian activity pattern they display diurnal variations in FGM levels (Sipari et al., 2017). Samples were collected always at the same daytime to minimize variation due to these daily FGM fluctuations (Touma et al., 2004). FGMs are excreted with a delay of 6–8 h in bank voles (Sipari et al., 2017). In order to sample the pre-trapping FGM levels, capture time in the trap was kept to <2 h during morning hours.

To obtain FGM samples directly in the field, we positioned a clean sheet of cardboard on the bottom of the activated trap. Fecal pellets were then directly collected after capture. Animals were released immediately at the site of capture and fecal samples were frozen at −29 °C.

Analysis of FGM was conducted using a 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (EIA, Touma et al., 2003) which has been successfully validated for evaluating adrenocortical activity in bank voles (Sipari et al., 2017). In short, the samples were defrosted quickly (10 min) by heating at 95 °C. Afterwards, samples were dried for 24 h at 60 °C and homogenized with mortar and pestle. Depending on the amount of feces collected, a portion of 0.03, 0.04 or 0.05 g of the dried homogenized mass was mixed with 1 ml of 80% methanol by shaking the vials intensely for 1 min by hand. The mixed samples were centrifuged at 2500 rotations per minute for 15 min and a 500 μl aliquot was stored frozen until EIA analysis (Sipari et al., 2017).

2.4. Activity and space use

In six out of the eight enclosures we conducted 24 h radiotelemetry in April at half moon, and in May at new moon (see supplements for time of day of different natural light phases). Each enclosure was equipped with an automated radiotelemetry system, consisting of eight four-element Yagi antennae (Winkler-Spezialantennen, Germany) connected to an automatic receiving unit (ARU; Sparrow System, USA) that logged signal strength per frequency and antenna (Ward et al., 2013). Two antennae were attached in each corner of an enclosure on a rack (height: 3.2 m, distance: 2.2 m, 40% angle to each other). Within each pair of antennae, we converted the distribution of signal strength among antennae into a bearing using linear regressions calibrated with stationary transmitters in the center of the enclosure and at enclosure walls. With four bearings from each corner of the enclosures, we then calculated the location of each transmitter in the logging interval via trigonometry.

Voles were live-trapped and fitted with radiotelemetry transmitters (transmitter: Holohil BD-2C, ~1 g) approximately 24 h before telemetry started so that they could get accustomed to the collars. In the half moon telemetry session 17 individuals and in the new moon session 13 individuals could be simultaneously tracked. The ARU scanned for each radio frequency every 7 min for 6 s (10 times per antenna, 80 scans). The median signal strengths on each antenna were used to calculate bearings and a location every 7 min (205 locations per animal in 24 h). Locations were further analyzed in the software Ranges 8 (Anatrack Ltd., United Kingdom). For each individual we estimated day range sizes by fixed kernels with selected cores containing 95% of all positions, representing the maximum area of the day range while excluding occasional excursions and errors. Although there is a serial dependence of observations, estimating day ranges by kernel densities is valid when using constant sampling intervals (De Solla et al., 1999).

For the analysis of activity patterns we used the variation among signal strengths (difference between two subsequently logged signals on the same antenna) as an indicator for activity: a large absolute delta in signal strength indicates that the transmitter is changing position or posture relative to the receiving antenna. This implies that an animal is active, while a small absolute delta in signal strength indicates that the transmitter was not moving between two logged signals. Since individual radio transmitters vary in signal strength with battery power and antenna length, we did not define an absolute technical threshold of delta signal strength

Table 1
Experimental schedule, with four bank vole (*Myodes glareolus*) populations living under artificial light at night (ALAN) and four control populations in large grassland enclosures; FGM – fecal glucocorticoid metabolites.

Year	Month	Experimental day	Experimental protocol (variables)
Phase 1			
2012	Nov–Dec	−12–0	Transfer of animals to enclosures
2013	Dec–Feb	11,42, 74	Live trapping (survival, body weight, FGM samples)
Phase 2			
	Mar	102	Additional animals to enclosures
	Mar–Apr	106,118,127	Live trapping (survival, body weight, FGM samples)
	Apr	130	Fitting radio collars
	Apr	132–135	Telemetry session at half moon (day range, activity, total distance)
	Apr–May	140, 150	Live trapping and removal of radio collars
	May	155	Fitting radio collars
	May	156–158	Telemetry session at new moon (day range, activity, total distance)
	May–June	168–192	Removal trapping Transfer of animals to laboratory

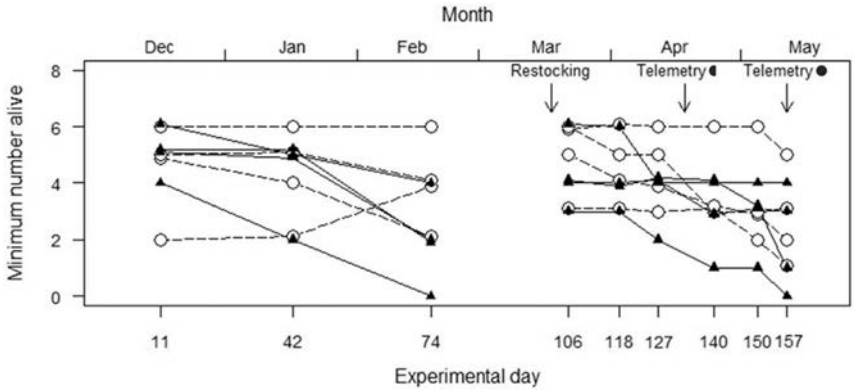

Fig. 2. Change in population size (minimum number of animals alive) of eight enclosed bank vole (*Myodes glareolus*) populations over winter (experimental day). Tick marks on x-axis indicate live trapping events. Enclosures with natural light regime (filled triangles, solid lines) and artificial light at night (open circles, dashed lines) are shown. Initial populations in November consisted of eight individuals. Similar to natural populations, only a small proportion of animals survived in winter. To obtain sufficient sample size a representation of both sexes per enclosure for telemetry at half moon and new moon, populations were restocked with three individuals per enclosure in March (Restocking).

to decide on activity. Instead we used a transmitter-specific threshold that defined 25% of fixes active for each transmitter separately. This value is between reports on bank vole activity (<20% (Górecki, 1968); >25% (Mironov 1990)). An exploratory analysis of 24 h raw data of several individual voles showed, that this threshold can be shifted between 10%–40%, robustly revealing individual activity patterns (example in supplementary material). However, with this method, we can not analyze differences in the total amount of activity between animals, but the distribution of activity in the day (Fig. 3).

One hour time periods of the day were compared between light treatment and control group in both telemetry sessions by

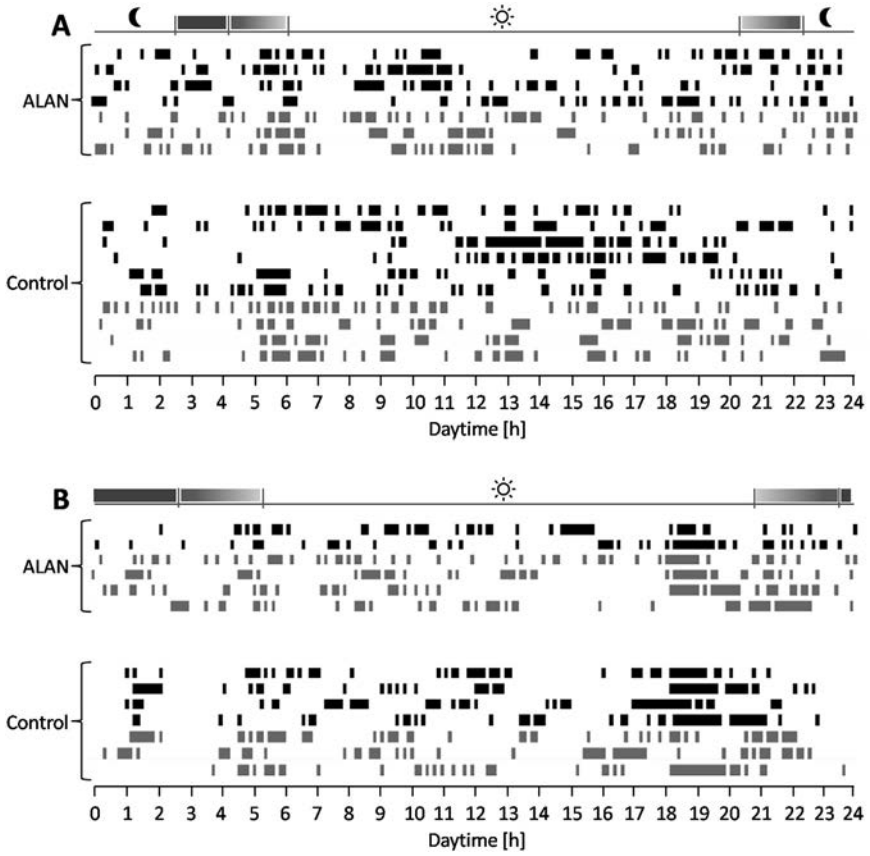

Fig. 3. Activity patterns of individual bank voles in large outdoor enclosures collected with automated telemetry during half moon (A) and new moon (B). Each line represents either a female (black) or male vole (grey). Natural light regime is shown above each graph, with sun and moon symbols indicating daylight and moonlight hours, shaded areas indicating dawn and dusk, and black bars time intervals without any natural light source. The dark areas of each line represent the time intervals the individual was active. Half of the enclosures were illuminated with dim solar garden lights (artificial light at night (ALAN)), the other half with natural light regime served as control.

calculating a time period specific activity index proposed by Halle (1995). This index I_a uses the following formula:

$$I_a = log\left[\frac{\frac{\sum a(bSR)}{\sum a}}{\frac{2}{24}}\right]$$

where $\sum$a (bSR) is the number of activity bouts during the respective hour and $\sum$a is the total number of activity records during 24 h, ranging from −1 to +1. A positive I_a indicates an increased activity during the focal time period compared to the average 24 h activity level, a negative I_a a lowered activity during the focal time period. The activity index was calculated separately for each of the 24 h of the day to identify preferred or avoided time periods. This was done with four different starting points of the time periods to decrease the chance of a type I error. Since tests with different starting points led to similar results (see supplementary material) we focus on results of one starting point of analyzed time periods (full hour).

2.5. Statistical analyses

All statistical analyses were performed with R version 3.0.2 (R Core Team, 2013). For each analyzed variable the mean is presented together with the standard deviation.

Linear mixed models (LMMs) were built using the R package lme4 (Bates et al., 2014) to analyze effects of light treatment, sex, and season (measured by experimental day) on body mass and FGM concentrations. Full models included an interaction of light treatment and sex. A separate model was built to analyze effects of light treatment, sex and telemetry session on day range size (kernels). The full model contained an interaction of light treatment and telemetry session.

To account for the nested design of several animals within a population, a random term was included ("individual" nested within "population"). As the residuals of the variables FGM concentration and day range size did not conform to a normal distribution, they were transformed via Box-Cox transformation. We confirmed a regular error distribution by plotting residuals versus fitted values and Q-Q plots. Full models including all variables and interactions were reduced via stepwise backwards model selection and comparing the Akaike Information Criterion (AIC). As we were mainly interested in the effects of the light treatment, this variable was never excluded from the models (see supplementary material for full and reduced models per variable). The explained deviance of the most parsimonious model was assessed for fixed effects alone (marginal R^2) and fixed effects and random effects together (conditional R^2) according to Nakagawa and Schielzeth (2013).

The post-hoc analysis of the LMMs included a Wald test (χ^2) to assess the significance of the fixed factors included in the minimal model. Whenever an interaction of light treatment and sex or telemetry session significantly influenced the dependent variable further analysis was conducted by using the R package "phia". Simple main effects for interactions were analyzed by evaluating the contrasts across the levels of one factor while the values of the other interaction factor were fixed. The significance level was adjusted for multiple testing according to Holm (De Rosario-Martinez, 2013).

As no GLMM could be fitted for analyzing the variables "activity index" and "individual survival", a Wilcoxon rank sum test was used to compare both light treatments. Individual survival was estimated by the minimum days animals were alive, while separate tests were conducted for individuals transferred into the enclosures in December and in March.

3. Results

3.1. Body mass and survival

Body mass of individual bank voles was on average 19.7 ± 3.3 g ($N_{Measurement}$ = 183). Artificial light at night as well as the release date had no influence on body mass while both season and sex had (Table 2). With seasonal changes (experimental day), mean body mass increased from 17.7 ± 1.7 g in November (N = 29) to 23.5 ± 2.2 g in April (N = 24). Averaged over all measurements, males had a higher body mass (20.5 ± 3.1 g, N = 92) than females (18.8 ± 3.2 g, N = 91).

On average, the minimum days animals were estimated to be alive in the experiment was 57.5 ± 64.0 days for animals transferred to enclosures in December (N = 65, maximum days possible = 168), and 36.8 ± 28.5 days for animals additionally transferred to the enclosures in March (N = 24, maximum days possible = 66). Survival did not differ between ALAN and control animals (December: U = 531, P = 0.97, N_{ALAN} = 32, $N_{Control}$ = 32; March: U = 90.5, P = 0.23, N_{ALAN} = 14, $N_{Control}$ = 10).

3.2. Activity

Voles showed polyphasic activity patterns with an activity peak shortly before sunrise irrespective of moon phase and light treatment (Fig. 4, mean I_a before sunrise: 0.27 ± 0.24) followed by a phase of decreased activity (mean I_a after sunrise: 0.00 ± 0.29).

At half moon, indices differed between ALAN and control animals in the afternoon ($U_{15:00\text{-}16:00}$ = 12.5, P = 0.032, N = 17) and shortly before midnight ($U_{22:00\text{-}23:00}$ = 59, P = 0.022, N = 17). Control animals showed lowered activity during the night (I_a at 22:00–23:00: −0.16 ± 0.24, N = 10) while ALAN animals did not (I_a at 22:00–23:00: 0.14 ± 0.15, N = 7). In the afternoon, control animals showed higher activity (I_a at 15:00–16:00: 0.28 ± 0.29, N = 10) than ALAN animals (I_a at 15:00–16:00: 0.01 ± 0.22, N = 7).

At new moon, the activity indices tended to differ between control and ALAN animals around midnight ($U_{23:00\text{-}00:00}$ = 35, P = 0.052, N = 13). Control animals showed lowered activity (I_a at 23:00–00:00: −0.29 ± 0.12, N = 7) while ALAN animals did not (I_a at 23:00–00:00: −0.06 ± 0.15).

3.3. Day range

Averaged over all 30 individuals, the size of the 95% kernel was 744 ± 375 m^2. The interaction of light treatment and telemetry session had a significant effect on day range, while sex had not (Table 2).

During new moon, day range was larger in the light treatments (1033 ± 344 m^2) than in controls (653 ± 408 m^2; post-Hoc test of the interaction: χ^2 = 5.79, df = 1, P = 0.032, Fig. 5) while during half moon there was no difference among light treatments (ALAN: 601 ± 371 m^2, control: 705 ± 312 m^2; post-Hoc test: χ^2 = 0.87, df = 1, P = 0.35). Day range did not differ among telemetry sessions for voles living under natural light conditions (half moon: 705 ± 312 m^2, new moon: 653 ± 408 m^2; post-Hoc test: χ^2 = 0.74, df = 1, P = 0.39). Within the ALAN treatment, 24 h day range was larger during new moon (1033 ± 344 m^2) than at half moon (601 ± 371 m^2; post-Hoc test: χ^2 = 9.38, df = 1, P = 0.005, Fig. 5).

3.4. Fecal glucocorticoid metabolites

In total, 67 fecal samples of 36 animals were collected and analyzed. On average, the concentration of FGM was 44.2 ± 33.7 ng/

Table 2
Bank vole populations living under artificial light at night (ALAN). Explained deviance of fixed factors (marginal R^2), fixed factors and random effects (conditional R^2) and results of Wald χ^2 tests for the variables of the minimal LMMs. Estimates and 95% confidence intervals (CI) are presented. Light indicates the effects of a long-term treatment with dim artificial light at night from winter to spring relative to control, season the effects of progressing season (experimental day, January to May), sex the effects of females compared to males, session the effects of different moon light intensity (half moon compared to new moon) during telemetry. Full models analyzing corticosterone and body mass contained light, season, and sex and an interaction of light and sex as fixed factors. The full model analyzing day range contained light, session, and sex and an interaction of light and session as fixed factors.

Dependent variable	N	Marginal R^2	Conditional R^2	Fixed factor	χ^2	P	Estimates	CI [2.5%, 97.5%]
Corticosterone level	67	0.405	0.435	Light	0.90	0.343	0.0139	[-0.0067; 0.0418]
				Season	46.64	>0.001	−0.0009	[-0.0011; −0.0006]
Body mass	183	0.353	0.600	Light	0.08	0.358	−0.514	[-1.604; 0.566]
				Sex	12.18	>0.001	−1.944	[-3.023; −0.866]
				Season	82.74	>0.001	0.035	[0.028; 0.043]
Day range	30	0.217	0.498	Light	0.61	0.434	−0.22	[-0.655; 0.217]
				Session	2.09	0.149	−0.21	[-0,514; 0.233]
				Light* Session	8.03	0.005	0.814	[0.202; 1.366]

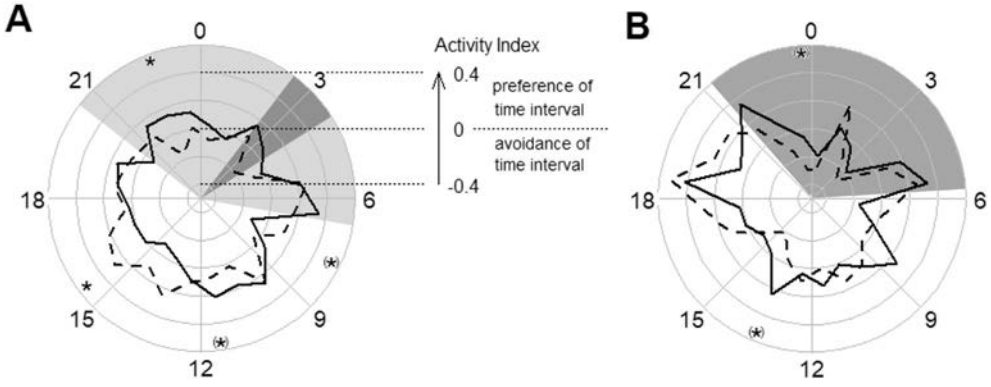

Fig. 4. Mean hourly activity indices over the course of 24 h of bank voles living in large outdoor enclosures during telemetry at half moon (A) and new moon (B). Mean values of animals living under a natural light regime (dashed lines, $N_{Half\ Moon} = 10$, $N_{New\ Moon} = 7$) and under artificial light at night (solid lines, $N_{Half\ Moon} = 7$, $N_{New\ Moon} = 6$) are shown. A light grey area marks nighttime between sunset and sunrise. A dark grey area marks the time interval without any natural light source (moonset to astronomical twilight). A negative or positive activity index shows that on average animals showed a decreased or increased activity in the focal time interval compared to the 24 h average activity level, respectively. (*) $P < 0.1$, *$P < 0.05$, **$P < 0.01$.

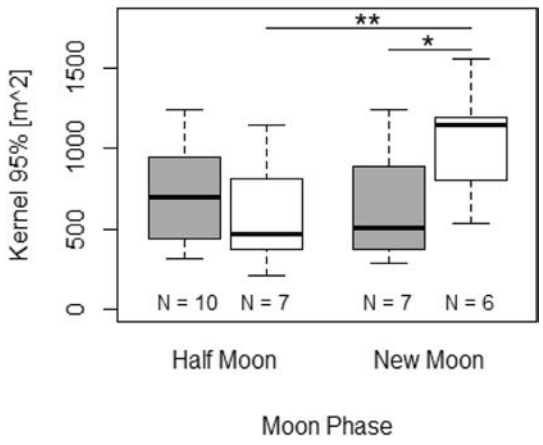

Fig. 5. Daily home range size of bank voles within 24 h based on 205 fixes per animal obtained by automated radiotelemetry. 95% day range kernels are displayed depending on telemetry sessions during half and new moon and light treatment (Control – grey boxes, ALAN – white boxes). Boxes show quartiles and median; * - $P < 0.05$, ** - $P < 0.005$.

0.05 g feces. Mean FGM levels increased with progressing season from 15.3 ± 5.6 ng/0.05 g feces (N = 7) in November to 60.9 ± 43.9 ng/0.05 g feces (N = 14) in April. Light treatment or sex of the animal had no effects on measured FGM concentration (Table 2).

4. Discussion

Our results suggest that artificial light at night (ALAN) may have been masking the natural light cycle and thus changed the activity pattern of small mammals in a field population. During telemetry at half moon animals living under natural light conditions showed reduced activity during the night which was not detected in the ALAN group (Fig. 4). As bank voles have activity peaks at twilight (Braun and Dieterlen, 2005), dim ALAN may have been mistaken as twilight conditions and thereby might override the endogenous clock and change the timing of activity phases of the individuals (Gaston et al., 2013). This effect is well known in birds which start their singing earlier in the day in areas where artificial night lighting is present (Miller, 2006). This change in activity could under natural conditions lead to a change in interspecific competition. It is known that bank voles decrease their nocturnal activity in presence of species with similar dietary needs, such as the wood mouse (Greenwood, 1978), to reduce competition by feeding at different times. ALAN may lead to a higher degree of temporal overlap of bank voles with other sympatric species and thus increase interspecific competition. To have a more complete understanding of the fitness effects of artificial light at night and therefore the development of populations, it should be investigated how ALAN influences the reproductive success and offspring survival of small mammals.

Day ranges at new moon were increased by ALAN. Rodents are known to adjust their foraging behavior to the intensity of moonlight (Prugh and Golden, 2014). Under ALAN voles may experience a

higher perceived predation risk as well as the perceived visibility to predators may increase. Voles may be more vigilant and deplete their food patches less thoroughly under ALAN and thus need to cover a larger area to forage sufficiently (Lagos et al., 1995).

Another possible explanation for increased space use could be an attraction of insects towards the lamps, which may serve as an additional food source for the bank voles. Throughout the different phases of the moon, brightness changes from approximately 0.215 lx at full moon to 0.001 lx at moonless nights (Austin et al., 1976). As large parts of the outdoor enclosures in this experiment have been subjected to artificial light intensities below 0.1 lx, there is the possibility that at half moon the artificial light sources were too weak to attract an increasing amount of insects, while during new moon they were strong enough. Further, telemetry at new moon was later in the season which most likely increased insect availability compared to the telemetry at half moon three weeks earlier. As insects are part of a bank voles' diet (Gebczynska, 1976; Hansson and Larsson, 1978), the experimental animals could have used the availability of disoriented insects around lamps for foraging. Therefore, the artificial lighting conditions may have allowed voles to visit light sources sequentially to forage on insects, resulting in larger day ranges. Similarly, studies on bats report an increased activity of certain species around street lamps as they exploit the increased insect availability (de Jong and Ahlén, 1991; Rydell, 1992) and ground beetles are also reported to aggregate at light sources near the ground (Eccard et al., 2018 (in revision)).

We found no evidence for a negative influence of very dim ALAN on body mass, FGM level and survival probability of voles, which was contrary to our predictions. Other studies report changes in glucocorticoid levels (Bedrosian et al., 2013) and body mass (Fonken et al., 2010) but these studies were conducted in the laboratory and under much higher light intensity (5 lx) which exceeds the brightness of a full moon. As bank voles spend large parts of their day below ground or below vegetation cover, and additionally the level of light pollution in our experiment was rather low, this may have reduced expected effects of artificial light on body condition and consequently survival.

5. Conclusions

The spread of artificial light at night is increasing steadily (Hölker et al., 2010a) and is now recognized as an environmental pollution which can have a negative impact on nature. Animals exposed to ALAN may suffer for example disorientation, circadian disruption and changes in competition and predation (Longcore and Rich, 2004). In this study we could show that even low intensity ALAN, common in urban regions via sky glow, was sufficient to change space use behavior and activity patterns in small mammals. Direct changes in body condition, FGM level and survival of voles were, however, not affected. Our results may indicate that behavioral flexibility of small mammals allows for compensation of some potential negative effects of ALAN. Certain small mammal species may even profit from illumination attracting insect prey, however no body weight changes under artificial light indicating better nutrition were recorded. Cascading effects on predators or on prey of small mammals remain to be investigated.

Authors contributions

JAE and JH designed the experiment. JH conducted fieldwork and analyzed the data. RP analyzed the corticosterone metabolite samples. JAE and JH wrote the manuscript; RP provided editorial advice.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.envpol.2018.03.107.

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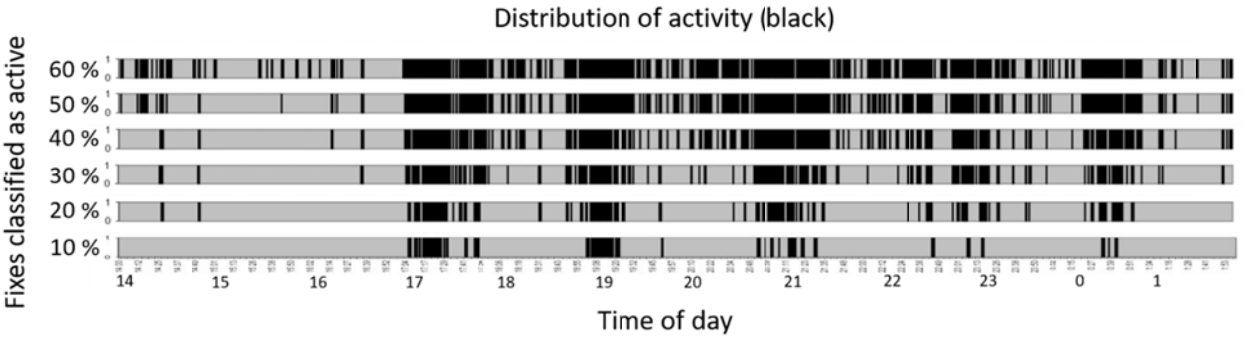
Supplementary Material

For the analysis of activity patterns we used the variation among signal strengths (difference between two subsequently logged signals on the same antenna) as an indicator for activity: a large absolute delta in signal strength indicates that the transmitter is changing position or posture relative to the receiving antenna. This implies that an animal is active, while a small absolute delta in signal strength indicates that the transmitter was not moving between two logged signals. Since individual radio transmitters vary in signal strength with battery power and antenna length, we did not define an absolute technical threshold of delta signal strength to decide on activity. Instead we used a transmitter-specific threshold that defined 25 % of fixes active for each transmitter separately.

In the figure we show exemplary that a distinct biological pattern emerges over a wide range of transmitter specific thresholds. Here we used automated telemetry signals from a collared ultradian, polyphasic vole (*Mictrotus arvalis*, male) in a large outdoor enclosure. Signals were received every minute at each of eight antennae. A transmitter specific threshold of maximum changes in signal strength across two subsequently logged signals in the same antenna was used to classify a given percentage of fixes as „active“ (black bars). Five activity phases are robustly revealed at any „active“ classification between 10-40% of fixes, and can be used in further analyses of distribution of activity over the day.


Distribution of activity (black)
Fixes classified as active
60 %
50 %
40 %
30 %
20 %
10 %
1
0
14
15
16
17
18
19
20
21
22
23
0
1
Time of day

Linear mixed models (LMMs) before (full) and after (minimal) model simplification. The random factor in all models is individual nested in enclosure; Light - light treatment, Season – season accounted for by sampling day, Session - telemetry session, ID - individual.

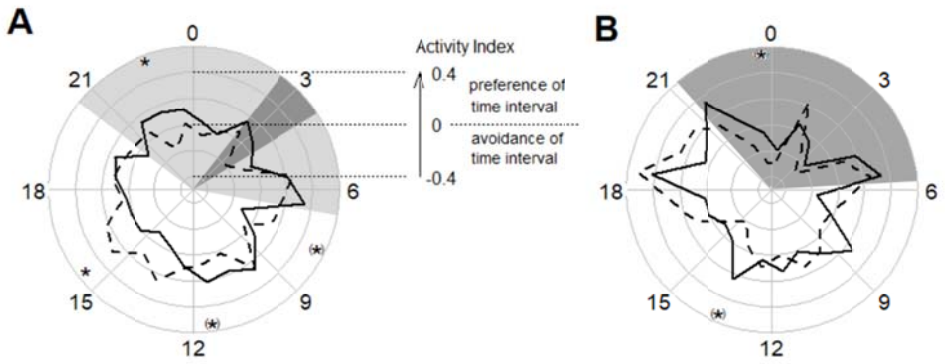
Dependent variable	**N**	**Transformation**	**Model complexity**	**Fixed factors**	**AIC**
FGM level	67	Box-Cox	Full	Light * Sex + Season	-198
			Minimal	Light + Season	-201
Body mass	183		Full	Light * Sex + Season	862
			Minimal	Light + Sex + Season	860
Day range	30	Box-Cox	Full	Light * Session + Sex	49
			Minimal	Light * Session	49

Time intervals (and their durations) of different natural light phases. These include the time from start of astronomical twilight to sunrise (dawn), from sunrise to sunset (day), from sunset to end of astronomical twilight (dusk), from end to start of astronomical twilight (night), from moonset to start of astronomical twilight at half moon telemetry and the corresponding time period at new moon telemetry (pre-dawn).

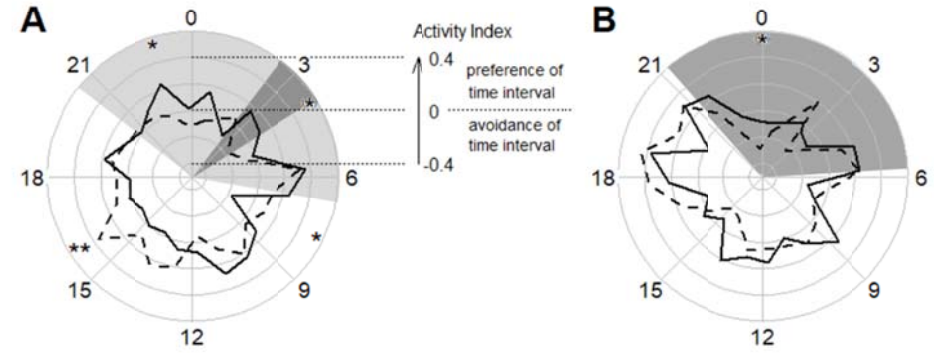
	Half moon		**New moon**	
Daytime	**Start - End (hh:mm)**	**Duration (hh:mm)**	**Start - End (hh:mm)**	**Duration (hh:mm)**
Dawn	03:51 – 06:09	02:18	02:26 – 05:22	02:56
Day	06:05 – 20:09	14:04	05:22 – 20:47	15:25
Dusk	20:09 – 22:25	02:16	20:47 – 23:46	02:59
Night	22:25 – 03:51	05:16	23:46 – 02:26	02:40
Pre-dawn	02:28 – 03:51	01:23	01:03 – 02:26	01:23

Mean hourly activity indices over the course of 24 h of bank voles using different starting points for the analyzed time intervalls. Voles were living in large outdoor enclosures during telemetry at half moon (A) and new moon (B). Mean values of animals living under a natural light regime (dashed lines, $N_{Half\ Moon} = 10$, $N_{New\ Moon} = 7$) and under artificial light at night (solid lines, $N_{Half\ Moon} = 7$, $N_{New\ Moon} = 6$) are shown. A light grey area marks nighttime between sunset and sunrise. A dark grey area marks the time interval without any natural light source (moonset to astronomical twilight). A negative or positive activity index shows that on average animals showed a decreased or increased activity in the focal time interval compared to the 24 h average activity level, respectively. (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$

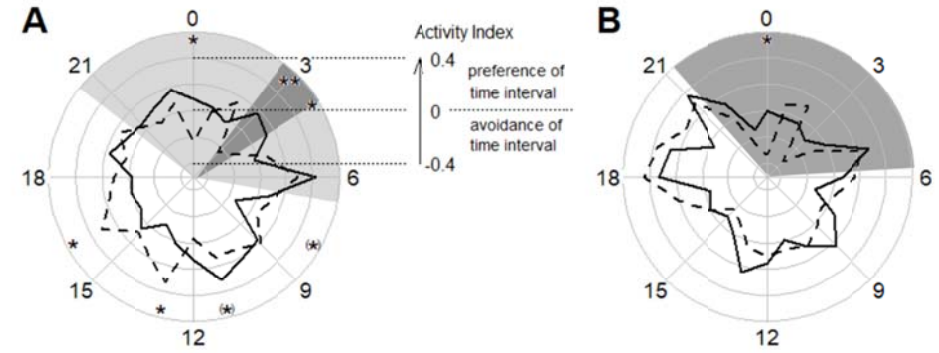
Time period start: full hour



Time period start: quarter of an hour



Time period start: half hour



Time period start: three quarters of an hour