



Nocturnal resting behaviour in urban great tits and its relation to anthropogenic disturbance and microclimate

Valentina Caorsi^{1,2} · Philipp Sprau³ · Sue Anne Zollinger² · Henrik Brumm²

Received: 16 May 2018 / Revised: 28 November 2018 / Accepted: 4 December 2018 / Published online: 25 January 2019
© The Author(s) 2019

Abstract

The ecological novelty of urbanisation poses many challenges to animals. We investigated whether anthropogenic disturbance (artificial light at night and noise) and abiotic factors in cities (temperature and humidity) predict nocturnal activity and rest in free-living urban great tits (*Parus major*). Our study is the first to relate nocturnal rest in wild birds to levels of noise pollution during the night, an issue that has been shown to be particularly damaging to human health. Unlike previous work on nocturnal behaviour of urban birds, we considered the combined effect of anthropogenic disturbance and urban microclimate to acknowledge that the Umwelt of an animal is composed of multiple environmental variables. Using infrared cameras, we observed the nocturnal resting behaviour as a proxy for sleep in 17 birds in nest boxes deployed across the city of Munich, Germany. Although we found marked differences in resting behaviour between individuals, this variation was not related to the measured environmental factors. This finding contrasts earlier studies that reported nocturnal resting behaviour of birds to vary with temperature and light exposure. Although we did not find evidence that urban environmental factors disrupt resting behaviour in great tits, their sleep might still be impaired by the anthropogenic disturbances. To elucidate this issue, further studies are necessary that, for instance, measure brain activity.

Significance statement

Urbanisation is a subject of growing concern among scientists, conservationists and policy makers alike. Yet surprisingly, little is known about the impact of urbanisation on wildlife. We investigated whether anthropogenic disturbance (artificial light at night and noise) and microclimate (temperature and humidity) predict patterns of nocturnal activity and resting behaviour in urban great tits (*Parus major*). Although patterns of resting behaviour differed markedly between individuals, this variation was not related to the measured environmental factors. Our findings are in contrast to previous studies on the effects of urban microclimate and light pollution. At the same time, they suggest that opposing effects of different urban ecological factors may level each other out and thus should be considered in combination.

Keywords Anthropogenic disturbance · Artificial light at night · Noise · *Parus major* · Sleep · Urbanisation

Communicated by C. M. Garcia

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00265-018-2624-1>) contains supplementary material, which is available to authorized users.

✉ Henrik Brumm
brumm@orn.mpg.de

¹ Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil

² Communication and Social Behaviour Group, Max Planck Institute for Ornithology, Seewiesen, Germany

³ Behavioral Ecology, Department of Biology, Ludwig Maximilians University of Munich, Munich, Germany

Introduction

Urbanisation is among the human activities causing the most drastic and permanent habitat transformations (McKinney 2002). These transformations include a loss of natural resources, habitat fragmentation, changes in environmental factors such as temperature and precipitation and an increase of anthropogenic disturbances, e.g. chemical, noise and light pollution (Grimm et al. 2008; Marzluff et al. 2008; Gil and Brumm 2014). Ultimately, the ecological changes associated with urbanisation cause exceptional environmental variation (Sprau et al. 2016), which may pose a threat to biodiversity (Kappelle et al. 1999). Increases in temperature, which are

typically observed in cities (“urban heat islands”), have been suggested to affect a whole suite of physiological, behavioural and ecological traits in animals, such as body growth, breeding phenology, reproductive success, predator-prey relationships and community composition (Avondet et al. 2003; Visser et al. 2006; Peach et al. 2008; Murphy et al. 2016; Brans et al. 2017; Schäfer et al. 2017).

Another characteristic of urban areas is the presence of artificial light. An increase in light intensity during the night may have fundamental ecological and evolutionary implications for animal populations, which may in time reshape entire ecosystems (Hölker et al. 2010). On an individual level, artificial lighting at night can alter behaviour, with often drastic effects on biological rhythms, activity budgets and reproduction (Kempnaers et al. 2010; Dominoni et al. 2013, 2014; Raap et al. 2015). In addition to artificial light and temperature changes, a wide range of species, from terrestrial to aquatic animals, are also affected by noise pollution (Brumm 2010; McGregor et al. 2013). Over the past decades, many studies have shown that anthropogenic noise may negatively affect animals on different systemic levels. An obvious effect of anthropogenic noise is on animal communication since noise can impair the detection of acoustic signals, which may disrupt, for instance, anti-predator or reproductive behaviours (Brumm 2013; Templeton et al. 2016). However, anthropogenic noise also has subtler, but nevertheless equally profound, impacts beyond signal masking. On a proximate level, chronic noise exposure may affect animal physiology, neural function, cellular ageing and gene expression (Kight and Swaddle 2011; Dorado-Correa et al. 2018; Kleist et al. 2018). In terms of behaviour and ecology, there is a growing body of evidence that anthropogenic noise can impair foraging, reduce reproductive success and change animal density and community structure (Barber et al. 2010).

Behavioural responses to the urban environment are usually studied during the active period of animals; however, disruptions during the inactive period (e.g. during the night for diurnal animals) are also crucial because sleep disturbance may have severe consequences. Sleep is a widespread and important behaviour in animals (Cirelli and Tononi 2008; Siegel 2008; Rattenborg et al. 2017), and many studies have shown that sleep deprivation can result in a wide range of negative health effects (Shaw et al. 2002; Stephenson et al. 2007; Andersen et al. 2009). The impact of anthropogenic disturbances on sleep has received the most attention in humans (Lewy et al. 1980; Begemann et al. 1997; Griefahn 2002; Michaud et al. 2008), while only few studies have investigated this topic in non-human animals. Urban birds are known to advance their activity to early morning and night hours, depending on the level of ambient light and noise pollution (Fuller et al. 2007; Dominoni et al. 2014). Moreover, experimental studies, applying artificial illumination inside nest boxes or cages, show that light exposure during the night

disrupts resting behaviour in birds (Raap et al. 2015; de Jong et al. 2016a; Sun et al. 2017). Similarly, artificial light from lamp posts was reported to reduce nocturnal rest in birds roosting outside nest boxes (Ouyang et al. 2017, but see Raap et al. 2017).

A crucial gap in our knowledge is whether current levels of noise pollution disrupt nocturnal resting periods in urban birds. Moreover, to our knowledge, no previous studies have considered the combined effects of urban factors, i.e. the synergistic impact of artificial light intensities, noise levels, temperature and humidity on nocturnal resting periods in urban birds. As birds have become a common and useful model system in the study of urban ecology (Marzluff 2001; Gil and Brumm 2014), approaching these questions in an urban avian species may be particularly relevant.

In this study, we investigated whether urban environmental factors, both anthropogenic and abiotic, predict nocturnal rest in free-living great tits (*Parus major*). Great tits are one of the commonest birds in Eurasian cities and previous studies on this species showed that nocturnal activity may vary with temperature (Stuber et al. 2015, 2017) and light intensity (Raap et al. 2015; de Jong et al. 2016b). However, it is not known whether these factors actually disrupt resting behaviour in urban habitats. Based on the previous literature, we predicted great tit resting behaviour during the night to be more disrupted (1) with increasing levels of artificial light and anthropogenic noise and (2) at higher temperatures. Unlike previous works, this study considers the combined effect of anthropogenic disturbance and urban microclimate, which may help to elucidate the influence of urbanisation on animal behaviour (Sprau and Dingemanse 2017).

Material and methods

Study site and data collection

Between 2 April and 3 May 2016, we observed nocturnal resting behaviour of great tits in the city of Munich, Germany (48° 8' 6.45" N 11° 34' 55.132" E). Great tits are secondary hole nesters, utilising natural holes in trees and artificial nest boxes (Perrins 1965). They are primarily active during the day and are considered nocturnal sleepers (Amlaner and Ball 1983; Stuber et al. 2015). During egg incubation and after hatching of the young, the female spends the night on the nest, whereas the male sleeps outside the nest cavity. This study was performed within the framework of a larger previous study (Sprau et al. 2016). From a total number of 157 great tit territories in the study population, we selected a subset of 23 territories. These 23 nest boxes were distributed across the entire city, thus covering a range of human disturbances on a gradient from highly disturbed habitats in the city centre to relatively undisturbed habitats in suburban areas

(Fig. 1). Territorial pairs bred in nest boxes deployed in the gardens of private homes of collaborating citizen scientists. For the analysis, we used only 17 of these nest boxes, the rest were excluded due to technical problems or to the excessive presence of ectoparasites in one nest, which is known to affect the nocturnal activity of infected birds (Christe et al. 1996). In order to investigate whether urban-induced environmental variation influences resting activity of female great tits during incubation, we chose locations of the nest boxes that allow environmental variation (Fig. 1). At each site, we measured four environmental factors: temperature ($^{\circ}\text{C}$), atmospheric humidity (%), artificial light intensity (lux) and nocturnal noise levels (dB(A) re. $20\mu\text{Pa}$). Measurements were taken at each nest box every minute during the time of observation using custom-made environmental loggers (MSR Electronic GmbH, Switzerland) installed outside the nest boxes approx. 10 cm above the entrance hole. The minimum noise level detectable by the loggers was 39 dB(A), which corresponds to the minimum noise level measured at night in urban bird habitats in previous studies (Fuller et al. 2007; Dominoni et al. 2016). Light levels were measured in lux, which is the luminous flux per square meter. A value of about 100,000 lx corresponds to direct sunlight, 100 lx to a dark overcast day and

0.05–0.3 lx to a full moon on a clear night (Ryer 1997; Kyba et al. 2017). Inside each nest box, an infrared digital Internet protocol camera (INSTAR GmbH, Germany) was installed to remotely monitor the birds' resting behaviour. Only the lens of the camera was visible to the birds, as the camera itself was concealed in the lid of the nest box. In order to minimise disturbance induced by the cameras, LEDs with a wavelength of 940 nm were used, a colour that birds cannot see. We recorded a still photograph every 1 s between 19:00 and 03:00 every night in each nest box for three consecutive nights during the incubation period to measure the activity of the females. However, only data for two nights could be used for three birds because of technical failure, resulting in a mean number of 2.8 analysed nights per bird. Pictures taken by the cameras were automatically stored on a server at the Ludwig Maximilians University. For technical reasons, the system was limited to a recording time of 8 h (i.e. 28,800 pictures) per night and nest box.

Data analysis

A single observer visually analysed all pictures using a MacBook pro. To exclude (unconscious) observer-

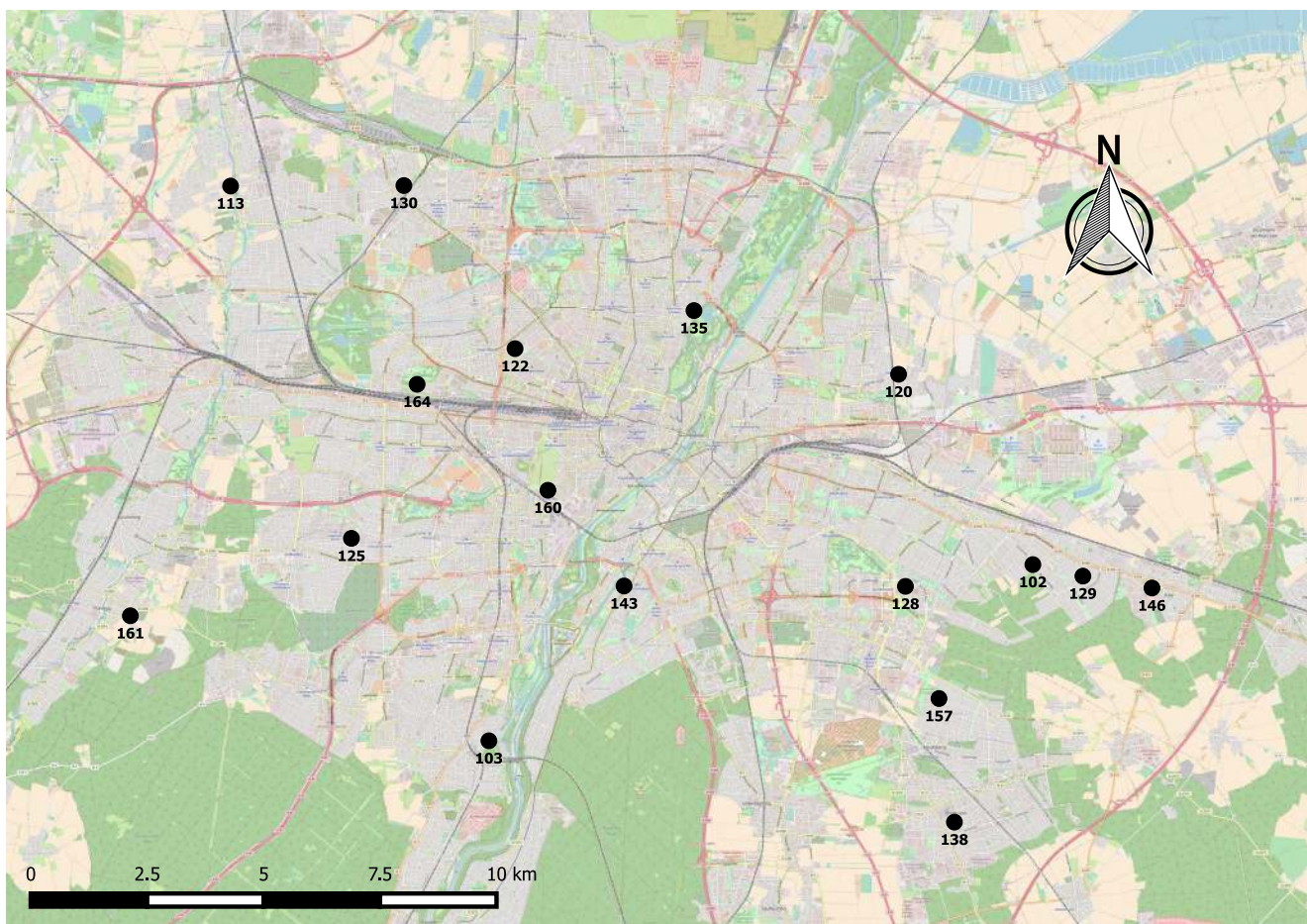


Fig. 1 Distribution of the nest boxes (black dots) in the city of Munich, Germany

expectancy biases (Traniello and Bakker 2015; Brumm et al. 2017), scoring of the images was done blindly, i.e. the person analysing the images was not informed about the environmental data of the nest boxes. For each night, we analysed all photographs by scoring the behavioural state depicted in each, and tallying the number of images that depicted each of two behavioural categories: (1) active, when the head was up, bill was out, facing forwards or the bird was actively moving inside the nest box, then considered awake (Online Resource Fig. S1A), or (2) inactive (resting), when the bird was in a “sleep posture”, with the bill pointed backwards, tucked under the scapulars (Fig. S1B) (Amlaner and Ball 1983). Since it is not possible to determine if a bird was physiologically asleep without recording brain activity, we used the “sleep posture” as a behavioural proxy for sleep, which we describe here as an “inactive” state. From the photographic counts, we then calculated (1) *the number of active bouts*, (2) *the duration of inactive bouts* and (3) *the proportion of night spent in active and inactive states*.

We calculated an average of the environmental factors for each nest box, using only the data taken during the picture recording times. Following Sprau et al. (2016), we excluded spurious noise events above 90 dB(A) (likely elicited by wind). As intended, the average environmental parameters varied markedly between sites. The mean temperature was 5.4 °C (SD = 4.0 °C, range: 0.2–17.0 °C). The mean ambient humidity was 77.1% (SD = 15.1%, range: 44.4–95.9%). The mean artificial light level during the night was 16.8 lx (SD = 19.4, range: 0–92.9 lx). Noise levels had a mean amplitude of 56.9 dB(A) SPL (SD = 20.4, range: 39.0–76.2 dB(A)).

Statistical analysis

We performed a principal component analysis (PCA) with varimax rotation to investigate whether our environmental factors (temperature, humidity, light and noise) could be summarised into a single axis (principal component). The PCA resulted in two components (PC1 and PC2) with eigenvalues higher than one, describing two orthogonal axes of environmental factors (Table 1). We fitted univariate mixed-effect models to estimate sources of variation in resting behaviour. We investigated sources of variation in each of the three focal behaviours (number of active bouts, duration of inactive bouts and proportion of night spent in each state) separately. Random effects included in the models were nest box and date. The two components resulting from the PCA and a variable separating the night into two halves (factor: early vs. late night) were fitted as fixed effects. The factor (early night: 1900–2300 h, late night: 2301–0300 h) was included because previous work found that nocturnal behaviour of great tits can vary with the period of the night (Stuber et al. 2015, 2017). We assumed a Gaussian error distribution for number of active bouts, duration of inactive bouts and

Table 1 Results of the PCA using the four environmental factors

	PC1	PC2	PC3	PC4
Standard deviation	1.37	1.09	0.88	0.41
Proportion of variance	0.47	0.30	0.20	0.04
Cumulative proportion	0.47	0.76	0.96	1.00
Noise [dB(A)]	0.47	−0.22	0.81	−0.27
Light (lux)	−0.41	0.70	0.26	−0.52
Temperature (°C)	−0.47	−0.66	−0.1	−0.57
Humidity (%)	0.62	0.13	−0.52	−0.57
Eigenvalues	1.87	1.18	0.78	0.17

proportion of the night spent in inactivity, which was confirmed by visual inspection of model residuals. All factors were further centred on their mean value (Kreft et al. 1995). For each specified relationship, we calculated the parameter estimate with its associated 95% credible interval. Credible intervals that do not cross zero indicate statistical significance in the frequentist’s sense (i.e. $p < 0.05$). All statistical analyses were performed in R environment (version 3.4.1) using the packages “stats” (version 3.1.27) (R Core Team 2016), “lme4” (version 1.1–7) (Bates et al. 2015), “ggplot2” (version 2.2.1) (Wickham 2009) and “dplyr” (version 0.7.4) (Wickham et al. 2017). The software QGIS (version 2.4.0) (QGIS 2017) was used to plot the map in Fig. 1.

Data availability

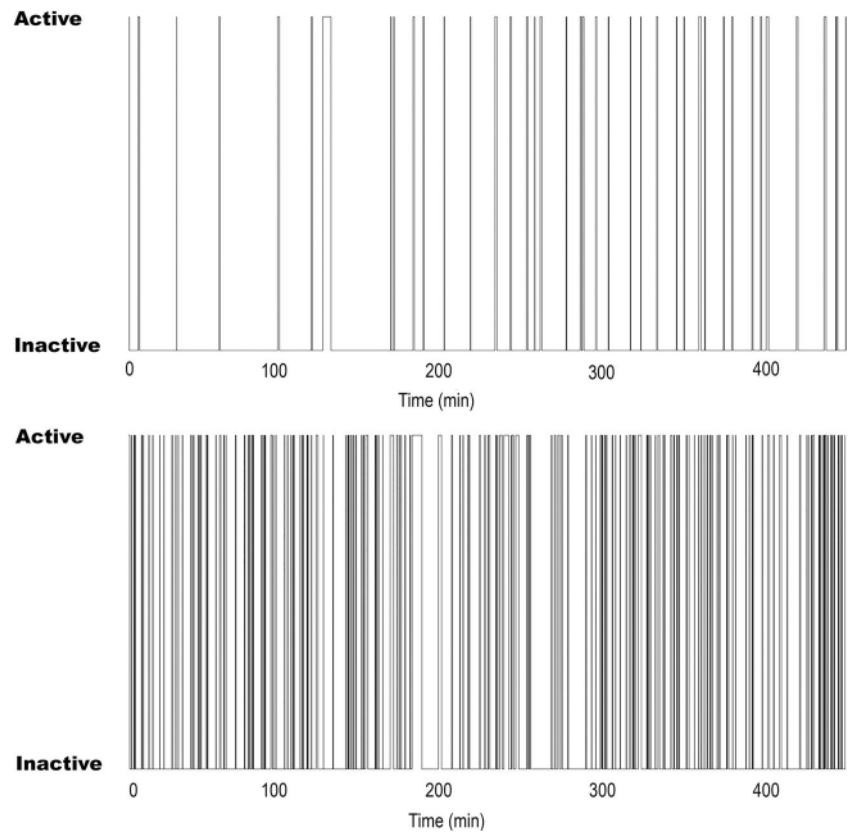
The datasets analysed during this study are available from the corresponding author upon request.

Results

Patterns of resting behaviour during the night varied notably between females (Fig. 2), with the most active individuals moving more than three times as often as the least active (mean: 84.5 ± 25.7 SD, range: 29–180). The duration of individual bouts of inactivity ranged between 1 and 2424 s (grand mean: 267.1 ± 47.1). On average, the birds spent 93.3% of the night in resting position, with 97.1% resting time in the most inactive night and 82.1% in the least inactive night.

However, this variation was not related to the composite measures of environmental factors (Table 2). Neither PC1 (humidity and noise) nor PC2 (temperature and artificial light) had an effect on the number of active bouts, the duration of inactive bouts or the proportion of the night spent at rest. When analysing artificial light and noise levels separately, models also did not show an effect of these factors on the number of active bouts [light: $\beta = 0.05$; -0.16 – 0.25 (95% CrI) and noise $\beta = 0.05$; -0.12 –

Fig. 2 Hypnogram showing the number and duration of active and inactive states of the least active bird (top) and the most active bird (bottom)



0.20] or on the duration of inactive bouts [light: $\beta = -0.05$; -0.32 – 0.20 and noise $\beta = -0.13$; -0.35 – 0.07] or on the proportion of night resting [light $\beta = -0.05$; -0.28 – 0.20 and noise $\beta = 0.01$; -0.18 – 0.18].

Discussion

Our study found that variation in nocturnal resting behaviour between female great tits was not related to the environmental

Table 2 Sources of variation in the number of active bouts, the duration of inactive bouts and the total duration of inactivity in relation to humidity and noise (PC1) and temperature and light (PC2, see Table 1). All models control for variation induced by time of night (early and late night) and

	Number of active bouts	Duration of inactive bouts	Proportion of night inactive
Fixed effects	β [CrIs]	β [CrIs]	β [CrIs]
Intercept	0.28 [– 0.34–0.79]	– 2.29 [– 22.19–19.73]	0.53 [– 0.10–1.14]
PC1	0.03 [– 0.19–0.25]	– 0.04 [– 0.31–0.22]	– 0.06 [– 0.31–0.19]
PC2	0.00 [– 0.17–0.18]	0.03 [– 0.19–0.24]	0.02 [– 0.18–0.21]
Time of night	0.14 [– 0.35–0.08]	0.00 [– 0.03–0.04]	– 0.36 [– 0.70–0.04]
Random effects	σ [CrIs]	σ [CrIs]	σ [CrIs]
Nest box	0.88 [0.58–2.15]	0.05 [0.33–1.23]	0.44 [0.29–1.09]
Day	0.03 [0.01–0.04]	0.00 [0.00–0.00]	0.00 [0.00–0.00]
Residual	0.25 [0.20–0.35]	0.66 [0.50–0.89]	0.66 [0.49–0.90]

factors ambient light, noise, temperature and humidity. Specifically, we did not find an effect of environmental factors on the number of active bouts, the duration of inactive bouts or on the proportion of time spent at rest during the night. This lack of evidence for an effect was observed when considering composite measures of environmental factors within the same model as well as when looking at the effects of artificial light and noise separately.

These findings contrast earlier studies that reported nocturnal resting behaviour of birds varied with temperature and

included random intercepts for nest box and day. We present fixed parameters (β) and random parameters (σ) with their 95% credible intervals (CrIs); effects with credible intervals that do not include zero are considered to be likely important

light exposure. For instance, free-ranging great tits were found to exhibit more nocturnal bouts of activity and to spend a greater proportion of the night active when temperatures were higher (Steinmeyer et al. 2010; Mueller et al. 2012; Stuber et al. 2015, 2017). Likewise, increased light intensities were found to reduce nocturnal rest in great tits, both in a correlative study (Stuber et al. 2015) as well as in response to experimental internal illumination of nest boxes (Raap et al. 2015, 2016; Stuber et al. 2017). When it comes to anthropogenic noise, we know of no previous study that has investigated whether noise affects bird resting behaviour or sleep. However, laboratory studies with other vertebrates have addressed the relation between environmental noise and sleep disturbances, and these studies found that chronic exposure to noise can permanently reduce and fragment sleep (Rabat 2007). Additionally, sleep deficits have been linked to compromises in the immune system (Majde and Krueger 2005), and animals chronically exposed to noise may even develop pathologies linked to poor sleep (McEwen and Wingfield 2003). However, in this study, we did not find an effect of noise levels, or any of our tested urban environmental factors on nocturnal resting behaviour in great tits.

Although all our nest boxes were located in urban and suburban areas, the data loggers registered a large variation of the environmental factors between recording sites and, thus, the lack of environmental correlates of disruptions of rest time cannot be explained by lesser variation in environmental factors in our study. Indeed, we deliberately chose the nest box locations to cover a wide range of noise and light levels. As a result, our variation in artificial light levels ranged between 0 and 92.2 lx, which is much greater than the variation of light levels that have been previously related to reduced nocturnal rest in great tits (Raap et al. 2016; Sun et al. 2017), although these studies used artificial illumination inside nest boxes, whereas we measured the natural variation of ambient urban light levels outside the nest boxes. In addition, our average nocturnal noise levels varied substantially between nest boxes and were well within the range of noise levels that induces behavioural changes in urban birds, including great tits (Brumm 2004; Dominoni et al. 2016; Zollinger et al. 2017). Although not explicitly planned during the design of the study, the average temperatures also varied markedly between our nest box sites, namely by 13 °C, which is similar to the temperature difference of 15 °C, and bigger than the 5 °C rise, that triggered a modification of great tit nocturnal rest in two previous studies (Lehmann et al. 2012; Stuber et al. 2017).

The discord between this study and previous work on temperature and light effects on resting behaviour in birds may be accounted for by our novel integrative approach that considers environmental variation as a unit. Ecological studies of urbanisation often focus largely on simple urban versus rural comparisons (Marzluff 2001; Marzluff and Rodewald 2008). Only recently have researchers started to integrate quantitative

environmental measures and their variation in studies on the impacts of urbanisation on life histories (Sprau et al. 2016). In this study, we tested multiple environmental factors within the same model, which acknowledges the complexity of urban habitats and, therefore could yield different results than studies including only one of these factors. The statistical difference between the two approaches is that in our case, variance is partitioned whereas in previous studies, variation is composed only of one factor. This partitioning may result in different effects levelling each other out in our study. However, as the Umwelt of an animal is composed of multiple environmental variables, it is important to consider the combined effects of external influences. Thus, we feel that an integrative approach is better suited to the investigation of responses of animals to the combination of various environmental variables. However, even when considering light pollution levels in isolation, we did not find an effect on nocturnal resting behaviour. These contrasts with previous studies may be, at least partly, accounted for by methodological differences. Previous studies used artificial illumination inside nest boxes or cages (Raap et al. 2015; de Jong et al. 2016a; Sun et al. 2017), whereas we measured the natural variation of urban light levels outside the nest boxes. Obviously, nest boxes and natural nesting cavities can shield birds, to some extent, from light pollution. Hence, our results might also be taken as a hint that the effects of light pollution may be reduced for birds sleeping in cavities. In line with this notion, Ouyang et al. (2017) found that great tits in artificially illuminated areas were less active during the night when roosting inside nest boxes compared to birds roosting outside nest boxes (but see Raap et al. (2017) for a critique).

Moreover, anthropogenic disturbances may also affect other biotic factors that could, in turn, influence nocturnal resting behaviour of birds. For example, if increased levels of noise or light pollution decrease predation risk during the night, great tits might be more likely to be active in less noisy/illuminated urban areas, which would mask an effect of these anthropogenic disturbances in our data. To further investigate this issue, one would need to assess whether light or noise pollution affects the density or the behaviour of nocturnal nest box predators. If it does, then artificial illumination inside the nest box, as used in previous experimental studies, may not be the most ideal method in terms of ecological relevance.

Another explanation for our findings could be that individuals that are better adapted to anthropogenic disturbances settle in areas with high levels of light and noise pollution. Phenotype-matching habitat choice has been suggested as an explanation for settlement patterns in relation to human disturbance in dunnocks, *Prunella modularis* (Holtmann et al. 2017). Moreover, it has been found that urban great tits differ in consistent behavioural traits from their rural conspecifics (Hardman and Dalesman 2018). It might well be that non-random distributions of great tit phenotypes also occur at

smaller spatial scales within cities, such that individuals that are less sensitive to nocturnal disturbance are more likely to settle in disturbed areas.

Alternatively, it is also possible that city great tits have habituated to the environment and therefore no correlation between the environment and resting behaviour could be found. So far, little is known about whether and how birds habituate to anthropogenic disturbance. A study on human-induced flight behaviour indicates that urban birds habituate faster than their rural conspecifics (Vincze et al. 2016). In addition, several reports suggest that animals may respond less to loud noise events after repeated exposure (Boudreau 1968; Weisenberger et al. 1996; Krausman et al. 1998). While American black ducks (*Anas rubripes*) habituated to experimental aircraft noise exposure and reduced their vigilance and flight behaviours over the course of several days, wood ducks (*Aix sponsa*) did not habituate (Conomy et al. 1998). Laboratory experiments on rodents demonstrated that habituation to noise often occurs only on the behavioural level, but animals can still be affected physiologically (Rabat 2007). Thus, even if urban birds are able to restore their resting behaviour in chronic noise, nocturnal noise exposure may still be harmful to them because covert micro-arousals and decreased sleep intensity might go unnoticed in the behavioural observations.

It is important to bear in mind that this study, like previous ones on environmental effects on “sleep” in wild birds (Steinmeyer et al. 2010; Raap et al. 2015, 2016; Stuber et al. 2015, 2017; Ouyang et al. 2017; Sun et al. 2017), did not measure sleep but used nocturnal resting behaviour as a proxy for it. While it is obvious that the scope for sleep is decreased when a bird is more active, a caveat of this behavioural proxy is that inactivity does not necessarily mean that a bird is indeed sleeping. Even without detectable differences in total sleep duration, environmental influences may still affect the quality of sleep (Aulsebrook et al. 2016). For instance, humans may subjectively habituate to nocturnal noise, in that they are not awakened by it, but noise events still cause responses of the autonomic nervous system, such as elevated heart rate and vasoconstriction of sleeping individuals (Muzet 2007). Moreover, it has been found that noise exposure can result in a suppression of sleep intensity in humans without affecting sleep duration, which could over the long-term have adverse effects on health (Tasali et al. 2008). This means that although we did not find evidence that urban environmental factors disrupt resting behaviour in great tits, their sleep might still be impaired by anthropogenic disturbance. To elucidate this issue, it is therefore necessary to advance from behavioural sleep correlates to measuring brain activity. Laboratory setups to record EEG patterns in birds (Rattenborg et al. 2004; Lesku et al. 2011) could be used to investigate whether sleep is affected by light and noise pollution. Moreover, as the progress in technology now enables researchers to measure EEG-defined sleep also in wild animals (Rattenborg et al. 2017), it

may be feasible in the near future to measure brain activity in free-ranging city birds. For this purpose, the integrative ecological approach that we used in this study may be particularly fruitful for future research on animal sleep in urban environments.

Acknowledgments We thank students and field assistants of the Behavioural Ecology group of the Ludwig-Maximilians-Universität München, as well as all citizen scientists for help with collecting the data. Walter Schimmel and Dietfried Molter are acknowledged for technical support and Sam Hardman, Samuel Kaiser, Julia Schäfer, Adriana Dorado, and Luke Eberhart-Phillips for discussions. Also, we thank Niels Rattenborg, Constantino Macías García, and two anonymous reviewers for their comments on the manuscript. We further thank the citizen scientists for hosting the nest boxes and providing access to the cameras.

Funding Information Open access funding provided by Max Planck Society. Research funding was provided by grants by the Deutsche Forschungsgemeinschaft to PS (award SP 1450/3-1) and HB (awards BR 2309/8-2 and BR 2309/9-1) and a research fellowship to VC awarded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES No. 88881.135522/2016-01).

Compliance with ethical standards

Ethical approval Permits to set up the nest boxes and collect the data were obtained from the Bavarian government and the Bavarian regional office for forestry LWF (permit numbers 55.2-1-54-2532-140-11; 55.2-1-54-2532-59-12). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Amlaner CJ, Ball NJ (1983) A synthesis of sleep in wild birds. *Behaviour* 87:85–119
- Andersen ML, Ribeiro DA, Bergamaschi CT, Alvarenga TA, Silva A, Zager A, Campos RR, Tufik S (2009) Distinct effects of acute and chronic sleep loss on DNA damage in rats. *Prog Neuropsychopharmacol* 33:562–567
- Aulsebrook AE, Jones TM, Rattenborg NC, Roth IITC, Lesku JA (2016) Sleep ecophysiology: integrating neuroscience and ecology. *Trends Ecol Evol* 31:590–599
- Avondet JL, Blair RB, Berg DJ, Ebbert MA (2003) *Drosophila* (Diptera: Drosophilidae) response to changes in ecological parameters across an urban gradient. *Environ Entomol* 32:347–358
- Barber JR, Crooks KR, Fristrup KM (2010) The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol Evol* 25:180–189
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48

- Begemann SHA, van den Beld GJ, Tenner AD (1997) Daylight, artificial light and people in an office environment, overview of visual and biological responses. *Int J Ind Ergon* 20:231–239
- Boudreau GW (1968) Alarm sounds and responses of birds and their application in controlling problem species. *Living Bird* 7:27–46
- Brans KI, Jansen M, Vanoverbeke J, Tüzün N, Stoks R, De Meester L (2017) The heat is on: genetic adaptation to urbanization mediated by thermal tolerance and body size. *Glob Chang Biol* 23:5218–5227
- Brumm H (2004) The impact of environmental noise on song amplitude in a territorial bird. *J Anim Ecol* 73:434–440
- Brumm H (2010) Anthropogenic noise: implications for conservation. In: Breed MD, Moore J (eds) *Encyclopedia of animal behavior*. Academic Press, Oxford, pp 89–93
- Brumm H (ed) (2013) *Animal communication and noise*. Springer-Verlag, Berlin
- Brumm H, Zollinger SA, Niemelä PT, Sprau P (2017) Measurement artefacts lead to false positives in the study of birdsong in noise. *Methods Ecol Evol* 8:1617–1625
- Christe P, Richner H, Oppliger A (1996) Of great tits and fleas: sleep baby sleep. *Anim Behav* 52:1087–1092
- Cirelli C, Tononi G (2008) Is sleep essential? *PLoS Biol* 6:e216
- Conomy JT, Dubovsky JA, Collazo JA, Fleming WJ (1998) Do black ducks and wood ducks habituate to aircraft disturbance? *J Wildl Manag* 62:1135–1142
- de Jong M, Jeninga L, Ouyang JQ, van Oers K, Spoelstra K, Visser ME (2016a) Dose-dependent responses of avian daily rhythms to artificial light at night. *Physiol Behav* 155:172–179
- de Jong M, Ouyang JQ, van Grunsven RHA, Visser ME, Spoelstra K (2016b) Do wild great tits avoid exposure to light at night? *PLoS One* 11:e0157357
- Dominoni D, Quetting M, Partecke J (2013) Artificial light at night advances avian reproductive physiology. *Proc R Soc B* 280:20123017
- Dominoni D, Carmona-Wagner EO, Hofmann M, Kranstauber B, Partecke J (2014) Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. *J Anim Ecol* 83:681–692
- Dominoni D, Greif S, Nemeth E, Brumm H (2016) Airport noise predicts song timing of European birds. *Ecol Evol* 6:6151–6159
- Dorado-Correa AM, Zollinger SA, Heidinger B, Brumm H (2018) Timing matters: traffic noise accelerates telomere loss rate differently across developmental stages. *Front Zool* 15:29
- Fuller RA, Warren PH, Gaston KJ (2007) Daytime noise predicts nocturnal singing in urban robins. *Biol Lett* 3:368–370
- Gil D, Brumm H (eds) (2014) *Avian urban ecology: behavioural and physiological adaptations*. Oxford University Press, Oxford
- Griefahn B (2002) Sleep disturbances related to environmental noise. *Noise Health* 4:57–60
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. *Science* 319:756–760
- Hardman SI, Dalesman S (2018) Repeatability and degree of territorial aggression differs among urban and rural great tits (*Parus major*). *Sci Rep* 8:5042
- Hölker F, Wolter C, Perkin EK, Tockner K (2010) Light pollution as a biodiversity threat. *Trends Ecol Evol* 25:681–682
- Holtmann B, Santos ESA, Lara CE, Nakagawa S (2017) Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. *Proc R Soc B* 284: 20170943
- Kappelle M, Van Vuuren MMI, Baas P (1999) Effects of climate change on biodiversity: a review and identification of key research issues. *Biodivers Conserv* 8:1383–1397
- Kempnaers B, Borgström P, Loës P, Schlicht E, Valcu M (2010) Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr Biol* 20:1735–1739
- Kight CR, Swaddle JP (2011) How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecol Lett* 14:1052–1061
- Kleist NJ, Guralnick RP, Cruz A, Lowry CA, Francis CD (2018) Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proc Natl Acad Sci U S A* 115:E648–E657
- Krausman PR, Wallace MC, Hayes CL, DeYoung DW (1998) Effects of jet aircraft on mountain sheep. *J Wildl Manag* 62:1246–1254
- Krefl IG, de Leeuw J, Aiken LS (1995) The effect of different forms of centering in hierarchical linear models. *Multivar Behav Res* 30:1–21
- Kyba C, Mohar A, Posch T (2017) How bright is moonlight? *Astron Geophys* 58:1.31–1.32
- Lehmann M, Spoelstra K, Visser ME, Helm B (2012) Effects of temperature on circadian clock and chronotype: an experimental study on a passerine bird. *Chronobiol Int* 29:1062–1071
- Lesku JA, Vyssotski AL, Martinez-Gonzalez D, Wilzeck C, Rattenborg NC (2011) Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? *Proc R Soc Lond B* 278: 2419–2428
- Lewy AJ, Wehr TA, Goodwin FK, Newsome DA, Markey SP (1980) Light suppresses melatonin secretion in humans. *Science* 210: 1267–1269
- Majde JA, Krueger JM (2005) Links between the innate immune system and sleep. *J Allergy Clin Immunol* 116:1188–1198
- Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, Donnelly R (eds) *Avian ecology and conservation in an urbanizing world*. Springer, Boston, pp 19–47
- Marzluff JM, Rodewald A (2008) Conserving biodiversity in urbanizing areas: nontraditional views from a bird's perspective. *Cities Environ* 1:6
- Marzluff JM, Shulenberg E, Endlicher W, Alberti M, Bradley G, Ryan C, Simon U, ZumBrunnen C (2008) *Urban ecology: an international perspective on the interaction between humans and nature*. Springer, Boston
- McEwen BS, Wingfield JC (2003) The concept of allostasis in biology and biomedicine. *Horm Behav* 43:2–15
- McGregor PK, Horn AG, Leonard ML, Thomsen F (2013) Anthropogenic noise and conservation. In: Brumm H (ed) *Animal communication and noise*. Springer-Verlag, Berlin, pp 409–444
- McKinney ML (2002) Urbanization, biodiversity, and conservation. *Bioscience* 52:883–890
- Michaud DS, Fidell S, Pearsons K, Campbell KC, Keith SE (2008) Review of field studies of aircraft noise-induced sleep disturbance. *J Acoust Soc Am* 39:12–23
- Mueller JC, Steinmeyer C, Kempnaers B (2012) Individual variation in sleep-wake rhythms in free-living birds. *Chronobiol Int* 29:1216–1226
- Murphy MO, Agha M, Mairret TA, Price SJ, Dorcas ME (2016) The effects of urbanization on body size of larval stream salamanders. *Urban Ecosyst* 19:275–286
- Muzet A (2007) Environmental noise, sleep and health. *Sleep Med Rev* 11:135–142
- Ouyang JQ, de Jong M, van Grunsven RHA, Matson KD, Haussmann MF, Meerlo P, Visser ME, Spoelstra K (2017) Restless roosts: light pollution affects behavior, sleep, and physiology in a free-living songbird. *Glob Chang Biol* 23:4987–4994
- Peach WJ, Vincent KE, Fowler JA, Grice PV (2008) Reproductive success of house sparrows along an urban gradient. *Anim Conserv* 11: 493–503
- Perrins CM (1965) Population fluctuations and clutch-size in the great tit, *Parus major* L. *J Anim Ecol* 34:601–647
- QGIS Development Team (2017) QGIS geographic information system. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>. Accessed 17 Dec 2017
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <http://www.R-project.org>

- Raap T, Pinxten R, Eens M (2015) Light pollution disrupts sleep in free-living animals. *Sci Rep* 5:13557
- Raap T, Pinxten R, Eens M (2016) Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environ Pollut* 215:125–134
- Raap T, Pinxten R, Eens M (2017) Rigorous field experiments are essential to understand the genuine severity of light pollution and to identify possible solutions. *Glob Chang Biol* 23:5024–5026
- Rabat A (2007) Extra-auditory effects of noise in laboratory animals: the relationship between noise and sleep. *J Am Assoc Lab Anim* 46:35–41
- Rattenborg NC, Mandt BH, Obermeyer WH, Winsauer PJ, Huber R, Wikelski M, Bencá RM (2004) Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biol* 2:e212
- Rattenborg NC, de la Iglesia HO, Kempnaers B, Lesku JA, Meerlo P, Scriba MF (2017) Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep. *Phil Trans R Soc B* 372:20160251
- Ryer A (1997) Light measurement handbook. International Light Inc, Newburyport
- Schäfer JE, Janocha MM, Klaus S, Tietze DT (2017) How weather instead of urbanity measures affects song trait variability in three European passerine bird species. *Ecol Evol* 7:4868–4880
- Shaw PJ, Tsononi G, Greenspan RJ, Robinson DF (2002) Stress response genes protect against lethal effects of sleep deprivation in *Drosophila*. *Nature* 417:287–291
- Siegel JM (2008) Do all animals sleep? *Trends Neurosci* 31:208–213
- Sprau P, Dingemans NJ (2017) An approach to distinguish between plasticity and non-random distributions of behavioral types along urban gradients in a wild passerine bird. *Front Ecol Evol* 5:92
- Sprau P, Mouchet A, Dingemans NJ (2016) Multidimensional environmental predictors of variation in avian forest and city life histories. *Behav Ecol* 28:59–68
- Steinmeyer C, Schielzeth H, Mueller JC, Kempnaers B (2010) Variation in sleep behaviour in free-living blue tits, *Cyanistes caeruleus*: effects of sex, age and environment. *Anim Behav* 80:853–864
- Stephenson R, Chu KM, Lee J (2007) Prolonged deprivation of sleep-like rest raises metabolic rate in the Pacific beetle cockroach, *Diploptera punctata* (Eschscholtz). *J Exp Biol* 210:2540–2547
- Stuber EF, Dingemans NJ, Kempnaers B, Mueller JC (2015) Sources of intraspecific variation in sleep behaviour of wild great tits. *Anim Behav* 106:201–221
- Stuber EF, Dingemans NJ, Mueller JC (2017) Temperature affects frequency but not rhythmicity of nocturnal awakenings in free-living great tits, *Parus major*. *Anim Behav* 128:135–141
- Sun J, Raap T, Pinxten R, Eens M (2017) Artificial light at night affects sleep behaviour differently in two closely related songbird species. *Environ Pollut* 231:882–889
- Tasali E, Leproult R, Ehrmann DA, Van Cauter E (2008) Slow-wave sleep and the risk of type 2 diabetes in humans. *Proc Natl Acad Sci U S A* 105:1044–1049
- Templeton CN, Zollinger SA, Brumm H (2016) Traffic noise drowns out great tit alarm calls. *Curr Biol* 26:R1173–R1174
- Traniello JFA, Bakker TCM (2015) Minimizing observer bias in behavioral research: blinded methods reporting requirements for *Behavioral Ecology and Sociobiology*. *Behav Ecol Sociobiol* 69:1573–1574
- Vincze E, Papp S, Preiszner B, Seress G, Bókony V, Liker A (2016) Habituation to human disturbance is faster in urban than rural house sparrows. *Behav Ecol* 27:1304–1313
- Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147:164–172
- Weisenberger ME, Krausman PR, Wallace MC, De Young DW, Maughan OE (1996) Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. *J Wildl Manag* 60:52–61
- Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer, New York
- Wickham H, Francois R, Henry L, Müller K (2017) dplyr: a grammar of data manipulation. R package version 0.7.4. <http://CRAN.R-project.org/package=dplyr>. Accessed 12 April 2018
- Zollinger SA, Slater PJB, Nemeth E, Brumm H (2017) Higher songs of city birds may not be an individual response to noise. *Proc R Soc B* 284:20170602

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.