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Urban house finches are more resistant to the effects of artificial light at night

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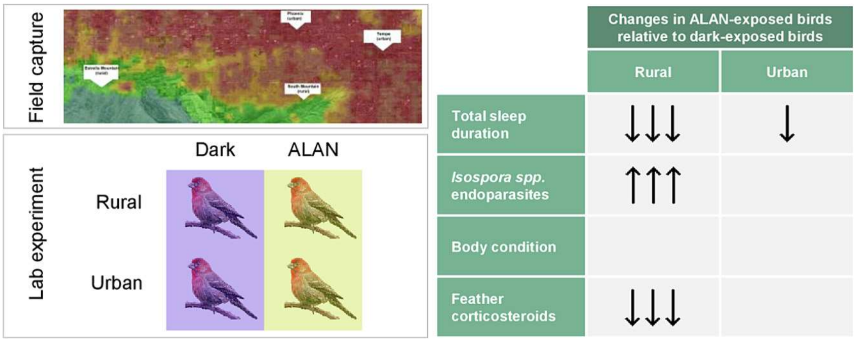
HIGHLIGHTS

- Wildlife may acquire resistance to the effects of artificial light at night (ALAN).
- Urban (but not rural) birds were overall resistant to experimental ALAN exposure.
- ALAN-exposed urban birds slept more and had fewer endoparasites than rural birds.
- ALAN-induced CORT_F suppression was mediated by ALAN-induced sleep loss.
- Urban birds were resistant to ALAN-induced corticosteroid dysregulation.

GRAPHICAL ABSTRACT



Changes in ALAN-exposed birds relative to dark-exposed birds	Rural	Urban
Total sleep duration	↓↓↓	↓
Isospora spp. endoparasites	↑↑↑	
Body condition		
Feather corticosteroids	↓↓↓	

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ABSTRACT

Rapid urbanization of habitats alters the physical, chemical, auditory, and photic environments of human and wild animal inhabitants. One of the most widespread transformations is caused by artificial light at night (ALAN), but it is not clear the extent to which individuals acclimate to such rapid environmental change. Here, we tested the hypothesis that urban birds show increased resistance to harmful behavioral, parasitological, and physiological effects of ALAN. We captured house finches (*Haemorhous mexicanus*), a bird that commonly inhabits cities and their natural surroundings, from two urban and two rural sites in Phoenix, Arizona, USA, which differ by both degree of urbanization and by multiple orders of magnitude in ALAN intensity, and placed them in a common garden laboratory setting. We exposed half of the birds from each habitat type to ecologically relevant levels of night lighting during the subjective night and found that, while ALAN exposure reduced sleep in both urban and rural birds, ALAN-exposed urban birds were able to sleep longer than ALAN-exposed rural birds. We also found that ALAN exposure increased the proliferation rate of an intestinal coccidian parasite (*Isospora* spp.) in both urban and rural birds, but that the rate of proliferation was lower in urban relative to rural birds. We found that night lighting suppressed titers of feather corticosterone in rural but not urban birds, suggesting that light impairs HPA function through chronic stress or suppression of its circadian rhythmicity, and that urban birds were again resistant to this effect. Mediation analyses show that the effect of ALAN exposure in rural birds was significantly sleep-mediated for feather corticosterone but not coccidiosis, suggesting a diversity of

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mechanisms by which ALAN alters physiology. We contribute further evidence that animals from night-lit habitats can develop resistance to ALAN and its detrimental effects.

1. Introduction

Humans have rapidly transformed Earth's surface and atmosphere over the last few centuries. For example, recent approximations suggest that global urban land area increased from ca. 450,000 km^2 in 1990 to 747,000 km^2 in 2010 (Grimm et al., 2008; Liu et al., 2014, 2018). The United Nations projects that nearly all human population growth through 2100 will occur in urban populations. The spread of global urbanization therefore presents one of the most geographically extensive and locally impactful forms of land use and land change in human history. With urbanization comes a plethora of associated environmental changes, such as natural habitat transformations and various types of pollution. Perhaps the most biologically novel, pervasive, and widespread component of city life is artificial light at night (ALAN). Falchi et al. (2016) estimated that about 40 % of Earth's land surface was light polluted in 2013–2014, a substantial increase from estimates just two decades earlier (Cinzano et al., 2001). They also showed that about 2 % of the globe is under “very high” nighttime light intensities (Falchi et al., 2016).

ALAN has strong biological impacts on many organisms (Horváth et al., 2009; Gaston et al., 2013; Le Tallec et al., 2013; Da Silva et al., 2015; Aulsebrook et al., 2018). Daytime and overnight light is often used as a natural cue for entraining biological clocks, which drive daily and annual variation in growth, physiology, and behavior, and ALAN can disrupt these natural cues (Pohl, 1999; Rani and Kumar, 2000; Dominoni, 2015). ALAN also can have direct and immediate impacts on behavior, including on sleep-wake activity (Phillips and Berger, 1992; Rattenborg et al., 2005; Yorzinski et al., 2015; Sun et al., 2017; Aulsebrook et al., 2018). Sleep is thought to perform several functions, such as improving immune activity (Bryant et al., 2004; Preston et al., 2009; Kuo and Williams, 2014; Raap et al., 2016a), consolidation of memory (Shank and Margoliash, 2009; Tononi and Cirelli, 2014), and energy conservation (Roth et al., 2010; Schmidt, 2014). Therefore, light pollution should have downstream impacts on both circadian traits and expression of traits that are directly controlled by sleep (Aulsebrook et al., 2021).

However, adaptive and plastic responses to ALAN could ameliorate some of the harmful sleep-loss-related physiological and behavioral effects (Dominoni et al., 2013a; Ulgezen et al., 2019). For example, Dominoni et al. (2013a) found that rural blackbirds exposed to ecologically relevant levels of ALAN increased activity more than urban conspecifics. There are also numerous examples of both vertebrates and invertebrates avoiding night-lit areas (Falcón et al., 2020), including at migratory stopover sites where birds are likely already sleep-deprived (Ferretti et al., 2019). It is possible that there is population-level adaptation or individual-level plasticity that increases physiological and behavioral resistance (shown by a dampened response) to ALAN. In this study, we used a common-garden experimental approach with wild-caught house finches (*Haemorhous mexicanus*) to test whether urban birds are more resistant to the hypothetical effects of exposure to ALAN; specifically, sleep behavior, parasite burden, body condition, and a long-term integrated measure of circulating corticosteroids, feather corticosteroids (CORT$_F$). Because of sleep's role in promoting multiple components of health, we predict that, if urban bird sleep is more resistant to ALAN than in rural birds (due to either selection or acclimation), urban birds will experience fewer sleep-health-related physiological costs (shown by either no effect in urban birds but an effect in rural birds, or a comparatively small effect in urban relative to rural birds). Additionally, we test whether the effects of light treatment on aspects of health are mediated by sleep duration.

Exposure to ALAN may positively or negatively alter indices of organismal health. Recent studies show that overnight exposure to ALAN increases circulating corticosteroids in birds, perhaps because of an activated stress response (Ouyang et al., 2015; Alaasam et al., 2018; Grunst et al., 2019; Dominoni et al., 2021). Because exposure to ALAN in cities is chronic, longer-term measures of corticosterone may be more appropriate. Corticosteroids are deposited from the blood into feathers, making this assay a long-term metric of corticosteroid secretion (Bortolotti et al., 2008). Based on these studies, we predict that long-term ALAN exposure should increase CORT$_F$ levels, but that the magnitude of this difference will be lower in urban than rural birds. Additionally, if urban birds are physiologically resistant to the sleep-restricting effects of ALAN, we predict that the intensity of infection with coccidian endoparasites (a common intestinal parasite in this bird, Duckworth et al., 2001; Giraudeau et al., 2014) will increase less in urban than rural birds. Because coccidia inhabit intracellular and extracellular spaces in host organisms, avian hosts mount a complex immune response consisting of both humoral and cell-mediated factors (Yun et al., 2000), any of which could potentially be impaired by ALAN (Ziegler et al., 2021). Finally, studies of growing nestling great tits (*Parus major*) show that experimental exposure to ALAN slowed growth (Raap et al., 2016b); here, we measured the body-mass change of fully-grown birds, and if ALAN has general effects on body mass regardless of age, we predict that ALAN would reduce body mass, but less so in urban finches.

2. Methods

2.1. Study area and subjects

The house finch is a species commonly used for studying biological impacts of urbanization (Fernández-Juricic et al., 2005; Weaver et al., 2018a; Hutton et al., 2021), due to its (1) abundance in rural, suburban, and urbanized areas in North America (Badyaev et al., 2020), (2) lack of migratory tendencies (including at our study sites) and short post-fledging dispersal distances, such that adults are exposed to similar local environments beginning at a young age and lasting throughout life (Badyaev et al., 2020), and (3) amenability to experimental captive studies. We captured finches from urban and rural areas in and near Phoenix, Arizona, USA, a large desert metropolis with an extensive urban-rural gradient of ALAN (Fig. 1a). Phoenix is one of the fastest growing cities in the United States; since 1990, the population has more than doubled from roughly 2 million to 4.6 million in 2021. Additionally, the land area of Phoenix has roughly doubled in the same timeframe. Thus, we studied finches in and around a city that has experienced extremely rapid growth.

We studied house finches at four different sites that vary both in their degree of urbanization and artificial light at night. Two sites, Phoenix (33.459810, −112.059289) and Tempe (33.419829, −111.933165; “urban sites”), are considerably more urbanized than the two “rural sites”, Estrella Mountain Regional Park (33.383067, −112.370096) and South Mountain Regional Park (33.350600, −112.076106). Site categorizations are based on multiple metrics of urban land use and land cover (captured via satellite imagery) and human population density (Giraudeau et al., 2014, 2018). These sites also differ greatly in their degree of ALAN exposure. The United States National Air and Space Association's and the United States National Oceanic and Atmospheric Association's Suomi-NPP satellite collects radiance data from Earth using the Day/Night Band from its Visible Infrared Imaging Radiometer Suite. Using cloud-free composite satellite data available from March 2014 (https://earthdata.nasa.gov/earth-observation-data/near-real-time/download-nrt-data/viirs-nrt), we estimated the radiance within a 1 km radius of each capture site, which should encompass the active range of finches caught at each capture site (Giraudeau et al., 2014). Indeed, our two urban sites have much higher levels of ALAN; from our darkest to brightest site, we found a two-order magnitude difference in mean ALAN intensity as measured in radiance (10^{-9} W/cm^2·sr; Fig. 1b).

From 21 to 27 May 2014, we captured house finches from the four sites (n = 64 total birds; Tempe: n = 16, Phoenix n = 15, South Mountain = 17, Estrella = 16; these were well balanced by sex and age across sites and treatment groups; Supplementary Table 1). Captured individuals with visible canary poxvirus (*Avipoxvirus* spp.) infection were released immediately and not included in the study, because this virus can quickly spread among and kill captive study subjects. All procedures were performed in compliance with relevant laws and institutional guidelines (including ARRIVE and the National Research Council's Guide for the Care and Use of Laboratory Animals), and were approved by the Arizona State University Institutional Animal Care and Use Committee (protocol #12-1234R).

2.2. Experimental setup

All birds were brought to the animal care facilities at Arizona State University — Tempe campus and then evenly split into treatment groups by site of origin and sex; individuals that could not be sexed were randomly split between groups as well. Birds were then placed in individual cages (0.40 m × 0.29 m × 0.21 m) within indoor, windowless climate-controlled rooms. The control and night-light-exposed treatment groups were housed in separate rooms. Within each room, the location of birds was randomized (birds were kept in bags and shuffled, then selected at random) to control for the potential confounding effects of differential exposure to light in varying locations throughout the housing room. The birds were provided with ad libitum access to food and water, and the indoor daytime photoperiod (14 h light:10 h dark) was set to approximate outdoor conditions at this time of year. We allowed the birds two weeks to acclimate to the captive environment before beginning the experimental treatment. Though the housing rooms were virtually identical, to negate any possible inter-room differences we swapped the experimental groups between the two rooms every eight days such that the treatment and control groups had approximately equal exposure to both rooms during the study.

To expose the treatment group to night lighting during the experiment, we placed three lights (7 W bulb; Meridian Lighting Company, Maryland Heights, MO) in each room (irradiance spectrum shown in Fig. 2), erected on PVC pipe "lamps" that held the light at roughly half the height of the rack. The control group was exposed to the same equipment setup (i.e., lights, wires, and stands). Night lights were only turned on when the ALAN-treated group occupied the room. Daytime lighting switched on instantaneously. This experimental portion of the study lasted 33 days. All birds were released at their capture sites after the study.

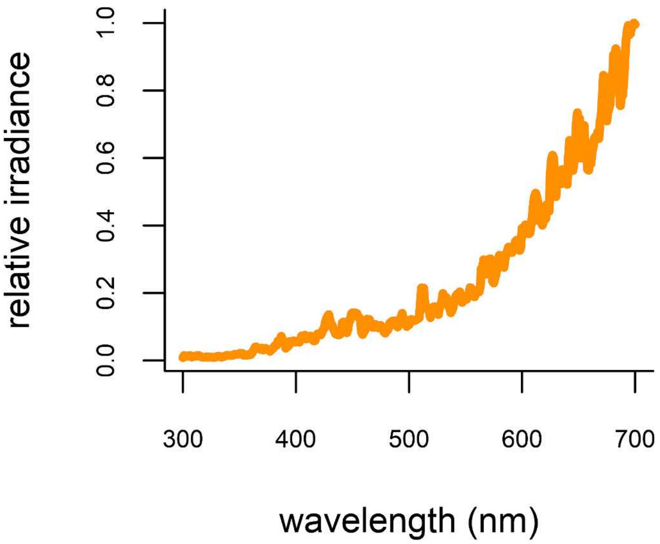

Fig. 2. Spectral composition of the artificial light used during the subjective night in this experiment. After allowing the bulb to warm, irradiance measurements were taken over 3 min in a dark room with an Ocean Optics spectroradiometer. The hue of the curve is matched to the calculated hue value (H3) of 613 nm.

Within the treatment room, several steps were taken to minimize inter-individual variation in light exposure; because the bird cages were placed on two separate racks, one night-light was placed on the far sides of both racks, and one was placed equidistant between both racks, and the lights on all sides of the racks were placed equidistant to the rack. The precise placements for each rack and light were marked on the floor within the rooms to ensure the treatment would be individually consistent over the duration of the experiment. At multiple points during the experiment, we measured the light exposure (in lux) for each individual during the subjective day and night by resting a light meter

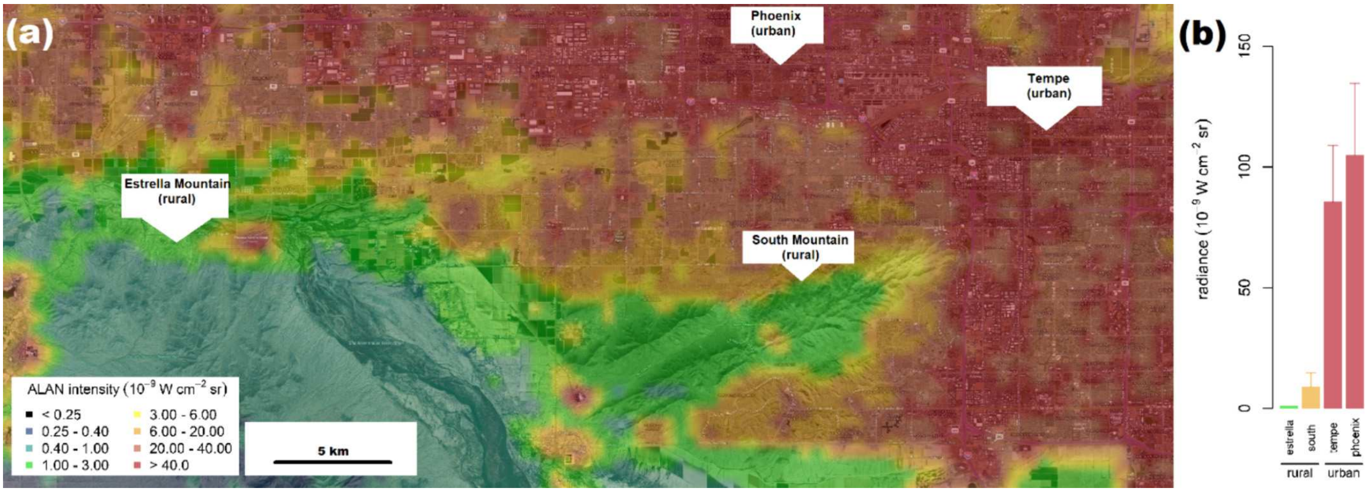

Fig. 1. (a) Light pollution intensity in and around Phoenix, AZ, USA, in March 2014. Data are originally from the NOAA Suomi-NPP satellite, and map visual is generated from: Jurij Stare, https://www.lightpollutionmap.info. House finches caught in this experiment originated from four separate sites, two of which are "urban" (Tempe and Phoenix) and two of which are "rural" (South Mountain and Estrella Mountain). Arrow tips indicate the precise location of finch captures. (b) Summary statistics (mean ± SD) of ALAN intensity in 1 km radius around each site.

(Control Company, Friendswood, TX) probe, directed upwards, at the center of the lower perch. We faced the probe upwards because the glossy white wall, floor, and ceiling surfaces of the room reflected the light omnidirectionally, resulting in a dim glow throughout the room. Light exposure was highly repeatable (Lin's concordance correlation coefficient, $r = 0.90$) at the individual/cage level throughout the experiment. The light meter could not resolve to the nearest 0.1 lx at very low light intensities (i.e. below 1 lx), and therefore detectable levels in this range were assumed to be 1 lx. Every bird in the control group was exposed to no amount of detectable light at night. Near the times of behavioral testing (see *Sleep Behavior* below), light exposure during the subjective day did not differ between treatments, sites of origin, or among trials (mean irradiance = 168 lx; analyses of variance (ANOVAs): all $p > 0.29$). Similarly, night light exposure did not differ between ALAN-exposed rural and urban birds (ANOVA: urban * treatment: $F_{1,54} = 0.0008$, $p = 0.98$), and the median level of light exposure for both groups was the same (1 lx). This illumination level closely aligns with the range of values that free-living and flying urban European blackbirds (*Turdus merula*) are exposed to at night (Dominoni et al., 2013b), suggesting that our ALAN treatment was ecologically relevant for urban settings.

Given that we could not include light intensity as a covariate in our main statistical models due to aliasing (see Statistical analyses section, below), we also tested whether variation in light intensity within the light-treatment groups had impacts on any of the variables measured in this study. We found no effect of light intensity on any of the study variables within light-treated birds, suggesting that a binary (ALAN-exposed vs. control) explanatory variable performs well. This is also expected because of the low levels of variability in light intensity in the treatment groups.

2.3. Body condition

At three times during the study (days 0, 16, and 32 of the experiment), we measured body mass with a digital scale to the nearest 0.1 g and tarsus length with digital calipers to the nearest 0.01 mm. As tarsus length significantly and positively predicted variation in body mass ($\beta = 0.75 \pm 0.15$, $t = 5.07$, $p < 0.001$), we extracted the residuals from this model as a metric of body condition for final analysis (Green, 2001).

2.4. Sleep behavior

To assess the sleep behavior of finches, we filmed individual finches on two separate occasions (experimental days 11–20 and 26–32) using infrared cameras (Swann, Santa Fe Springs, CA) at night. We focused our sleep-behavioral analyses on the final hour of the subjective night (Zeitgeber time 23–24), because a recent meta-analysis shows that light pollution appears to have the largest impacts on behavior towards the end of the night (Sanders et al., 2021), and because studies of activity of free-living birds show that urban birds have advanced activity onset and overall activity (by about 40 min), but no difference in the timing of the end of daily activity (Dominoni et al., 2013a). Additionally, the urban-rural difference in sleep activity appears to precipitate towards the end of the night (Dominoni et al., 2013a). We scored sleep behaviors using the open-source software CowLog (Hänninen and Pastell, 2009). Sleep was operationally defined as either the adoption of sleep-specific postures (i.e. ‘back sleep’, which often conceals the eyes under feathers), or eye closure that lasts longer than a blink (approx. 4 s; Amlaner and Ball, 1983, Hutton et al., 2018). When a bird was in a sleep-specific posture and subsequently left this posture, or eyes were closed and subsequently re-opened, this was scored as the end of a sleep bout. Sleep duration is reported in total number of seconds spent sleeping during the recording period. The scoring of all videos was performed by one individual (PH) who was blind to the site of origin, individual identity, experimental treatment, and time-point of recording. From these behavioral observations, we calculated total sleep duration, the number of sleep bouts, and the average sleep bout length. Total sleep duration was strongly and positively correlated with both number of sleep bouts ($\rho = 0.78$, $p < 0.001$) and average sleep bout length ($\rho = 0.71$, $p < 0.001$). The number of sleep bouts was not related to average sleep bout length ($\rho = -0.08$, $p = 0.64$). Sleep behaviors were highly repeatable within individuals for the two trials (Lin's concordance correlation coefficient, sleep duration: $r = 0.76$, number of sleep bouts: $r = 0.63$, mean sleep bout length $r = 0.77$), so we averaged the values in the two trials for analysis.

2.5. Coccidian endoparasites

To assess the effects of ALAN exposure on coccidiosis, at the beginning (day 0) and end (day 32) of experimental treatment, we estimated the prevalence and severity of gastrointestinal endoparasitism by isosporan coccidian protozoans, following previously established fecal collection (Giraudeau et al., 2014) and float methods (Brawner et al., 2000). Shedding of coccidian oocysts through the feces peaks in the late afternoon, so at 1600 h on these days we replaced the paper lining of bird housing cages, and after an hour returned to collect the fresh feces and preserved them in a 2.2 % potassium dichromate solution. After fecal float and microscope slide preparation, we scored coccidian oocyst load using a 0–5 integer ranking that is based on a logarithmic scale (a score of 0 = no oocysts, 1 = 1–10 oocysts, 2 = 11–100 oocysts, 3 = 101–1000 oocysts, 4 = 1001–10,000 oocysts, and 5 = >10,000 oocysts). All fecal samples were prepared and scored by one individual, and a subset were re-examined by a second individual to determine measurement repeatability (Lin's concordance correlation coefficient, $r = 0.96$). Both individuals were blind to both the experimental treatment and population of origin for each sample, thereby negating any potential biases.

2.6. CORT$_F$

Steroid hormones such as corticosterone are deposited in growing bird feathers (Bortolotti et al., 2008). As feather molt occurs over weeks, corticosteroids deposited in feathers (CORT$_F$) are an integrated measure of corticosteroid circulation during feather development. In house finches, CORT$_F$ levels in tail feathers are similar to levels in body feathers, suggesting that tail feathers reliably reflect general whole-plumage CORT$_F$ levels (Lendvai et al., 2013). At the beginning of the experimental treatment, we plucked the right outermost tail feather of each bird to assess pre-experimental corticosteroid titers. At the end of the experiment, this tail feather had regrown and was plucked again. Therefore, the post-treatment feather provides a metric of corticosteroid circulation and excretion during the experiment.

We assayed CORT$_F$ based on previously published methods (Lendvai et al., 2013) using radioimmunoassay in singlet, due to low sample volumes. Previous studies from this lab in house finches (Lendvai et al., 2013) that were able to run duplicates of samples showed a low intra-assay coefficient of variance (5.06 %). To account for the likely confounding effect of variation in feather length between individuals, we regressed whole-feather corticosterone amount on feather length (after removing the calamus). As expected, feather length significantly predicted total corticosterone amount ($\beta = 0.76 \pm 0.079$, $t = 9.59$, $p < 0.001$), so we analyzed the residuals from this model.

2.7. Statistical analyses

All statistics were performed in the R computing environment (Version 4.4.0) with a significance level of $\alpha = 0.05$. To test the effects of light treatment and habitat urbanization on sleep behaviors, we produced three separate generalized linear models using R package *lme4*. The response variables in these models were number of sleep bouts, total sleep duration, and mean duration of sleep bouts. These data were right-skewed, so we used a gamma error term, but because there were multiple birds with no sleep bouts during our 1 h/night observation window, we first added a pseudo-count of 1 to each data point for those models. The predictors in these models were habitat urbanization (urban vs. rural), experimental treatment (ALAN vs. dark), and their interaction.

To test how ALAN affects body condition, CORT$_F$, and coccidiosis score, we made a separate linear mixed model with each variable as the response variable, and with time, urbanization, light treatment, and all their higher-order interactions as predictors. We also included individual identity as a random effect to prevent pseudo-replication. Models were tested using Type 3 (Wald) tests, which use the χ^2 test statistic, using R package *car*. Pairwise comparisons were done via the Tukey method using R package *emmeans*.

While we evenly split ages and sexes into the experimental treatment groups to avoid potential confounding effects with treatment (Supplementary Table 1), we also tested whether age or sex had any effect in our models by adding an additional age or sex term to the main interaction term in each model.

Lastly, we tested how sleep duration might mediate any effects of light treatment on health-related dependent (e.g. coccidiosis, CORT$_F$) variables. Prior to mediation analysis, we tested whether sleep duration significantly predicted the change in any dependent variables using linear models (standardized regression coefficients were generated using R package *effectsize*). We only tested mediation for variables that met the criteria for mediation analysis, including a significant direct effect of light pollution on the dependent variable, a significant effect of light pollution on the mediator (sleep duration) variable, and a significant effect of the mediator variable on the dependent variable. Mediation was analyzed by structural equation models for urban and rural birds separately. We created mediator models, which are linear models where the effects of light treatment and total sleep duration are set as predictors of the dependent variable (change in value from pre-treatment to post-treatment for coccidia or CORT$_F$). Next, we created outcome models, which include the effect of light treatment on total sleep duration (the mediator variable). Using the mediator and outcome models, we ran bootstrapped (1000 simulations) causal mediation models using the *mediation* package in R.

3. Results

3.1. Baseline comparisons

With our random group assignment, prior to the experimental ALAN treatment, there were no significant differences among groups for baseline body condition (all $p > 0.84$), CORT$_F$ (all $p > 0.72$), or coccidiosis (all $p > 0.12$).

3.2. Sleep behavior

We found that our ALAN treatment significantly impacted house finch sleep behavior and depended on urbanization (Fig. 3, Table 1). There was a significant effect of the treatment * urbanization interaction on sleep bout duration and overall sleep duration (but not number of bouts; Fig. 3, Table 1). Specifically, sleep bout duration in urban birds was less sensitive to experimental exposure to ALAN than in rural birds (Fig. 3, Supplementary Table 2). In other words, ALAN had disproportionately strong reductive effects on the average duration of sleep bouts in rural compared to urban birds (Fig. 3b, Supplementary Table 2). This partially explains why ALAN-exposed rural birds showed a disproportionately large reduction in total sleep duration (Fig. 3c, Supplementary Table 2); interestingly, 64 % of those rural birds did not sleep at all during the hour before sunrise, whereas only 25 % of ALAN-exposed urban birds did not sleep at all in the hour before sunrise. For comparison, all birds in dark rooms slept at least once during our sampling interval. We found no main effect of urbanization on any of the sleep behaviors (Fig. 3, Table 1). Overall, these results strongly suggest that

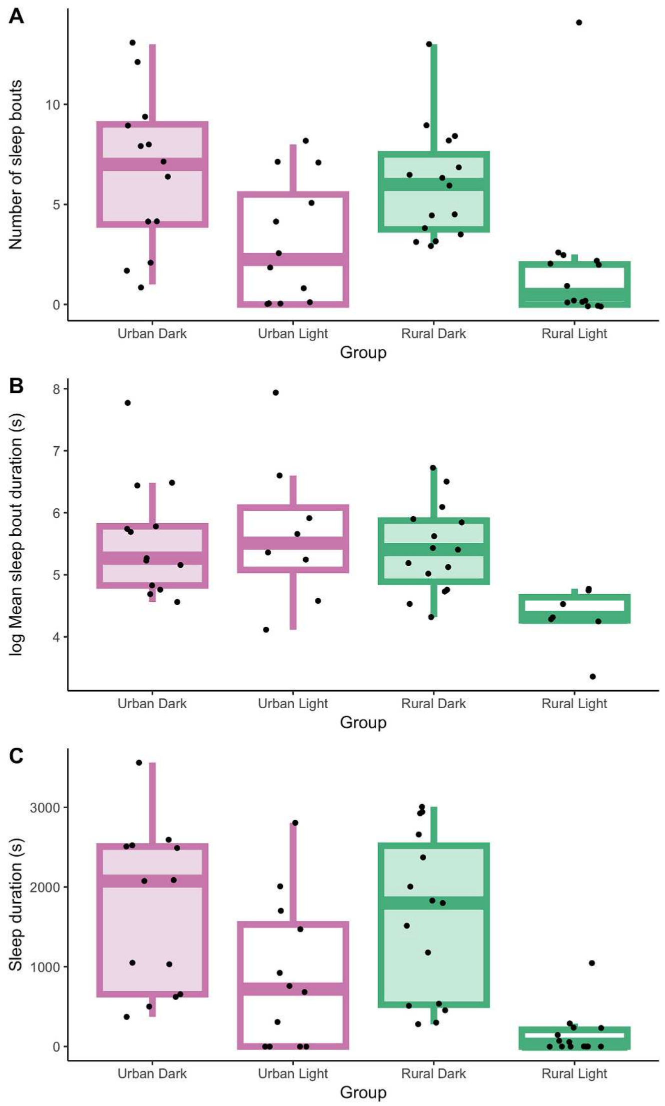

Fig. 3. Artificial light at night affects sleep traits in house finches. (a) Rural and urban birds exposed to ALAN had fewer sleep bouts than control finches, and the magnitude of difference was similar for both urban and rural birds. (b) Rural, but not urban, finches exposed to ALAN slept for less time per bout. (c) Rural and urban birds exposed to ALAN slept less than controls, but the magnitude of this difference was greater among rural birds. Points represent mean data from individuals across two separate behavioral trials, boxes represent the 1st, 2nd, and 3rd quartiles, and whiskers represent the range of values (excluding outliers).

Table 1
Model outputs showing the effects of ALAN treatment, urbanization, and their interaction on the number of sleep bouts, mean sleep bout duration, and total sleep duration of house finches. Bolded *p* values indicate significant (*p* value < 0.05) terms.

Response	Predictor	χ^2	df	*p* value
# of sleep bouts	Urbanization	0.033	1	0.85
	Treatment	8.58	1	**0.0033**
	Urbanization * treatment	0.79	1	0.375
Mean sleep bout duration	Urbanization	0.91	1	0.34
	Treatment	4.81	1	**0.028**
	Urbanization * treatment	5.21	1	**0.022**
Total sleep duration	Urbanization	0.011	1	0.92
	Treatment	24.74	1	**<0.001**
	Urbanization * treatment	13.15	1	**<0.001**

rural birds are disproportionately sensitive to ALAN, and that, consistent with our prediction, urban birds conversely are more resistant and sleep comparatively more in spite of the environmental nightlight disturbance.

When testing the effects of age in our models, we found only one significant effect: that the differential response of sleep bout frequency between urban and rural birds was relatively strong in hatch-year compared to after-hatch-year birds. Because the effect of ALAN on sleep bout frequency was not significantly dependent on urbanization, and because ages were evenly assigned to treatment groups, we believe this has no major effect on the interpretation of our results.

3.3. Body condition

We found that body condition was not dependent on the interaction between experimental ALAN exposure and urbanization; however, there were significant effects of urbanization * time and treatment * time (Fig. 4a, Table 2). Over the study duration, the condition of light-treated birds (independent of urbanization) changed significantly differently than control birds, but post-hoc analyses reveal no significant differences between treatment groups at any point (Supplementary Table 3). Similarly, the condition of urban birds changed significantly differently than rural birds, but again, post-hoc analyses reveal no differences between treatment groups (Supplementary Table 3).

3.4. CORT$_F$

We found that CORT$_F$ levels significantly depended on the interaction between urbanization and ALAN exposure (Fig. 4b, Table 2); although control rural birds nearly doubled in CORT$_F$, ALAN completely blocked this rise in rural night-lit birds (Supplementary Table 4). Additionally, we found that urban birds, regardless of their treatment, had similar CORT$_F$ levels at the end of the study (Supplementary Table 4).

3.5. Endoparasitism

Coccidian parasite burden significantly depended on the interaction between urbanization and ALAN exposure (Fig. 4c, Table 2). At the end of the experiment, we found that ALAN-exposed rural birds harbored higher levels of coccidian endoparasites than rural dark controls, but there was no significant difference between ALAN and control urban birds (Supplementary Table 4). Because coccidiosis is scored on a logarithmic scale, ALAN exposure caused rural birds to become roughly ten times more parasitized than rural controls. Urban birds, however, were statistically unaffected by exposure to ALAN, as at the end of the study, both light-treated and dark controls had statistically similar and low levels of coccidiosis (Supplementary Table 4).

3.6. Mediation by sleep duration

Given that light treatment had significant effects on coccidiosis and CORT$_F$, we sought to understand whether reduced sleep duration under light exposure significantly mediated these effects (Fig. 5). Because only rural birds met the criteria for mediation analysis, we restricted the analyses to this population. Prior to mediation analysis, we found that sleep duration significantly predicted the change in CORT$_F$ (standardized $\beta = 0.63 \pm 0.36$, $t = 3.4$, $p = 0.003$) and coccidiosis (standardized $\beta = -0.38 \pm 0.36$, $t = -2.05$, $p = 0.05$) over the duration of the experiment. Mediation analysis showed that the change in coccidiosis is not significantly mediated by sleep duration (ACME: $\beta = -0.06$ [−2.13, 1.38, 95 % CI], $p = 0.89$), however the change in CORT$_F$ is significantly mediated by sleep duration (ACME: $\beta = -6.78$ [−22.5, −0.18, 95 % CI], $p = 0.042$).

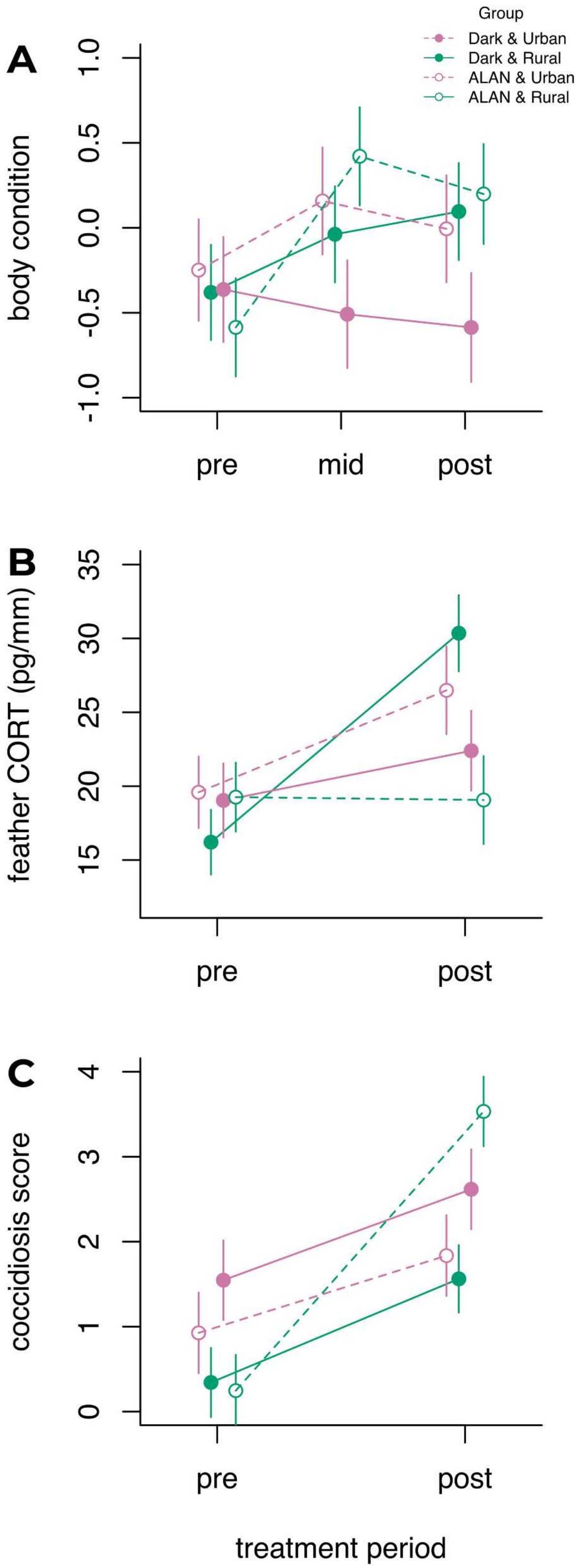

Fig. 4. Experimental exposure to artificial light at night impacts house finch physiology and parasite burden. (a) Body mass was not dependent on ALAN or site of origin. (b) Exposure to ALAN caused lower feather CORT in rural compared to urban house finches. (c) Exposure to ALAN caused an increase in coccidiosis score in rural but not urban finches. Points represent group means and vertical bars represent standard error of the means.

Table 2
Model outputs showing the effects of ALAN treatment, urbanization, time, and their interactions on body condition, feather CORT ($CORT_F$), and coccidiosis score of house finches. Bolded p values indicate significant (p value < 0.05) terms.

Response	Predictor	χ^2	df	p value
Body condition	Time	8.20	2	**0.016**
	Urbanization	0.26	1	0.61
	Treatment	0.002	1	0.96
	Time * urbanization	7.74	2	**0.021**
	Time * treatment	7.48	2	**0.023**
	Urbanization * treatment	0.29	1	0.58
	Time * urbanization * treatment	0.50	2	0.77
$CORT_F$	Time	22.76	1	**<0.001**
	Urbanization	0.72	1	0.40
	Treatment	0.90	1	0.34
	Time * urbanization	6.065	1	**0.014**
	Time * treatment	10.58	1	**0.0011**
	Urbanization * treatment	0.27	1	0.60
	Time * urbanization * treatment	7.75	1	**0.005**
Coccidiosis score	Time	7.86	1	**0.0050**
	Urbanization	4.27	1	**0.039**
	Treatment	0.046	1	0.82
	Time * urbanization	0.039	1	0.84
	Time * treatment	11.51	1	**<0.001**
	Urbanization * treatment	0.40	1	0.52
	Time * urbanization * treatment	5.57	1	**0.018**

4. Discussion

Here we reveal two major and general phenotypic effects of ALAN on a North American bird species that is common to both natural and urban environments. First, we found that finches from urban populations were comparatively resistant (relative to rural finches) to our experimental ALAN exposure. Thus, some (e.g., sleep, disease resistance, glucocorticoid regulation) ALAN-driven effects might be ameliorated through the development of physiological or behavioral accommodations to ALAN. Few studies have tested this hypothesis, but those that do often find support for adaptation or acclimation by urban animals to urban-related stimuli (Dominoni et al., 2013a; Tennessen et al., 2018). The evolution of resistance to human-induced rapid environmental changes may be widespread among animals, and the development of resistance could help explain urban-rural differences in animal community structures (Blair, 1996; McKinney, 2002; Banville et al., 2017).

Second, we contribute more evidence that ALAN has behavioral and physiological impacts on birds. Urban finches were comparatively resistant to the sleep-suppressing effects of ALAN exposure; we found that ALAN (independent of urbanization) reduced the number of sleep bouts, the mean duration of sleep bouts, and total sleep duration in house finches, but the reduction of total sleep time and mean sleep bout duration was weaker in urban finches. Sleep is homeostatically (and possibly allostatically) regulated in most birds (Martinez-Gonzalez et al., 2008; Lesku et al., 2011; Raap et al., 2016c), is thought to have a number of important physiological functions across animals, and forgoing sleep can have significant behavioral and physiological costs (Cooper et al., 2019). Multiple studies in numerous taxa, including birds, have shown

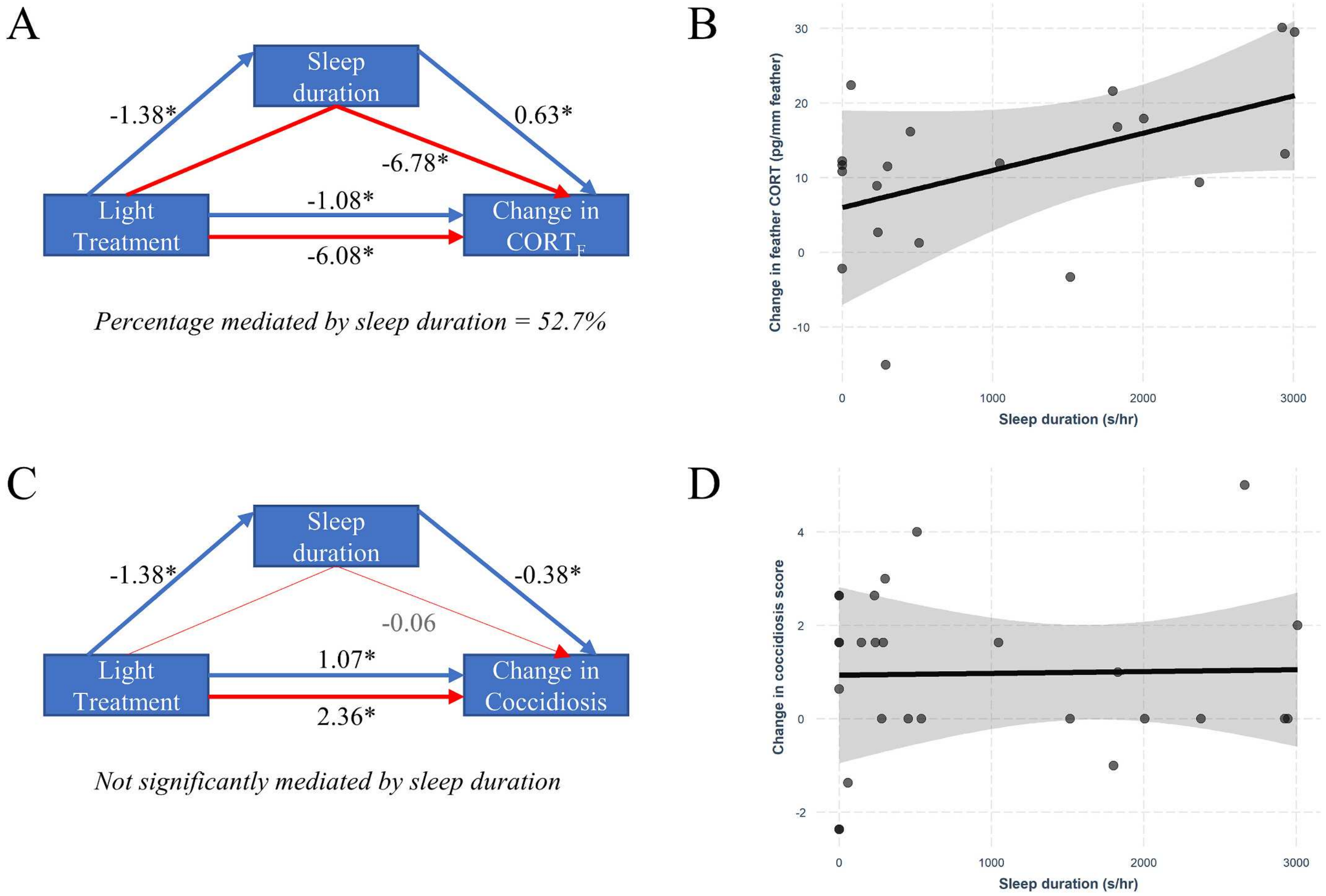

Fig. 5. The effect of light treatment in rural birds is significantly mediated by sleep duration for $CORT_F$ but not coccidiosis. In (A, C) blue arrows represent univariate effects, and red arrows represent effects from mediation models. Significant effects are marked with an asterisk and corresponding arrows and text are bolded. In (B, C), scatterplots show the indirect effect mediated by sleep duration by using partial residuals that account for the effect of light treatment in rural birds.

that ALAN decreases overnight sleep (Raap et al., 2015, 2016c, 2017a; Sun et al., 2017; Aulsebrook et al., 2018), or physiological markers of sleep (Ouyang et al., 2017), and increases night-time locomotor activity both in the laboratory and wild settings (Dominoni et al., 2013a; Ouyang et al., 2017, 2018; Alaasam et al., 2018). Thus, it is possible that ALAN-driven sleep loss could have multiple downstream effects on physiology and behavior.

We also found that ALAN exposure had limited effects on $CORT_F$ levels and coccidiosis in urban relative to rural birds. One hypothesis could be that ALAN affects sleep, corticosteroid regulation, and disease resistance independently, and therefore that urban birds have developed resistance to ALAN independently for each of these parameters (Raap et al., 2017b; Dominoni et al., 2021; Ziegler et al., 2021). Alternatively, in light of the health-promoting effects of sleep (Rattenborg et al., 2007), we may have found urban resistance in these traits because they are controlled by sleep. Mediation analysis supported this hypothesis for $CORT_F$, showing that a significant portion of the effect of light treatment was mediated by sleep duration. However, future studies should experimentally test this by reversing the sleep-restricting effects of ALAN (via e.g., sleep-inducing substances; Malek et al., 2019) to assess whether this also restores the original state of other health-related indices such as $CORT_F$. In contrast, we found that the effect of light treatment on coccidiosis was not significantly mediated by sleep duration, suggesting that sleep loss provides a link between light pollution and physiology for some traits, but others are mediated by factors beyond sleep. Therefore we provide evidence that light pollution affects physiology through both sleep-mediated and non-sleep-mediated pathways in wild birds.

We found that $CORT_F$ increased in all groups by the end of the experiment, except for ALAN-exposed rural birds, again suggesting urban resistance. Dominoni et al. (2021) recently found a similar result in a study of wild forest and urban blue tit nestlings, such that rural ALAN-exposed had low $CORT_F$ levels relative to unexposed controls, and urban ALAN-exposed nestlings had higher $CORT_F$ levels relative to unexposed controls. Such urban-dependent responses of $CORT_F$ to ALAN exposure may carry-over into adulthood, as we show here. Interestingly, they also find that $CORT_F$ levels were positively related to fledging success in ALAN-exposed birds, suggesting that the relatively low $CORT_F$ levels in ALAN-exposed rural birds is a sign of poor health (Dominoni et al., 2021). Here, we also show that this effect may be sleep-dependent. Other studies have tested the effects of ALAN on plasma CORT (taken during the day). In multiple species, ALAN increased circulating CORT (Ouyang et al., 2015; Alaasam et al., 2018; Dominoni et al., 2021). These opposing results for different measures of CORT are interesting and call for a better understanding of why $CORT_F$ is comparatively lower in rural birds in response to ALAN, while plasma CORT levels are greater. Though past circadian studies find increased CORT during subjective night under bright continuous light (Zani de Souza et al., 2001), dim ALAN could potentially decrease circulating CORT levels during night (when previous studies have not measured it), or it could reduce stress reactivity to challenging events. Alternatively, plucking of tail feathers for $CORT_F$ measurement could induce metabolic changes required for feather regrowth (Hoshino et al., 1988), and ALAN has been shown to alter metabolism in birds (Yadav et al., 2022). Thus, we may see relatively low $CORT_F$ in rural ALAN exposed birds because of broader metabolic disruption. Regardless of the potential fitness consequences, urban house finches appear resistant to ALAN-driven $CORT_F$ suppression.

We found that urban birds were resistant to the large effect of ALAN on coccidian infection in rural finches. Coccidian infections have been linked to poor body condition in free-living birds (Brawner et al., 2000; Hõrak et al., 2004; Pap et al., 2011), which may be due to how these parasites inhabit and damage the gastrointestinal tract and reduce digestive efficiency (Meitern et al., 2016). Similarly, Ouyang et al. (Ouyang et al., 2017) showed that experimental ALAN exposure increased malarial infection in wild adult great tits. Increased parasite or pathogen burden may be caused by a weakened immune response, but empirical evidence for harmful effects of ALAN on immune function in other bird species is mixed (Raap et al., 2016a; Ouyang et al., 2017; Saini et al., 2019). We further show that the effect of ALAN exposure on coccidiosis was not sleep-dependent, suggesting direct or circadian impacts of light on immune function. Future studies might use transcriptomic approaches in the gut of coccidian-infected birds to better understand how light exposure alters anti-parasite immune responses.

Lastly, we also tested the hypothesis that ALAN alters body condition but found no clear significant effect in either urban or rural birds. Alaasam et al. (2018) tested a similar hypothesis in a study on adult zebra finches and found that experimental ALAN exposure had no significant effect on body mass, even when accounting for potential differences in food intake between ALAN-exposed and control birds. Because birds from laboratory studies have been fed ad libitum food (i.e. permitting overnight access for ALAN-exposed animals), this may have prevented effects on body mass that were observed in wild birds (Raap et al., 2016b). In this study, we observed that ALAN-exposed finches fed at night, but control finches did not. Interestingly, Ulgezen et al. (2019) found that exposure to ALAN increases daily energy expenditure in great tits. Future studies might better test the impact of ALAN on body condition and energetics by limiting overnight food access and/or tracking foraging and other energy uses in ALAN-exposed birds.

Here we address a major question in whether and how animals respond to anthropogenic environmental change, such as urbanization and the associated elevations in local night-lighting. Similar to our findings on light pollution, a recent experiment on sound pollution showed that anthropogenic-noise-exposed rural wood frogs (*Rana sylvatica*) had decreased immune function and increased CORT, but frogs from naturally noisy environments were resistant to the physiological effects of noise (Tennessen et al., 2018). Multiple recent reviews address the mechanisms of phenotypic change in these new ecosystems (Hopkins et al., 2018; Rivkin et al., 2018). Empirical studies now probe whether these phenotypic changes are the result(s) of genetic mechanisms (adaptation, drift, etc.) and/or developmental or behavioral plasticity. Although we uncovered multiple phenotypic differences between urban and rural finches in response to ALAN (this study) and other anthropogenic activities (e.g. human presence; Cook et al., 2017, Weaver et al., 2018a, 2018b), we have not tested for adaptive genetic differences between urban and rural house finch populations. However, a genome-wide study of great tits identified multiple genes under selection in several European cities (Salmón et al., 2021), and one of the most common genes under selection was *HRT7* which is involved in serotonin signaling and sleep regulation (Monti, 2011). Future studies should test whether genes under selection in urban or night-lit areas play any roles in sleep or responsiveness to light.

The experimental setup was limited for several reasons. In past studies, we had captured finches from a larger gradient of urbanization of up to seven sites (Giraudeau et al., 2014). Here, we captured finches from the two most urban and most rural sites from this gradient; capturing finches from a greater number of sites would better reflect responses of finches across the entire gradient (including e.g., suburban sites) instead of only the extremes. In this study we had access to only two environmentally controlled rooms for housing of finches during the experiment, which could lead to finches reacting to specific conspecifics in the same room. Given the balanced randomization of finches of various sites, sexes, and ages across the two groups, and the observation that inter-individual communication (e.g. contact calls) is nearly constant during the day and absent during the night, we feel this likely had little impact on the results. Lastly, we measured the amount of exposure to night-lighting at the individual level but were unable to resolve the amount of light between 0.1 and 1 lx, but given that these limited measurements showed similar amounts of lighting between ALAN-exposed urban and rural birds, and the absolute difference in light exposure in this range was small, we expect this had little impact on our conclusions. Future studies might take these limitations into consideration during experimental design.

ALAN is rapidly expanding across the globe and can be ecologically, physiologically and behaviorally costly to natural wildlife populations. One major future goal for the conservation of biodiversity will be to understand the types and magnitudes of ALAN's costs and benefits in various taxa and landscapes. Given prior work and our findings here, another emerging question is whether and how certain species or populations of animals can acclimate or adapt to ALAN and other types of anthropogenic environmental changes (Rivkin et al., 2018).

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CRediT authorship contribution statement

Pierce Hutton: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ádám Z. Lendvai:** Writing – review & editing, Supervision, Resources, Methodology, Investigation. **Jószef Németh:** Writing – review & editing, Supervision, Resources, Methodology, Investigation. **Kevin J. McGraw:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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