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PHYSIOLOGICAL ECOLOGY – ORIGINAL RESEARCH

Illuminating the physiological implications of artificial light on an insectivorous bat community

Zachary M. Cravens[1] · **Justin G. Boyles**[1]

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Abstract

Global light pollution threatens to disturb numerous wildlife species, but impacts of artificial light will likely vary among species within a community. Thus, artificial lights may change the environment in such a way as to create winners and losers as some species benefit while others do not. Insectivorous bats are nocturnal and a good model to test for differential effects of light pollution on a single community. We used a physiological technique to address this community-level question by measuring plasma ß-hydroxybutyrate (a blood metabolite) concentrations from six species of insectivorous bats in lit and unlit conditions. We also recorded bat calls acoustically to measure activity levels between experimental conditions. Blood metabolite level and acoustic activity data suggest species-specific changes in foraging around lights. In red bats (*Lasiurus borealis*), ß-hydroxybutyrate levels at lit sites were highest early in the night before decreasing. Acoustic data indicate pronounced peaks in activity at lit sites early in the night. In red bats on dark nights and in the other species in this community, which seem to avoid lights, ß-hydroxybutyrate remained relatively constant. Our results suggest red bats are more willing to expend energy to actively forage around lights despite potential negative impacts, while other, generally rarer species avoid lit areas. Artificial light appears to have a bifurcating effect on bat communities, whereby some species take advantage of concentrated prey resources, yet most do not. Further, this may concentrate light-intolerant species into limited dark refugia, thereby increasing competition for depauperate, phototactic insect communities.

Keywords Bat–insect interactions · β-Hydroxybutyrate · Light pollution · LED · Plasma metabolite analysis

Introduction

Global light pollution has increased dramatically during the twentieth and twentyfirst centuries as a result of rapid urban development (Hölker et al. 2010a). Currently, nearly 90% of Europe and over half of North America are estimated to experience light-polluted skies (Falchi et al. 2016). Yet, these light intensity levels have remained relatively constant over the last several decades, while increases in light pollution extent have occurred recently in developing areas with higher than average species richness (Koen et al. 2018). The use of artificial light at night (ALAN) is widespread and a major threat to biodiversity (Hölker et al. 2010b), especially for nocturnal animals such as bats that are adapted to life in dark environments (Voigt and Lewanzik 2011).

Many species are affected by ALAN as 30% of vertebrates and > 60% of invertebrates are considered nocturnal (Hölker et al. 2010b). The impacts of light pollution on species are wide ranging, and include effects on physiology, behavior, reproduction, and predator–prey interactions (Bradshaw and Holzapfel 2010; Longcore and Rich 2004). Importantly though, artificial light may not affect all species in the same way. For example, the behavior of moth prey around artificial light has variable effects on their predators, as Cape serotine bats in lit areas were found to consume six times more moths than in unlit areas (Minnaar et al. 2015), while orb-weaver spiders had significantly fewer moths fly into their webs in the presence of artificial light (Yuen and Bonebrake 2017). Such variation suggests artificial light may have community-level

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✉ Zachary M. Cravens
zcravens@siu.edu

[1] Cooperative Wildlife Research Laboratory, Department of Zoology, Southern Illinois University, Carbondale, IL 62901, USA

effects and recent work has demonstrated artificial light can alter community structure and composition in invertebrate communities (Davies et al. 2012) and fish communities (Bolton et al. 2017). Importantly, even closely related and morphologically similar species might respond differently to artificial light (Cravens et al. 2018), thereby potentially tipping the competitive balance in some communities.

Insectivorous bats are a good model to test community-level effects of artificial light. The impact of artificial lighting on bat behaviors is wide ranging and includes effects on foraging and commuting, emergence, roosting, breeding, and hibernation (as reviewed in Stone et al. 2015). Negative impacts on these behaviors could have reduced fitness costs. For instance, artificial lighting around bat roosts can lead to a delayed nightly emergence (Downs et al. 2003). By delaying emergence, bats can miss the peak in insect abundance around dusk (Jones and Rydell 1994), which could be particularly detrimental to pregnant or lactating females who have increased energetic demands (Kurta et al. 1989).

While bats, in general, appear to prefer dark environments (Lima and O'Keefe 2013), there are numerous observations of bats foraging around artificial light (Acharya and Fenton 1999; Hickey et al. 1996; Polak et al. 2011; Schoeman 2016). Concurrently, artificial light induces phototaxis in aerial insects, leading to unusually high densities around lights (van Langevelde et al. 2011). It has been proposed that light-tolerant bats take advantage of larger and higher densities of prey around artificial light, which could offset predation risks from flight in a lit environment (Tomassini et al. 2014). If this is the case, widespread ALAN in the nocturnal environment could significantly alter bat–insect interactions and foraging behaviors with cascading effects on the food web and ecosystem functioning (Cravens et al. 2018; Minnaar et al. 2015).

If ALAN alters foraging behaviors, we should also expect to see energetic effects on these bats. Thus, we evaluated the effect of artificial light on energy metabolism in an insectivorous bat community through plasma metabolite analysis (Boyles et al. 2016; McGuire et al. 2009). We experimentally manipulated naturally dark areas with an artificial light treatment known to cause shifts in prey selection (Cravens et al. 2018; Minnaar et al. 2015), and measured ß-hydroxybutyrate levels from bats captured in both lit and unlit environments. We also measured bat activity from acoustic recordings in lit and unlit conditions. We predicted an increase in foraging success and activity in artificial light treatments relative to naturally dark areas.

Materials and methods

Study site

Our study was conducted in a nine-county region of western Missouri, USA, during summer (May–August) 2017. The study area lies primarily within the Ozark Highlands physiographic region, a heavily forested landscape dominated by oak–hickory forests. Along the western edge of our study area, the land begins to transition to Osage Plains, a region historically dominated by prairie but now heavily converted to agriculture with limited forest and woodlands (Raeker et al. 2010). In general, there is low to moderate light pollution across the study area, interspersed with small urban areas of higher concentrations of light pollution. No major cities are located in the study area.

Experimental design

We erected temporary lights along naturally dark forest roads or streams on public lands and had two experimental conditions: unlit (control) and lit (light pollution treatment). Distance between lit and unlit sites was at least 2 km to minimize overlap in foraging ranges by individual bats, but sites were chosen with similar habitat and landscape features. At lit sites, we used 50 W LED (Shenzhen Lepower Opto Electronics Co., China) producing 5600 lumens at 4000 K. We used LED lighting as it is replacing older outdoor lighting styles, such as mercury vapor. Lights were elevated 3 m from the ground on a metal pole and powered by a 12 V lead acid battery. We used mist nets to capture bats along forested roads or streams at 17 paired lit and unlit sites, for a total of 34 netting locations, throughout the summer. We netted at each survey site for three nights, and ran lights for all three nights from 21:00 to 05:00. On the first two nights, we captured bats at an unlit control site and on the third night, we captured bats at lit sites (Cravens et al. 2018; Minnaar et al. 2015). Delaying capture at lit sites until the third night allowed bats to become accustomed to the lit condition, as well as provide time for them to choose to forage in the newly lit environment. We make no assumption that all bats captured at lit sites were necessarily foraging around the lights; moreover, we expect some species may be less prone to foraging at lights than others and, therefore, show less-pronounced shifts in feeding rates and activity levels. We do assume that all captured bats, at either lit or unlit sites, would have encountered artificial lights, at least once, within their home range prior to capture. Nets were placed in flyways within 25 m of the light in an appropriate netting location.

We recorded bats acoustically (SM2Bat + and SM4ZC; Wildlife Acoustics, Maynard, Massachusetts, USA) from 20:00 to 06:00 on each of three sampling nights at all lit and unlit sites, and added additional sampling nights if there was a period of rain or high winds longer than 30 min. We elevated detectors two meters on a metal pole away from clutter that could affect echolocation calls. At lit sites, we placed detectors within 0.5 m of the light source. We identified bat species from our acoustic detector recordings using Kaleidoscope Pro v3.1 automated identification software (Wildlife Acoustics, Maynard, Massachusetts, USA). Little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) are difficult to differentiate acoustically, so we combined calls identified as either of those species. We pooled calls, identified to each species, into 15-min intervals, and report data from the second night of recording.

We measured plasma ß-hydroxybutyrate concentrations from six species of insectivorous bats in naturally dark and artificially lit conditions. ß-hydroxybutyrate is generally considered a fasting metabolite and increases during fasting to power metabolic processes when dietary triglycerides are low (Balasse and Féry 1989; Jenni-Eiermann and Jenni 1991; Laffel 1999; Robinson and Williamson 1980). While the mechanism is not understood, available data indicate ß-hydroxybutyrate paradoxically increases in both captive and free-living bats after feeding (McGuire et al. 2009) and has thus been used as a proxy for foraging success (Boyles et al. 2016; McGuire et al. 2009; Sommers et al. 2017; we discuss the implications of these competing interpretations in the discussion). We removed bats from the net and collected a small (< 75 µl) blood sample from the interfemoral vein by puncturing the vein with a 26-gauge needle and collecting blood with a 75-µl heparinized hematocrit tube (Fisher Scientific, Waltham, MA; Hooper and Amelon 2014). All blood samples were collected within 10 min after removing the bat from the net. After blood collection, we centrifuged blood samples (10 min at 2000*g*; Fisher Scientific Mini Centrifuge) to obtain 10 µl of plasma which was used to quantify ß-hydroxybutyrate concentration with a handheld meter (STAT-Site M ß-HB; Stanbio Laboratory, Boerne, Texas USA; Sommers et al. 2017).

We expect foraging success to be highly temperature dependent because both bats and their insect prey are more active on warmer nights; thus, ß-hydroxybutyrate levels are also likely temperature dependent. However, we designed our experiment specifically to determine the effect of light pollution on ß-hydroxybutyrate levels. Thus, to account for temperature, we used residuals from a regression of mean nightly ambient temperature against ß-hydroxybutyrate in all further analyses. We then used general linear models in program R to test the effects of treatment (lit, unlit), minutes after sunset (because the effect of the lights may change as ambient light changes), and treatment*minutes after sunset interaction for each bat species. We used this approach because we were interested in the effect from the light treatment and not concerned with the effect of environmental variables, as these have been well established in the literature (Erickson and West 2002; Erkert 1982). We used a generalized linear model (function glm) in program *R* to test the effects of treatment (lit, unlit), site (lit and unlit combined), and minutes after sunset in 15-min intervals to compare acoustic activity across the night for each bat species. Because our response variable (total bat calls) is count data, we used a Poisson model with a log link. We qualitatively compared temporal patterns in ß-hydroxybutyrate to activity estimated with acoustic detectors for each species of bat.

Results

We collected blood samples from 169 bats ($n = 66$ lit and $n = 103$ unlit) over 36 nights ($n = 11$ lit and $n = 25$ unlit) during summer 2017 (10 June–14 August). We included samples in our statistical analysis from five species (big brown bats (*Eptesicus fuscus*); red bats (*Lasiurus borealis*); gray bats (*Myotis grisescens*); evening bats (*Nycticeius humeralis*); and tri-colored bats (*Perimyotis subflavus*)) and excluded little brown bats because of small sample size ($n = 1$). We excluded two outliers, one from a big brown bat and one from a red bat, and as their removal did not change the results qualitatively we are reporting results with these samples excluded (Online Resource 1). We measured acoustic activity across 16 paired lit and unlit locations from 10 June–8 August 2017. The automated identification software regularly identified little brown bats from acoustic recordings, so those data are included below (although some of these calls may have been produced by Indiana bats).

Both blood metabolite and acoustic data suggest similar, species-specific patterns: red bats actively forage around lights to take advantage of concentrated prey resources likely gaining some benefit, while big brown and gray bats avoid lit areas and thus gain no such benefit. Specifically, the interaction between minutes after sunset and light treatment was significant in red bats ($t = 3.782$, $P < 0.001$); ß-hydroxybutyrate levels were highest just after sunset and declined throughout the night in artificially lit sites, while at naturally dark sites, ß-hydroxybutyrate levels were lowest just after sunset and increased throughout the night (Fig. 1). Overall activity, as indicated by acoustic recordings, was greater at lit sites across the entire night ($\chi^2 = 52.1$, $df = 1$, $P < 0.001$), with two distinct periods during the night when red bat activity appears highest at lit sites relative to unlit sites (Fig. 2): one immediately after sunset corresponding to the highest ß-hydroxybutyrate levels for this species, and another approximately 300 min after sunset. Interestingly,

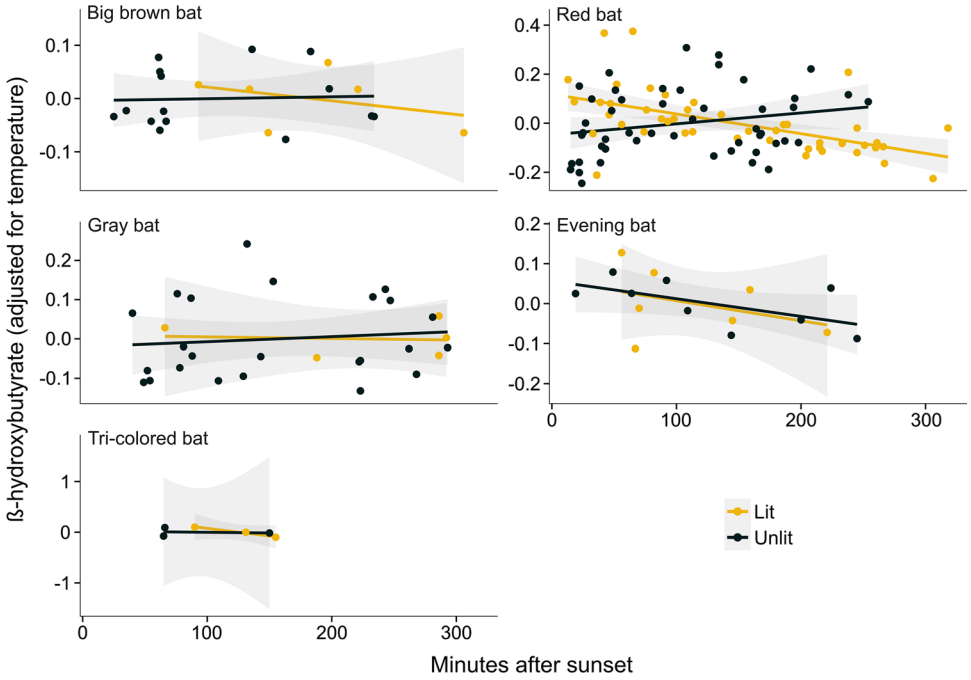

Fig. 1 Changes in ß-hydroxybutyrate concentrations across the night in the five species of insectivorous bats between artificially lit (● , yellow line) and naturally dark (● , black line) conditions. Values along the *y*-axis represent the range of residual values from a regression of temperature and ß-hydroxybutyrate to account for an effect of temperature (color figure online)

the only red bats we captured after approximately 250 min after sunset were around artificial lights.

Blood metabolite and acoustic data for big brown bats and gray bats indicate avoidance of lit areas. Plasma ß-hydroxybutyrate levels were not significantly different between treatments, across the night, or in the treatment*minutes after sunset interaction for either big brown bats or gray bats ($P > 0.54$ in all cases). Both species were more active at unlit sites than lit sites (big brown bats: $\chi^2 = 114.3$, $df = 1$, $P < 0.001$; gray bats: $\chi^2 = 683.1$, $df = 1$, $P < 0.001$). Notably, when comparing the difference in activity between lit and unlit sites for each 15-min interval throughout the night, activity is rarely greater at lit sites for big brown bats and gray bats (Fig. 3). Taken together, this strongly indicates these species appear to be actively avoiding lit areas.

It is difficult to compare β-hydroxybutyrate levels with acoustic activity for evening and tri-colored bats. Plasma metabolite levels for evening bats were quite similar between treatments ($t = -0.017$, $P = 0.987$) with no significant interaction between the main effects ($t = 0.114$, $P = 0.911$), suggesting this species may be avoiding lit areas. Tri-colored bats may also be avoiding lit sites as their plasma metabolite levels were again very similar between treatments ($t = -1.331$, $P = 0.315$) and no interaction between main effects ($t = 1.251$, $P = 0.337$), although interpretation is limited given our small sample size. However, care should be taken when interpreting evening and tri-colored bat acoustic data. The Kaleidoscope software is known to commonly confuse evening and tri-colored bats with more common red bats (Ford 2017). Qualitatively, the activity patterns of these two species track closely with red bats (Figs. 2, 3), so we suspect these patterns are an artifact of the identification process, not a biological pattern. While we have no blood metabolite data for the two Myotis species (Indiana bats and little brown bats), acoustic data indicate activity is significantly greater at unlit sites relative to lit sites ($\chi^2 = 43.6$, $df = 1$, $P < 0.001$; Fig. 2).

Discussion

Our data show taxon-specific effects of short-term changes in ALAN from isolated lights in otherwise naturally dark areas on foraging and activity levels in an insectivorous bat community. Although subjective, qualitatively our acoustic data suggest red bats may actively forage around artificial lights, and ß-hydroxybutyrate levels indicate they likely are gaining some benefit in doing so, regardless of the exact interpretation of ß-hydroxybutyrate levels (see below). The other species in the community appear to avoid foraging around artificial light and showed no observable difference in ß-hydroxybutyrate between experimental treatments. This is the first study, to our knowledge, demonstrating that ALAN can modify behavior sufficiently to cause knock-on effects on physiology and energetics, and because the effects are not the same on all species, ALAN might further affect competitive balance in a community.

Bats adapted for faster flight in relatively open habitats are generally considered to be light-tolerant species (Rowse et al. 2016). Red bats have a moderate aspect ratio, high wing loading, and are fast flyers with limited (relatively speaking) maneuverability (Norberg and Rayner 1987).

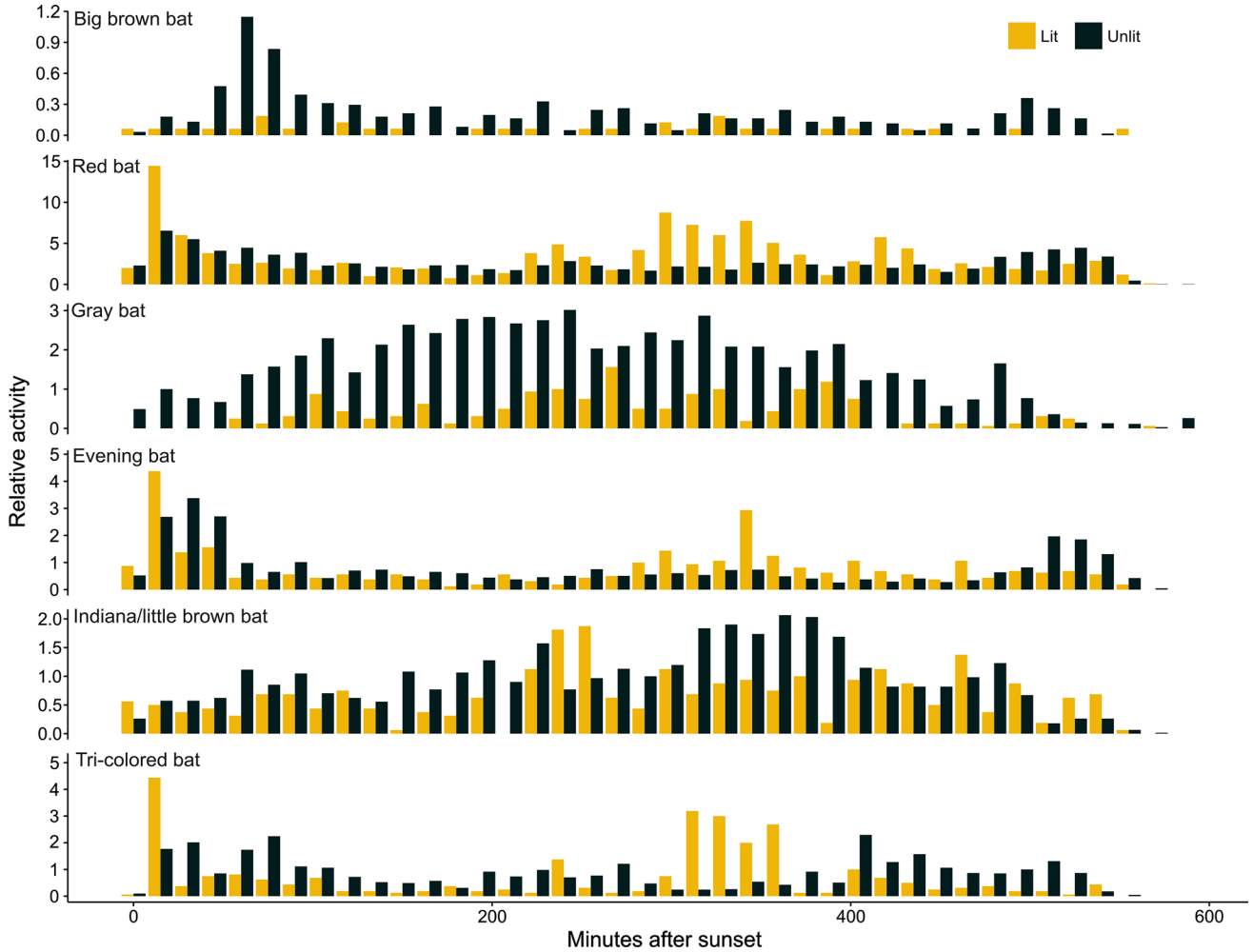

Fig. 2 Comparison of relative bat activity, summed in 15-min intervals, across the night between experimental treatments for each bat species. Calls of common red bats are often misidentified as rarer evening bats and tri-colored bats by the identification software so the patterns for these two species should be interpreted with care. Calls of the Indiana and little brown bats were combined as a single species group as they are very difficult to distinguish acoustically (color figure online)

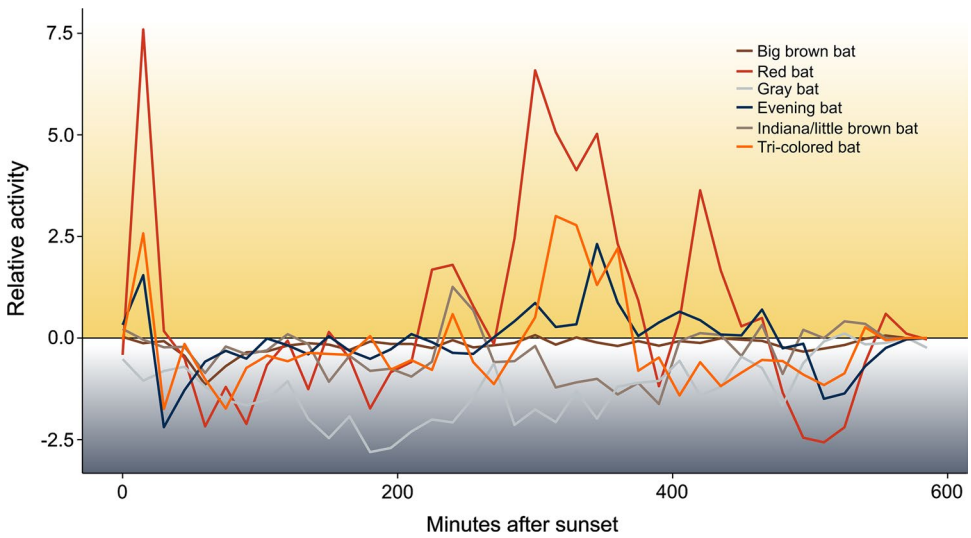

Fig. 3 Difference in relative abundance between treatments for each 15-min interval, based on call data from Fig. 2. Higher positive values represent greater activity at lit sites, while higher negative values indicate greater activity at unlit sites (color figure online)

They have been the focus of numerous studies on bats and artificial light (Acharya and Fenton 1992, 1999; Hickey et al. 1996), and these studies have consistently shown artificial light to have an attractive effect on red bats. Conversely, slower flying species adapted for flight in cluttered habitat tend to be light intolerant (Rowse et al. 2016) as slower flight may make bats vulnerable to predation in open, lit environments. Big brown bats and gray bats, while not necessarily clutter adapted, do have lower aspect ratios, lower wing loadings, and are slower fliers than red bats (Norberg and Rayner 1987). Our data suggest these two species, especially gray bats, avoid lit areas (Fig. 2). Acoustic data suggest the other Myotis species in the community (little brown and Indiana bats) are also light averse (Fig. 2). Evening bats are not fully clutter adapted, but are weak fliers (Norberg and Rayner 1987). Although the acoustic data may be unreliable for evening bats, this species showed no change in ß-hydroxybutyrate levels between treatments. Further, evening bats did not alter diet, at least with respect to Lepidoptera and Coleoptera, in the presence of artificial light (Cravens et al. 2018), suggesting they are not actively taking advantage of increased prey densities around artificial light.

We recorded the highest ß-hydroxybutyrate levels in red bats foraging around lights shortly after sunset, with a marked decrease throughout the rest of the night. There were no significant trends in ß-hydroxybutyrate levels throughout the night in other species. Unlike in most other animals, ß-hydroxybutyrate levels in bats appear to behave contrary to physiological norms, increasing with food intake (McGuire et al. 2009). Thus, previous papers measuring ß-hydroxybutyrate levels in bats have interpreted increased ß-hydroxybutyrate as an indicator of increased foraging efficiency and energy intake (Boyles et al. 2016; McGuire et al. 2009). Using this interpretation, our data suggest red bats forage heavily around lights shortly after sunset and gain energetic benefits by doing so, but do not forage around artificial light late in the night, and thus gain no energetic benefit. This is incongruous with acoustic data which indicate a second peak in red bat activity late in the night (Fig. 2). Under this interpretation, the other species in this community avoid lights and thus gain no benefit of increased prey densities around lights, regardless of time of night.

Our acoustic and capture data hint that interpreting ß-hydroxybutyrate levels in bats as a proxy of foraging success might be problematic, and that ß-hydroxybutyrate might behave as it does in other species. Ketogenesis, or the production of ß-hydroxybutyrate and other ketone bodies in the liver, occurs during periods of low food availability to provide fuel to the brain, muscles, and other organs (Flatt 1972). Thus, ß-hydroxybutyrate levels increase with fasting (Balasse and Féry 1989; Féry et al. 1996; Jenni-Eiermann and Jenni 1991; Robinson and Williamson 1980). Temperate-zone, insectivorous bats generally only forage on the wing for 2–8 h each night (Kurta et al. 1989). For the remainder of the daily cycle they stay in roosts and do not feed, so we might expect ß-hydroxybutyrate levels to increase throughout the day, peaking immediately before the nightly foraging period. If this were the only driver of high β-hydroxybutyrate, we would expect to see elevated levels in all species early in the night, which we do not.

Our data suggest ß-hydroxybutyrate may be a better indicator of the energy source powering flight than of foraging success in bats, as it has been interpreted in the past. Although most commonly thought of as a fasting metabolite, elevated levels of ketone bodies can also be found during prolonged or intense exercise (Evans et al. 2017, 2018; Féry and Balasse 1983; Laffel 1999; Wahren et al. 1984) and exercise-trained muscles oxidize ß-hydroxybutyrate more efficiently than muscles from sedentary individuals (Winder et al. 1973). Thus, we might expect to see elevated ß-hydroxybutyrate in bats undertaking intense foraging shortly after leaving the roost and before they can metabolize exogenous energy sources. If red bats are taking advantage of high densities of insects around lights (particularly moths) immediately after beginning foraging (Rydell et al. 1996), they may be powering flight through ketogenesis. The same reasoning may explain why ß-hydroxybutyrate levels are high in little brown bats living at high latitudes, where foraging bouts are necessarily short and intense because of limited darkness (Boyles et al. 2016). The difference in ß-hydroxybutyrate patterns between red bats in the two treatments in this study may relate to what the bats were doing when captured. During the artificial light treatments, red bats were likely foraging (as indicated by high, sustained acoustic activity), while red bats captured in naturally dark conditions were likely commuting to foraging areas (because they normally forage in open areas, not over roads and streams where we captured them). The relatively lower flight costs of straight flight during commuting (Grodzinski et al. 2009; Voigt and Holderied 2012; Voigt et al. 2010a) should impose lower energetic demands, and thus less need for an upregulation of ketogenesis. Interestingly, red bats were only captured late in the night around lights, and these individuals universally had low ß-hydroxybutyrate levels (Fig. 1). This would suggest foraging around lights provides more energy than foraging in naturally dark areas, and as the night progresses, red bats fuel increasingly more flight through dietary proteins and fatty acids (Voigt et al. 2010b, 2012). ß-hydroxybutyrate levels do not decrease throughout the night in any of the species which avoid lights or in red bats at naturally dark sites. Further, both acoustic data and capture data suggest red bats are not highly active late in the night at naturally dark sites. If so, energy intake may never be high enough in the absence of artificial light, when insect densities are presumably low, for metabolized dietary sources to fully replace ketone bodies in powering flight.

Regardless of the interpretation, there are clearly bifurcating effects of artificial light in this bat community as the represented species did not all have the same response. If ß-hydroxybutyrate is interpreted as has been in past wildlife studies, it represents a proxy for foraging success (i.e. it goes up when bats actually consume insects). Using this interpretation, the marked increase in ß-hydroxybutyrate early in the night suggests red bats alone are gaining an energetic benefit. However, if the ß-hydroxybutyrate signal is increasing with exercise, it represents a proxy for foraging intensity (i.e. the effort bats are willing to expend to pursue a resource). Under this flight interpretation, the significant increase we see, again solely in red bats, suggests they are willing to invest more energy for foraging, strongly hinting that they are gaining some benefit. Thus, our study indicates red bats, with a morphological propensity for fast flight, are either: (1) gaining an energetic benefit from increased foraging success or (2) displaying a willingness to expend energy to take advantage of insect concentrations around lights, despite other negative impacts of artificial lights. At the same time, other, often rarer species seem incapable or unwilling to either directly benefit or expend the energy to benefit from foraging around lights.

The production and use of ketone bodies may have other physiological benefits for bats beyond powering flight during periods of intense activity when dietary sources are not available. For example, ketogenesis inhibits lipolysis, which serves to maintain endogenous energy stores and muscle glycolysis, allowing for fattening and recharge of muscle glycogen (Maizels et al. 1977; Féry et al. 1996; Mikkelsen et al. 2015; Jenni-Eiermann 2017). Thus, we might expect to see ß-hydroxybutyrate used heavily to power flight during periods when storing fat is imperative, such as immediately before hibernation. In support of this prediction, some of the highest ß-hydroxybutyrate levels measured in bats to date were from little brown bats during the pre-hibernation fattening period in Ontario (McGuire et al. 2009).

The unique combination of circadian cycles, high-fat diet, and an unusually expensive mode of locomotion might explain why ß-hydroxybutyrate levels appear to increase with energy intake in insectivorous bats (McGuire et al. 2009). In the lab, bats are fed without foraging. However, in the field highly energetically expensive foraging occurs at the end of a daily fast when circulating triglyceride levels are low. Insectivorous, aerial-hawking bats never naturally intake energy without flying, so flight and feeding might be physiologically linked in these species, and a reliance on a low-carbohydrate diet might mean that dietary energy is not immediately available to power foraging. Feeding might signal the liver to increase ketogenesis in insectivorous bats, even without flight. An interesting test of this hypothesis would be to measure ß-hydroxybutyrate levels in frugivorous or nectivorous bats, which can metabolize dietary energy almost instantly to power flight (Voigt and Speakman 2007). In these species, ketones may be less important energetic substrates for powered flight and, therefore, may be less physiologically linked to flight.

Our results shed additional light on the complex interactions of the bat–insect–light system. Some species, such as red bats, seem to be at an advantage relative to other species in areas with artificial light. However, red bats may not need the advantage of higher insect concentrations as they are ubiquitous on the landscape and among the most common species in the region. Other species in the area, particularly those in the genus Myotis, are rare and becoming rarer. This is a pattern seen in European bat communities as well, whereby species that are light tolerant are common on the landscape and those which are light averse tend to be rare or threatened (Lacoeuilhe et al. 2014; Stone et al. 2009, 2012). In addition to limiting spatial extent, the negative impacts of light pollution on light-intolerant species may be further compounded by decreasing prey resources in naturally dark areas where they forage (Eisenbeis 2006; Longcore and Rich 2004). The low capture rates (and activity levels from the acoustic data) of those species around lights would suggest that despite being caught near the light, they may just be commuting through. Thus, artificial lights may be helping common species, such as red bats, by concentrating resources but actively hurting other, rarer species by both limiting their distribution on the landscape and concentrating insects where these species will not forage. As this study may be most applicable in more heterogeneously lit landscapes, as opposed to uniformly lit urban areas, conservation practitioners should ensure protected lands have only necessary night lighting around infrastructure and work with lighting engineers to minimize impacts of artificial light on imperiled bat populations.

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Author contribution statement ZMC and JGB conceived and designed the experiments. ZMC performed the experiments. ZMC analysed the data and wrote the manuscript. JGB contributed to the interpretation of results and provided editorial input on the manuscript. Both authors approve the final version of the manuscript.

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Compliance with ethical standards

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

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. Further, experiments reported herein were approved by the Southern Illinois Institutional

Animal Care and Use Committee (protocol: 15-044) and conducted under permits from the Missouri Department of Conservation (permit #17126) and the US Fish and Wildlife Service (permit no. TE82666A-2).

Data accessibility The datasets generated during and/or analyzed during the current study will be available in the Dryad Digital Repository.

References

Acharya L, Fenton MB (1992) Echolocation behaviour of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) attacking airborne targets including arctiid moths. Can J Zool 70:1292–1298. https://doi.org/10.1139/z92-180

Acharya L, Fenton MB (1999) Bat attacks and moth defensive behaviour around street lights. Can J Zool 77:27–33. https://doi.org/10.1139/cjz-77-1-27

Balasse EO, Féry F (1989) Ketone body production and disposal: effects of fasting, diabetes, and exercise. Diabetes Metab Rev 5:247–270

Bolton D et al (2017) Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. Sci Total Environ 576:1–9. https://doi.org/10.1016/j.scitotenv.2016.10.037

Boyles JG et al (2016) Physiological and behavioral adaptations in bats living at high latitudes. Physiol Behav 165:322–327. https://doi.org/10.1016/j.physbeh.2016.08.016

Bradshaw WE, Holzapfel CM (2010) Light, time, and the physiology of biotic response to rapid climate change in animals. Annu Rev Physiol 72:147–166. https://doi.org/10.1146/annurev-physiol-021909-135837

Cravens ZM, Brown VA, Divoll TJ, Boyles JG (2018) Illuminating prey selection in an insectivorous bat community exposed to artificial light at night. J Appl Ecol 55:705–713. https://doi.org/10.1111/1365-2664.13036

Davies TW, Bennie J, Gaston KJ (2012) Street lighting changes the composition of invertebrate communities. Biol Lett 8:764–767. https://doi.org/10.1098/rsbl.2012.0216

Downs NC, Beaton V, Guest J, Polanski J, Robinson SL, Racey PA (2003) The effects of illuminating the roost entrance on the emergence behaviour of *Pipistrellus pygmaeus*. Biol Conserv 111:247–252. https://doi.org/10.1016/s0006-3207(02)00298-7

Eisenbeis G (2006) Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: Rich C, Longcore T (eds) Ecological consequences of artificial night lighting. Island Press, Washington, DC, pp 281–304

Erickson JL, West SD (2002) The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterol 4:17–24. https://doi.org/10.3161/001.004.0103

Erkert HG (1982) Ecological aspects of bat activity rhythms. Plenum Press, New York

Evans M et al (2017) Metabolism of ketone bodies during exercise and training: physiological basis for exogenous supplementation. J Physiol 595:2857–2871

Evans M et al (2018) Effect of acute ingestion of ß-hydroxybutyrate salts on the response to graded exercise in trained cyclists. Eur J Sport Sci 18:376–386. https://doi.org/10.1080/17461391.2017.1421711

Falchi F et al (2016) The new world atlas of artificial night sky brightness. Sci Adv 2:25. https://doi.org/10.1126/sciadv.1600377

Féry F, Balasse EO (1983) Ketone body turnover during and after exercise in overnight-fasted and starved humans. Am J Physiol 245:E318–E325

Féry F, Plat L, Melot C, Balasse EO (1996) Role of fat-derived substrates in the regulation of gluconeogenesis during fasting. Am J Physiol Endocrinol Metab 270:E822–E830. https://doi.org/10.1152/ajpendo.1996.270.5.e822

Flatt JP (1972) On the maximal possible rate of ketogenesis. Diabetes 21:50–53. https://doi.org/10.2337/diab.21.1.50

Ford WM (2017) USGS Test Report 12. U. S. Geological Survey Ecosystems Division, United States Department of The Interior

Grodzinski U, Spiegel O, Korine C, Holderied MW (2009) Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? J Anim Ecol 78:540–548. https://doi.org/10.1111/j.1365-2656.2009.01526.x

Hickey MBC, Acharya L, Pennington S (1996) Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. J Mammal 77:325–334. https://doi.org/10.2307/1382804

Hölker F et al (2010a) The dark side of light: a transdisciplinary research agenda for light pollution policy. Ecol Soc. https://doi.org/10.5751/es-03685-150413

Hölker F, Wolter C, Perkin EK, Tockner K (2010b) Light pollution as a biodiversity threat. Trends Ecol Evol 25:681–682. https://doi.org/10.1016/j.tree.2010.09.007

Hooper SE, Amelon SK (2014) Handling and blood collection in the little brown bat (*Myotis lucifugus*). Lab Animal 43:197–199. https://doi.org/10.1038/laban.543

Jenni-Eiermann S (2017) Energy metabolism during endurance flight and the post-flight recovery phase. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 203:431–438. https://doi.org/10.1007/s00359-017-1150-3

Jenni-Eiermann S, Jenni L (1991) Metabolic responses to flight and fasting in night-migrating passerines. J Comput Physiol B Biochem Syst Environ Physiol 161:465–474. https://doi.org/10.1007/s00359-017-1150-3

Jones G, Rydell J (1994) Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philos Trans R Soc B Biol Sci 346:445–455. https://doi.org/10.1098/rstb.1994.0161

Koen EL, Minnaar C, Roever CL, Boyles JG (2018) Emerging threat of the 21st century lightscape to global biodiversity. Glob Chang Biol 24:2315–2324

Kurta A, Bell GP, Nagy KA, Kunz TH (1989) Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). Physiol Zool 62:804–818. https://doi.org/10.1086/physzool.62.3.30157928

Lacoeuilhe A, Machon N, Julien J-F, Le Bocq A, Kerbiriou C (2014) The influence of low intensities of light pollution on bat communities in a semi-natural context. PLoS One 9:e103042. https://doi.org/10.1371/journal.pone.0103042

Laffel L (1999) Ketone bodies: a review of physiology, pathophysiology and application of monitoring to diabetes. Diabetes Metab Res 15:412–426. https://doi.org/10.1002/(sici)1520-7560(199911/12)15:6%3c412:aid-dmrr72%3e3.0.co;2-8

Lima SL, O'Keefe JM (2013) Do predators influence the behaviour of bats? Biol Rev 88:626–644. https://doi.org/10.1111/brv.12021

Longcore T, Rich C (2004) Ecological light pollution. Front Ecol Environ 2:191–198. https://doi.org/10.1890/1540-9295(2004)002%5b0191:elp%5d2.0.co;2

Maizels EZ, Ruderman NB, Goodman MN, Lau D (1977) Effect of acetoacetate on glucose metablolism in the soleus and extensor digitorum longus muscles of the rat. Biochem J 162:557–568

McGuire LP, Fenton MB, Faure PA, Guglielmo CG (2009) Determining feeding state and rate of mass change in insectivorous bats using plasma metabolite analysis. Physiol Biochem Zool 82:812–818. https://doi.org/10.1086/605951

Mikkelsen KH, Seifert T, Secher NH, Grøndal T, van Hall G (2015) Systemic, cerebral and skeletal muscle ketone body and energy

metabolism during acute hyper-D-beta-hydroxybutyratemia in post-absorptive healthy males. J Clin Endocrinol Metalol 100:636–643. https://doi.org/10.1210/jc.2014-2608

Minnaar C, Boyles JG, Minnaar IA, Sole CL, McKechnie AE (2015) Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. J Appl Ecol 52:522–531. https://doi.org/10.1111/1365-2664.12381

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammaila, Chiroptera) - wing adaptations, flight performance, foraging strategy and echolocation. Philos Trans R Soc Lond Ser B Biol Sci 316:337–419. https://doi.org/10.1098/rstb.1987.0030

Polak T, Korine C, Yair S, Holderied MW (2011) Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. J Zool 285:21–27. https://doi.org/10.1111/j.1469-7998.2011.00808.x

Raeker G, Fleming J, Morris M, Moser K, Trieman T (2010) Missouri's forest resource assessment and strategy: seeking a sustainable future for Missouri's forest resources. In: Missouri Department of Conservation UFS, Northern Research Station (ed), Jefferson City, Missouri

Robinson AM, Williamson DH (1980) Physiological roles of ketone bodies as substrates and signals in mammalian tissues. Physiol Rev 60:143–187. https://doi.org/10.1152/physrev.1980.60.1.143

Rowse EG, Lewanzik D, Stone EL, Harris S, Jones G (2016) Dark matters: the effects of artificial lighting on bats. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer, New York, pp 187–213

Rydell J, Entwistle A, Racey PA (1996) Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76:243–252. https://doi.org/10.2307/3546196

Schoeman MC (2016) Light pollution at stadiums favors urban exploiter bats. Anim Conserv 19:120–130. https://doi.org/10.1111/acv.12220

Sommers AS, Boyle WA, McGuire LP (2017) Validation of a field-ready handheld meter for plasma ß-hydroxybutyrate analysis. J Field Ornithol 88:399–404. https://doi.org/10.1111/jofo.12233

Stone EL, Jones G, Harris S (2009) Street lighting disturbs commuting bats. Curr Biol 19:1123–1127. https://doi.org/10.1016/j.cub.2009.05.058

Stone EL, Jones G, Harris S (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. Glob Chang Biol 18:2458–2465. https://doi.org/10.1111/j.1365-2486.2012.02705.x

Stone EL, Harris S, Jones G (2015) Impacts of artificial lighting on bats: a review of challenges and solutions. Mammal Biol 80:213–219. https://doi.org/10.1016/j.mambio.2015.02.004

Tomassini A, Colangelo P, Agnelli P, Jones G, Russo D (2014) Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or urbanization? J Biogeogr 41:944–953. https://doi.org/10.1111/jbi.12248

van Langevelde F, Ettema JA, Donners M, WallisDeVries MF, Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. Biol Conserv 144:2274–2281. https://doi.org/10.1016/j.biocon.2011.06.004

Voigt CC, Holderied MW (2012) High manoeuvring costs force narrow-winged molossid bats to forage in open space. J Comp Physiol B Biochem Syst Environ Physiol 182:415–424. https://doi.org/10.1007/s00360-011-0627-6

Voigt CC, Lewanzik D (2011) Trapped in the darkness of the night: thermal and energetic constraints of daylight flight in bats. Proc R Soc B Biol Sci 278:2311–2317. https://doi.org/10.1098/rspb.2010.2290

Voigt CC, Speakman JR (2007) Nectar-feeding bats fuel their high metabolism directly with exogenous carbohydrates. Funct Ecol 21:913–921. https://doi.org/10.1111/j.1365-2435.2007.01321.x

Voigt CC, Schuller BM, Greif S, Siemers BM (2010a) Perch-hunting in insectivorous Rhinolophus bats is related to the high energy costs of manoeuvring in flight. J Comp Physiol B Biochem Syst Environ Physiol 180:1079–1088. https://doi.org/10.1007/s00360-010-0466-x

Voigt CC, Sorgel K, Dechmann DKN (2010b) Refueling while flying: foraging bats combust food rapidly and directly to power flight. Ecology 91:2908–2917. https://doi.org/10.1890/09-2232.1

Voigt CC, Sorgel K, Suba J, Keiss O, Petersons G (2012) The insectivorous bat *Pipistrellus nathusii* uses a mixed-fuel strategy to power autumn migration. Proc R Soc B Biol Sci 279:3772–3778. https://doi.org/10.1098/rspb.2012.0902

Wahren J, Sato Y, Ostman J, Hagenfeldt L, Felig P (1984) Turnover and splanchnic metabolism of free fatty acids and ketones in insulin-dependent diabetics at rest and in response to exercise. J Clin Investig 73:1367–1376. https://doi.org/10.1172/jci111340

Winder WW, Baldwin KM, Holloszy JO (1973) Exercise-induced adaptive increase in rate of oxidation of ß-hydroxybutyrate of skeletal muscle. Exp Biol Med 143:753–755. https://doi.org/10.3181/00379727-143-37406

Yuen SW, Bonebrake TC (2017) Artificial night light alters nocturnal prey interception outcomes for morphologically variable spiders. Peerj 5:e4070. https://doi.org/10.7717/peerj.4070