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Contrasting effects of street light shapes and LED color temperatures on nocturnal insects and bats

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Abstract

Street lights are important light sources that contribute to artificial light at night (ALAN). To date, ecological impacts of individual LED properties (color temperature, dimmability) have been studied, while interactions between light properties or aspects of luminaire design have not been addressed. However, the design of luminaires can influence ALAN impacts as the shape determines the spatial distribution of light and its visibility in the environment. This may cause amplifying or mitigating effects. We assessed the relative individual and interacting effects of two LED luminaire designs and three LED color temperatures (1750 K, 3000 K, 4000 K) on nocturnal insect abundance, bat foraging and feeding activity. We considered a standard LED luminaire shape with focused light emission and a luminaire shape with a diffusor to scatter the light spatially, leading to increased visibility of the light in the environment. During 104 nights, we trapped 51263 nocturnal insects of which 97% were caught at lights and 3% at dark sites. For bats, up to 44.8% fewer acoustic signals were recorded at dark sites. We caught 31% insects at LEDs with1750 K, 34% and 35% at 3000 K and 4000 K, respectively. Thus, color temperatures of 1750 K proved less detrimental than 3000/4000 K. Effects of luminaire shape led to an increase (16%) of trapped insects for luminaires with diffusors compared to the standard shape. In addition, luminaires with diffusors amplified the effects of LED color (+12% insects at 1750 K/3000 K; +25.6% at 4000 K). In contrast, bat foraging activity was independent of the light treatments while bat feeding activity was increased by 21.5% at standard luminaire shapes. Likely, intense straylight at diffused lights negatively affects the target-focused echolocation by deterring the bats. We concluded that ecological impacts of luminaire shape are an important, yet underestimated variable in light-pollution impact research.

Keywords: ALAN; artificial light at night; light pollution; experimental biodiversity assessment; light impact; nocturnal biodiversity; LED; light mitigation measure; peri-urban; luminaire shape

Introduction

Recent decades have seen a drastic decline in insect abundance and diversity (Dirzo, Young, Galetti, Ceballos, Isaac et al. 2014; Hallmann, Sorg, Jongejans, Siepel, Hofland et al. 2017; Rhodes 2018). This decline is the result of a

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combination of increased agricultural intensification and habitat reduction (Brooks, Bater, Clark, Monteith, Andrews et al. 2012; Habel, Samways & Schmitt 2019) due to urbanization along with a simultaneous increase in light pollution (Bates, Sadler, Grundy, Lowe, Davis et al. 2014; van Langevelde, Braamburg-Annegarn, Huigens, Groendijk, Poitevin et al. 2018). Consequences of light pollution are far-reaching, as continued declines in insect populations (Desouhant, Gomes, Mondy & Amat 2019; Owens, Cochard, Durrant, Farnworth, Perkin et al. 2019) also imply lowered genetic diversity and thus less adaptive capacity to changing environmental conditions (Vanden Broeck, Maes, Kelager, Wynhoff, WallisDeVries et al. 2017). Therefore, mitigation measures to reduce lighting impacts are imperative (Davies & Smyth 2018; Hoelker, Bolliger, Davies, Giavi, Jechow et al. 2021) and studies are required to investigate the potential of emerging lighting technologies (Hölker, Moss, Griefahn, Kloas, Voigt et al. 2010; Kyba, Hanel & Holker 2014).

Among the light sources in urban and peri-urban areas, street lights are an important contributor to artificial light at night (ALAN) (Falchi, Cinzano, Duriscoe, Kyba, Elvidge et al. 2016). Although indispensable to the functioning of human society (Boyce 2019), ALAN interferes mostly negatively with organismic physiology, life history traits, daily activity patterns, with impacts cascading to higher hierarchical levels of populations and communities (reviews by Desouhant, Gomes, Mondy & Amat, 2019; Owens & Lewis, 2018; and a meta-analysis by Sanders, Frago, Kehoe, Patterson & Gaston, 2021) and ecosystem services (Giavi, Blosch, Schuster & Knop 2020; Giavi, Fontaine & Knop 2021; Knop, Zoller, Ryser, Erpe, Horler et al. 2017).This calls for efficient mitigation strategies to minimize the ecological impact of ALAN while ensuring that human needs are met when planning outdoor lighting projects (Doulos, Sioutis, Kontaxis, Zissis & Faidas 2019; Jagerbrand 2020).

Among LED properties, the ecological effects of color temperature on nocturnal biodiversity are widely researched. A general trend in the literature shows that cooler color temperatures have more negative effects on nocturnal biodiversity compared to warmer color temperatures (insects (Longcore, Aldern, Eggers, Flores, Franco et al. 2015; Somer-Yeates, Hodgson, McGregor, Spalding & ffrench-Constant 2017) but see (Bolliger, Hennet, Wermelinger, Blum, Haller et al. 2020c), mammals (Fuller, Raghanti, Dennis, Kuhar, Willis et al. 2016; Spoelstra, van Grunsven, Ramakers, Ferguson, Raap et al. 2017), biomass of primary producers (Grubisic, van Grunsven, Manfrin, Monaghan & Holker 2018)). Lowered LED light levels (dimming) can reduce the attraction of light for insects and bats, counteracting the negative effects of neutral white color temperature (Bolliger, Hennet, Boesch, Wermelinger, Pazur et al. 2020b; Rowse, Harris & Jones 2018). Yet, additional luminaire parameters may reduce or amplify ecological impacts. For example, the luminaire's design, particularly luminaire shape, drives the spatial distribution of light and defines how bright the emitted light is perceived in the surroundings. While LED street lights are designed to focus the emitted light on the road, there are various commercially available luminaire housing shapes that also distribute the light into the broader environment.

We provide an ecological assessment of combined and relative impacts of two light treatments (two luminaire housing shapes with (a) standard focused and (b) increased light distribution into the environment using diffusors, as well as three LED color temperatures (1750 K, 3000 K, 4000 K) on nocturnal insect and bat activity. Research questions included: (1) what is the relative role of luminaire shape with respect to light color in driving nocturnal insect abundance and bat activity? (2) are there differentiated responses of individual taxonomic insect groups (Lepidoptera, Coleoptera, Diptera, Neuropterida, Heteroptera, Hymenoptera, Ephemeroptera, Trichoptera) or bat guilds (short-range (SRE), mid-range (MREs) and long-range echolocators (LRE)) as a function of light color and luminaire shape? First, we expect to collect fewer insects and - correspondingly, as bats prey on insects − lower bat activity given warmer LEDs (1750 K, 3000 K) compared to neutral-white LED color temperatures (4000 K). Second, because luminaire housing shapes determine the spatial distribution of light into the surroundings, we expect that luminaires with diffusors, which increase the light distribution into the environment, amplify impacts of LED colors on nocturnal insects and bats. To date we are not aware of any ecological assessment investigating impacts of LED luminaire shapes individually or in combination with other lighting properties such as different color temperatures.

Materials and methods

Study site

The study site was a street section of 1.5 km located in Weiningen, Canton of Zürich, in the Swiss lowlands (Rebbergstrasse, 47.42 N, 8.44 E; Fig. 1). Weiningen (413 m a.s.l.) is a peri-urban settlement (4832 habitants, 12/2018) dominated by single-family homes in the immediate vicinity of Zürich. The landscape is dominated by settlements, interspersed with forests, vineyards and intensively managed agricultural areas (Fig. 1).

Light treatments

We investigated effects of two light treatments on insect abundance and bat activity at the study site of Weiningen (Fig. 1) between May 20 and August 30, 2019 during a total of 104 nights. Along the study road (Fig. 1), 29 state-of-the-art LED street lights of the type SL20 micro, Siteco Switzerland AG, were installed and maintained by the EKZ (cantonal electricity company of Zürich). The two light treatments were: three LED color temperatures (1750 K,

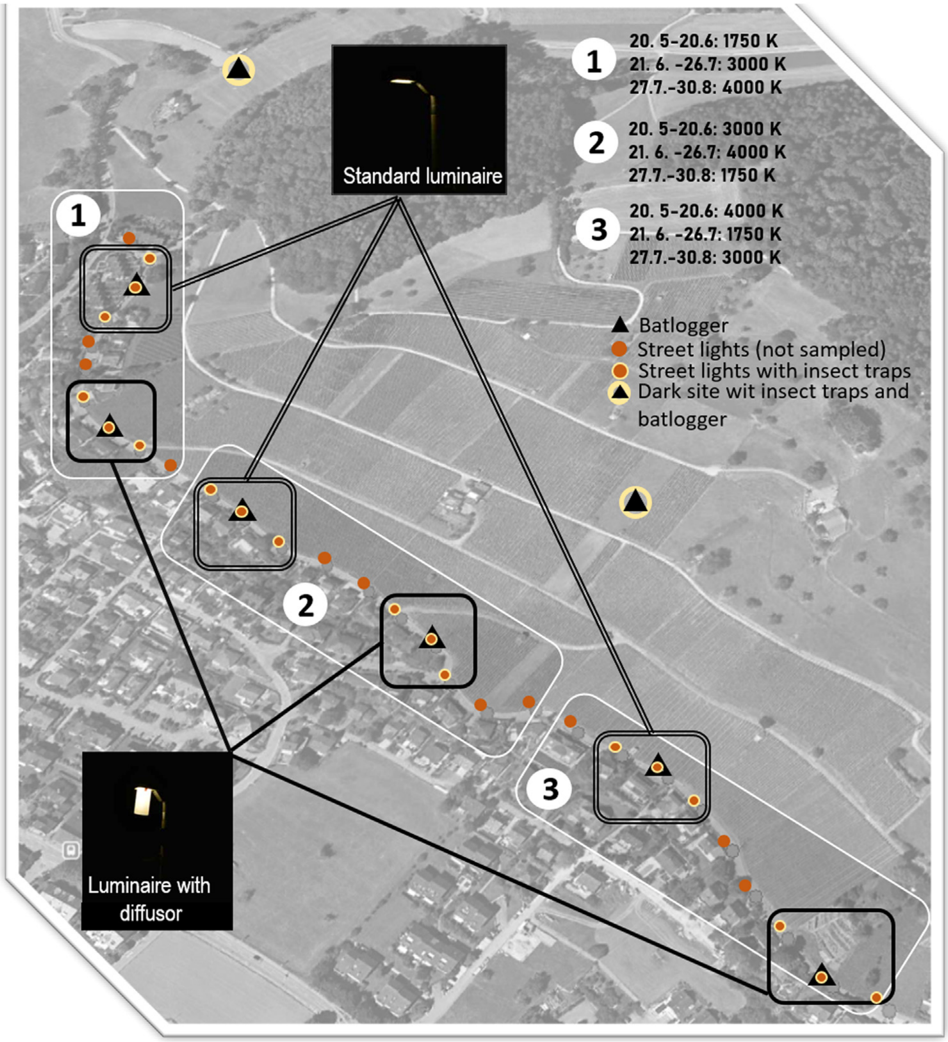

Fig. 1. Set-up of the street light experiment (two luminaire shapes (luminare with diffusors and standard luminaires) and three LED light colors (1750 K, 3000 K, 4000 K)). Black boxes with single line: luminaires with diffusors; black boxes with double extended line: standard luminaire shape; white boxes: LED-color swapping scheme according to the dates listed in the figure (Google Earth, 2021).

3000 K, 4000 K) and two luminaire shapes (standard focused and increased spatial light distribution, Fig. 1). The spectral composition of the three LED color temperatures is shown in Appendix A: Fig. 1.

To mimic luminaire shapes with increased light distribution into the environment, we mounted white, opaque Plexiglas tubes (hereafter "diffusors") to the standard LED luminaires, Fig. 1). The diffusors (transmittance 44%) had a diameter of 150/140 mm and a length of 245 mm. To ensure that the luminous flux (lm) of both luminaire forms (standard and with diffusor) and for all LED colors remained comparable, each luminaire combination (with/without diffuser for all three luminaire colors) was measured at the Swiss Metrological Institute METAS in Bern. The changes in luminous flux caused by color temperature were adjusted so that all luminaires exhibited comparable luminous flux values (Table 1). The diffusor reduced the luminous flux by 22%. This means that lights with diffusor were somewhat "darker" than the standard shapes. However, as the spatial distribution of light was the intended effect of the diffusor, we had to accept this. The desired changes in the spatial distribution of the light caused by diffusors are shown in Appendix A: Fig. 2. Luminaires with diffusors also distributed the light into areas > 75° that remained dark with standard luminaires without diffusors. The diffusors thus fulfill the desired effect of radiating the light into the environment. (Appendix A: Fig. 2).

The study site with the 29 street lights was divided into six sections each containing groups of three street lights (Fig. 1). The three street lights in each group were equipped with insect traps, and batloggers were installed at the center light of each group (Fig. 1). This resulted in a total of three replicates per treatment (Fig. 1). However, because the three replicates were spatially dependent, they should be referred to as pseudo-replicates. Between the six groups, two to three street lights with the same treatments (luminaire shape, color

Table 1. Standardization of the luminous flux (lm) for standard luminaires to ensure that the luminous flux is comparable for all luminaires. The diffusor reduces the luminous flux by 22%.

Color temperature	Standardized luminous flux	Percentage of nominal luminous flux	Power consumption
1750 K	2343 ± 62 lm	100%	33 W
3000 K (warm white)	2313 ± 64 lm	Dimmed to 57%	22 W
4000 K (neutral white)	2372 ± 63 lm	Dimmed to 49%	19 W

temperature) as the adjacent group served as non-sampled buffers (Fig. 1). The groups were alternately equipped with standard luminaires and luminaires with diffusors (Fig. 1). Two dark sites (light poles without luminaries but equipped with insect traps and batloggers) served as controls (Fig. 1). The luminaire shapes remained fixed throughout the duration of the experiment. To counteract local effects at the street lights, the three LED colors were rotated (Fig. 1) so that each light was subject to all three light colors during the experiment. The detailed rotation scheme is listed in Fig. 1: the lights were installed on 20.5. 2019, a first exchange between LED colors was performed on 20.6. 2019 after 30 nights, a second rotation took place on 27.6. 7. 2019 after 36 nights (Fig. 1).

Insect abundance

Flying nocturnal insects were sampled with automated flight intersection traps (Bolliger, Collet, Hohl & Obrist 2020a) mounted on street-light poles at a height of about 4 m. The automated traps ensured that the nightly sampling duration was exactly the same for all traps and optimized trap handling as insect collection was reduced to one visit per site and week (Bolliger et al. 2020a). The traps are based

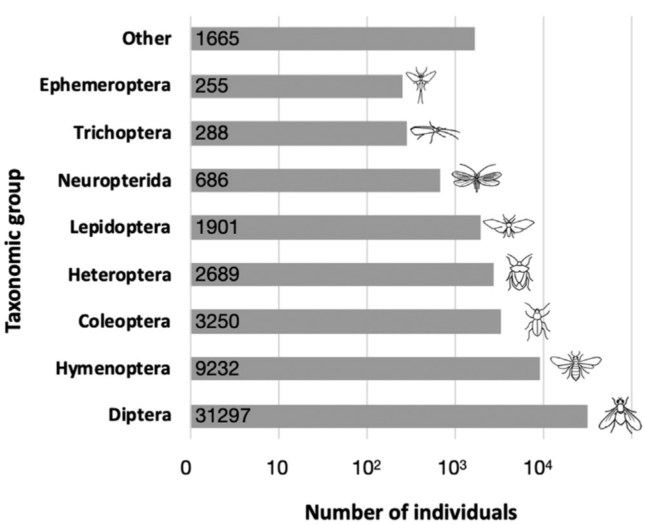

Fig. 2. Number of caught insect individuals assigned to eight taxonomic groups. “Other” encompassed individuals that were not considered for further analysis. Abundances are plotted on a log scale and the numbers of insects are given inside the bars.

on a widely used (Bolliger et al. 2020b; Gossner, Lachat, Brunet, Isacsson, Bouget et al. 2013), commercially available flight intersection trap (Polytrap ®). While the flight interception trap itself remained unchanged, the sampling was automated. A turntable under the flight intersection trap’s funnel, moved by a battery-powered motor, was equipped with seven cups for trapping during seven nights and a pass-through hole to release insects when not sampling (Bolliger et al. 2020a). Each cup contained water with a biocide (Rocima GT, Acima AG, CH-9471 Buchs/Rohm and Haas Co.) The traps were only active at night and the exact sampling period (sunset-sunrise) was electronically controlled by the firmware of the trap (Bolliger et al. 2020a). A passage hole in the trap freed accidentally caught insects during daytime. After seven nights, the cups with the samples corresponding to seven nights were collected and the traps were restarted for another week of sampling. The caught insects were stored in alcohol and sorted into nine groups with the help of a binocular: Diptera, Coleoptera, Heteroptera, Hymenoptera, Lepidoptera, Trichoptera, Ephemeroptera, Neuropterida and Other. The category “Other” referred to infrequently trapped insects that could not be assigned to any of the eight insect groups.

Insect dry biomass

Insect dry biomass was used as a proxy to estimate the amount of prey available for bats foraging at the street lights. The insect biomass was pooled per night and treatment and dried in paper bags at 60°C for 72 hours in a Heraeus drying cabinet. After drying, the insects were stored in a desiccator and weighed at an accuracy of 0.0001 g (0.1 mg) on a Mettler AE240 scale. If a sample’s weight was recorded as 0.0000 g, it was rounded to 0.0001 g.

Bat foraging and feeding activity

Bats emit ultrasound vocalizations in flight when orienting and hunting. Techniques sensitive to ultrasound thus allow to eavesdrop on these acoustically conspicuous species (Froidevaux, Zellweger, Bollmann & Obrist 2014). A total of six batloggers (Elekon AG, Luzern, Switzerland; http://www.batlogger.com) were mounted at the central street light pole of each treatment group at a height of 4 m (Fig. 1). Additionally, a batlogger was installed at each of the two dark sites (Fig. 1). The batloggers recorded echolocation calls from bats. Recordings were triggered by sinusoidal signals in the ultrasound range (‘period trigger’ set in batloggers). Echolocation calls of bats passing between 15 min before sunset and 15 min after sunrise elicited recording sequences of 1.5 - 10 sec duration, which were stored on SD memory cards as WAV files for later offline-analysis. The acoustic signals were recorded at a sampling rate of 312.5 kHz at 16-bit sampling depth. Once a week, the memory cards were retrieved to download the data and the logger batteries were recharged. The recorded bat signals were processed using BatScope 4.1 (Obrist & Boesch 2018). This software is available at no costs (http://www.batscope.ch) and cuts recorded bat vocalization sequences into single echolocation calls and measures their temporal and spectral characteristics. This allows statistical assignment of calls to bat species and summarizes the probability of species match for each sequence. Automated species classifications of all recorded sequences were manually verified and assigned to species groups in unclear situations. This process guarantees high identification accuracy and avoids errors typically occurring in unsupervised machine identification (Russo & Voigt 2016; Rydell, Nyman, Eklöf, Jones & Russo 2017). The bat recordings were finally assigned to functional groups (Frey-Ehrenbold, Bontadina, Arlettaz & Obrist 2013) as follows: LRE = Long Range Echolocator (species foraging at long distances; genus *Eptesicus, Nyctalus* and *Vespertilio*), MRE = Mid Range Echolocator (species that hunt closer to structured vegetation but also in the open; genus *Hypsugo* and *Pipistrellus*) and SRE = Short Range Echolocator (species that mainly hunt near or within structured vegetation; genus *Barbastellus, Myotis* and *Plecotus*).

To quantify not only the search for prey (foraging activity) but also actual feeding attempts, we checked for final or feeding buzzes in our recordings (insect capture attempts of the bats; Griffin, 1958). Sequences containing feeding buzzes were reliably found (and visually controlled) in the recordings by filtering for sequences containing at least five successive calls of decreasing call intervals, which were all shorter than 80 ms.

Individual bats tend to circle around street lights repeatedly. To decrease the chance of miscounting such behavior as repeated passes, we binned the activity of single species in five-minute intervals. Thus, one or more passes of the same species within five minutes was counted as a single activity measure − summing up to a possible total count of 12 individuals of each species per hour.

As occasionally batloggers quit service before the end of the experimental treatment period, we were forced to weight the recorded activity with the actual observation times, thus determining a relative activity of foraging and feeding attempts. We transformed these percentage values with the ‘logit’ transformation (R package car V. 3.0-10) prior to statistical analyses, but for better readability, we plot untransformed relative activities in the figures.

Statistical analysis

We used generalized linear mixed-effect models (GLMM, package lme (Bates, Machler, Bolker & Walker 2015)) to assess the relative effects of two light treatments (standard luminaires and luminaires with diffusors as well as three color temperatures (1750 K, 3000 K, 4000 K)) on nocturnal insect abundance and bat foraging and feeding activity. We fitted GLMMs using a negative binomial error distribution to account for overdispersed count data (Zuur, Ieno & Elphick 2010). Dependent variables were insect abundance (all insects and each insect group individually), bat foraging, and bat feeding activity calculated for all bats as well as for each guild separately (mid-range (MRE), long-range (LRE), short-range echolocators (SRE)). The dependent variables were fitted to the light treatments as fixed effects. Two random effects were considered. To account for intrinsic changes during time (e.g. insect development), a unique identifier was assigned to each sampled night (night 1 - night 104); to implicitly consider the very local site conditions at each street light, each of the 18 street lights obtained an identifier (Fig. 1).

The explanatory variables entering the models were checked for multicollinearity using the variance inflation factor VIF (R package car V. 3.0-10). Model performance was assessed using R^2 (R^2GLMM) and the Akaike information criterion (AIC) for the full model.

Results

Insect abundance

Overall, 51263 insects were trappedd at 18 street lights during 104 nights of sampling between May 20 and August 30, 2019 (Fig. 2). Diptera was the most frequently caught insect group with almost 3.5 times more individuals than the second frequent group, Hymenoptera. The number of individuals caught of the groups Coleoptera, Heteroptera and Lepidoptera ranged between 3250 and 1901, whereas Neuropterida, Ephemeroptera and Trichoptera had lower sample numbers between 680 and 250 (Fig. 2). The insect abundance at lights was on average 97% higher compared to the number of insects caught at the dark sites (Fig. 3). This shows continued attraction of insects to street lights even in peri-urban areas where nighttime illumination has been prevalent for many decades.

The regression results for insect abundance are shown in Appendices B and C. VIF values of 1 indicated that the predictors were independent (Appendix B). The regression results for individual and combined parameters showed that luminaire shape was a strongly determining factor for all insects and all insect groups (Appendix C). The R^2 indicated overall good model performance with values between 0.5 and 0.8 except for Trichoptera (R^2=0.32) and Ephemeroptera (R^2=0.03).

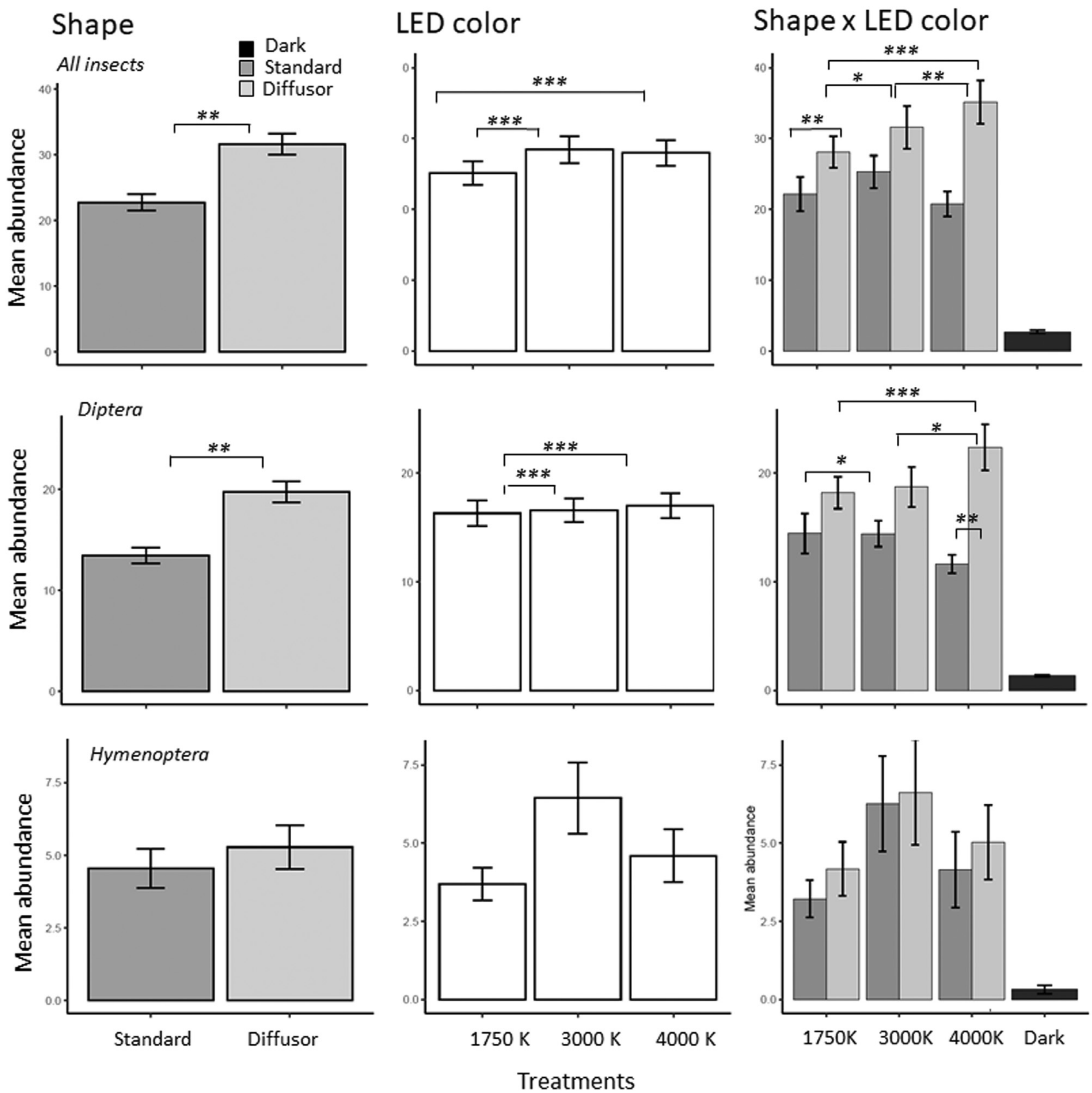

Fig. 3. Mean insect abundance (± standard error) as a function of two light treatments: luminaire shape and LED color temperatures. The left and the middle columns show GLMM results for impact of light treatments luminaire shape (luminaires with diffusor (Diffusor) and standard luminaires (Standard)) + three LED color temperatures (1750 K, 3000 K, 4000 K). The right column shows results for combined impacts for luminaire shapes:color temperatures. Indicated are only statistically significant comparisons. Please note that dark sites are shown for visual comparison only and did not enter the statistical analyses. Statistical levels of significance: *** < 0.001 ** < 0.01, * < 0.05. Regression tables and contrasts are reported in Appendix C).

At luminaires with diffusors, we caught on average 16% more insects compared to standard lights (Fig.3, Appendix C). These effects were statistically significant for all insects (+16% on average), the insect groups Diptera (+19%), Coleoptera (+18%) and Heteroptera (+22.9%; Appendix C). In contrast, luminaire shape did not statistically significantly affect Hymenoptera, Lepidoptera and Trichoptera, although there was a distinct trend towards more insects caught at luminaires with diffusors for Trichoptera (+ 14.8% on average), Lepidoptera (+11.7%) and for Hymenoptera (+7.5% Fig. 3). Ephemeroptera and Neuropterida were not sensitive to luminaire shapes (Fig. 3).

We caught 31% insects at LEDs with1750 K, 34% and 35% at 3000 K and 4000 K, respectively. Thus, color temperatures of 1750 K proved less detrimental than 3000/4000 K (Fig. 3; Appendix D). These effects were statistically

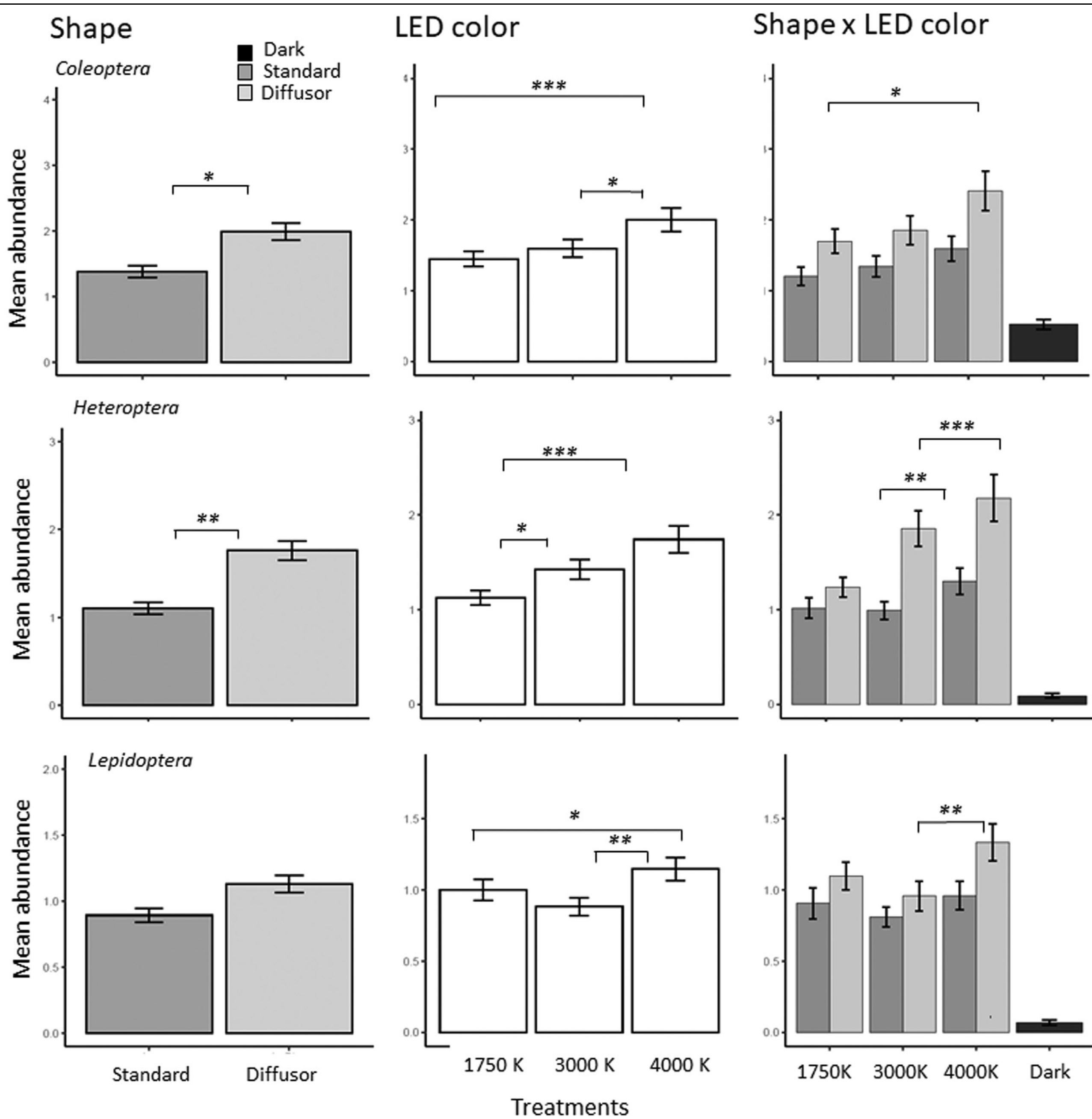

Fig. 3 Continued.

significant for the total number of insects (+4%), and for Diptera (+2%) and Heteroptera (+10%; Fig. 3). When comparing 3000 K to 1750 K, statistically significantly more specimens were caught for all insects (+4%), and the groups Diptera (+1%) and Heteroptera (+7%). For lights with 4000 K compared to 1750 K overall more insects (+4%), more Diptera, (+2%), Coleoptera (+3%), Heteroptera (14%), Lepidoptera (+4.8%) and Hymenoptera (+6%; Fig. 3) were caught. The remaining groups, Trichoptera, Ephemeroptera, and Neuropterida, did not respond statistically significantly to LED color temperatures (Fig. 3).

Interacting effects of luminaire shape and color temperatures showed that the combination of colder color temperatures and diffusors generally increased the number of caught insects, and luminaires with diffusors amplified the differences in captured insects between 1750 and 4000 K (Fig. 3, Appendix D). On average up to +31.8% more individuals (Diptera) were caught at luminaires with diffusors for lights with 3000/4000 K. Diffusors for 1750 K lights amplified the number of caught insects maximally +17% (for Coleoptera; Fig. 3). We therefore conclude that luminaire shape is a more consistent and stronger driver for the number of captured insects than the three LED color temperatures considered here. In addition, the color temperature of 1750 K appeared less detrimental than color temperatures of 3000 K and 4000 K, respectively (Appendix D).

Bat activity

Overall, we recorded 38045 bat passes which fell into 16223 activity intervals of five minutes, occupying 1994 bat feeding bins (Appendix E: Fig. 1). For both, relative bat foraging and relative feeding activity, the vast majority occurred in the guild of mid-range echolocators (MREs; Appendix E: Fig. 1). Long- (LRE) and short-range echolocators (SRE) were observed only in very small numbers at street lights compared to MREs which made up over 94% of the observations (Appendix E: Fig. 1; Appendix F). In addition, MREs showed a 44.8% higher activity at street lights compared to records in dark areas, while SRE and LRE exhibit lower or similar record numbers in dark areas compared to records at street lights (Appendix F).

As a consequence of the low numbers of records for LREs and SREs (Appendix E: Fig. 1), we only fitted GLMMs for the total number of bat records and for MREs. The variables luminaire shape and color temperature had VIF values around 1 for bat foraging and feeding activity (Appendix G), indicating no evidence of multicollinearity (Zuur et al. 2010). The regressions did not explain bat foraging nor feeding activity (Appendices H, I) with R^2 around 0. Our interpretations of these results are therefore only qualitative.

In strong contrast to insects, bats seemed to avoid luminaires with diffusors. Both, bat foraging and feeding activity were reduced by 40% given luminaires with diffusors (Figs. 4-5). In contrast, responses to color temperatures did not matter for both, relative bat foraging and feeding activity (Figs. 4-5). Interactions between luminaire shapes and color temperatures showed that bats preferred standard luminaire shapes when foraging (Fig. 5), while the overall response to different color temperatures remained weak.

Discussion

We provided an ecological impact assessment of combined and relative impacts of luminaire shapes and three LED color temperatures (1750 K, 3000 K, 4000 K) on nocturnal insects and bat foraging and feeding activity. The two luminaire shapes encompassed a standard LED luminaire emitting light in a focused way and an LED luminaire with a diffusor to enhance the distribution of light into the surroundings. First, we showed that LED color temperatures matter for insects. There was a distinct and overall statistically significant trend towards more insects captured at warm-white (3000 K) and neutral-white (4000 K) compared to LEDs with 1750 K (Fig. 3). This finding is in line with other studies reporting more detrimental effects of cooler LED color temperatures on insects [(Somer-Yeates et al. 2017; van Geffen, van Eck, de Boer, van Grunsven, Salis et al. 2015), but see (Bolliger et al. 2020c; Longcore et al. 2015; Macgregor, Pocock, Fox & Evans 2019)]. Between 3000 K and 4000 K, however, differences in captured insects were only significant for Lepidoptera (Fig. 3). An explanation might be that the peak in the blue range at about 450 nm - to which insects are reportedly particularly sensitive - is only strongly developed for the neutral-white LEDs at 4000 K. LEDs of 3000 K exhibited only a small and LEDs of 1750 K no peak at all in blue spectrum (Appendix A: Fig. 1).

Second, luminaire design may have a significant impact on the ecological environment when considering nocturnal insect abundance. Standard, well focused luminaire shapes reduced the impacts on nocturnal insect abundance by between 28% and 37%. These effects were statistically significant for all insects and the groups Diptera, Coleoptera and Heteroptera (Fig. 3).

Third, combined effects of luminaire shape and color temperatures showed that generally more insects were caught at street lights with diffusors and cooler color temperatures. On average 92% more Diptera specimens were caught given lights with diffusors at 4000 K, while the treatment combination of lights with diffusors and 1750 K yielded up to 40% more individuals belonging to Coleoptera. We therefore conclude that luminaire shape is a more consistent and stronger driver for the number of captured insects compared to the three LED color temperatures considered here.

In contrast to insects, effects of the light treatments on bats were only minor. Bat foraging activity did not show any statistically significant response pattern to treatments of luminaire shape and color temperatures (Fig. 4). However, there was a trend towards 21.5% more foraging activity at standard luminaire shapes compared to luminaires with diffusors for all bats and for MREs (mid-range echolocators; Fig. 4). This relationship was significant for bat feeding activity (Fig. 5). Similar to the response pattern of insects, bats (MREs) were up to 44.8% less active at dark sites. The activity of LREs and SREs was low at the luminaires and at the dark sites (Appendix F). Thus, while MREs may have adapted to or even profited from exposure to lights attracting more insects, LREs and SREs seemed to avoid settled areas altogether. Especially species classified as SREs are mostly listed as critically endangered (CR), endangered (EN) or vulnerable (VU) in the recent Chiroptera Red List (Bohnenstengel, Krättli, Obrist, Bontadina, Jaberg et al. 2014), stressing that more attention needs to be paid to the long list of ALAN-intolerant bat species. MREs seemed affected by (higher) LED color temperature (activity ratios 1750 K:3000 K:4000 K~1:0.8:0.9) as well as by luminaires with diffusors (activity ratio Standard:Diffusor 1:0.8) in their foraging flight around the lights (Fig. 4). However, when closely approaching the lights equipped with diffusors in their attempt to catch the insects in their feeding flight (Fig. 5),

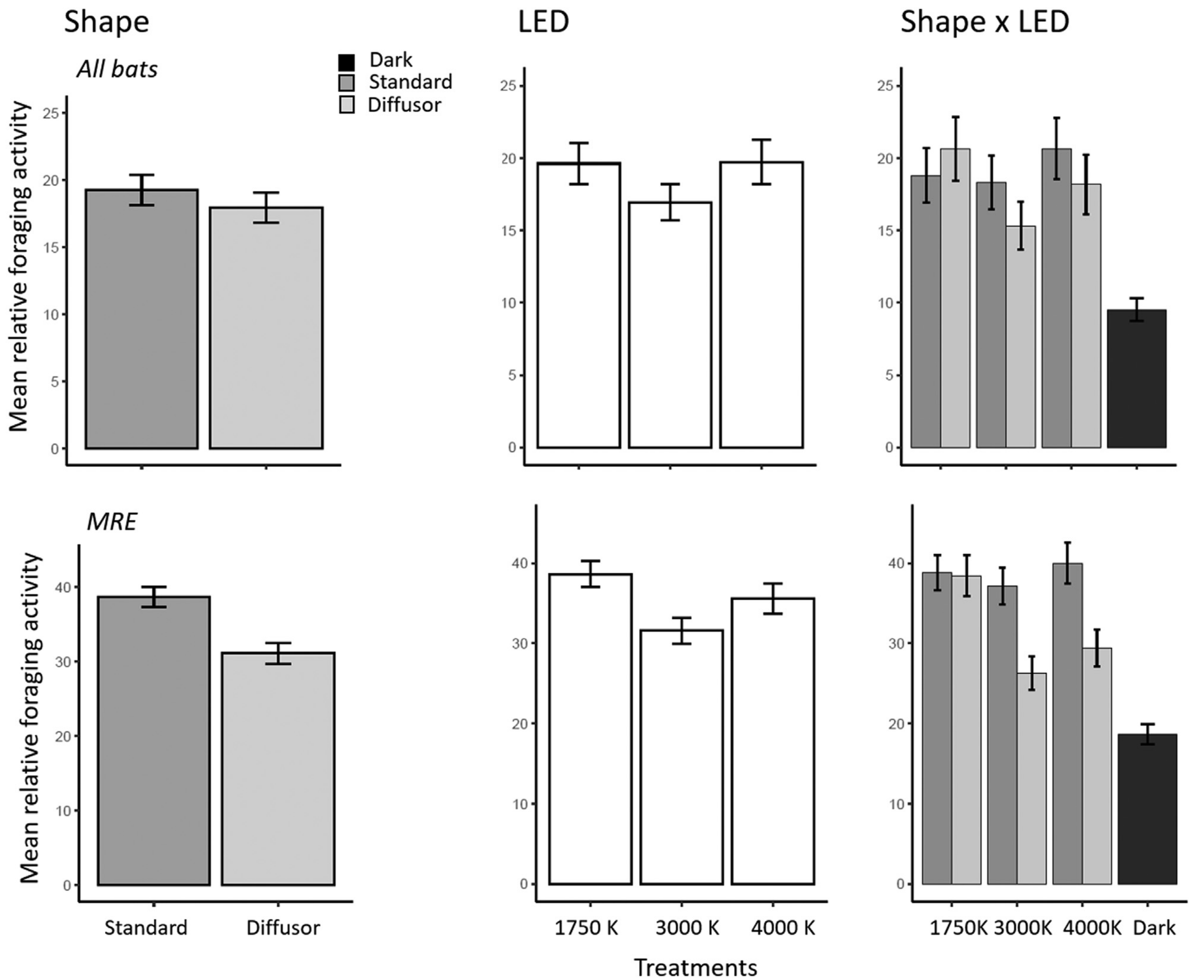

Fig. 4. Mean relative foraging activity of bats (± standard error) as a function of luminaire shape (luminaire with diffusor (Diffusor) and standard luminaires (Standard)) and three LED color temperatures (1750 K, 3000 K, 4000 K). MRE: mid-range echolocators. The left and the middle columns show GLMM results for impact of light treatments luminaire shape (luminaires with diffusor (Diffusor) and standard luminaires (Standard)) + three LED color temperatures (1750 K, 3000 K, 4000 K). The right column shows results for combined impacts for luminaire shapes:color temperatures. Indicated are only statistically significant comparisons. Please note that dark sites are shown for visual comparison only and did not enter the statistical analyses. Statistical levels of significance: *** < 0.001 ** < 0.01, * < 0.05. Regression tables and contrasts are reported in Appendix H).

they seemed to shy away from luminaires with diffusors (ratio Standard:Diffusor 1: 0.6), especially at higher LED color temperatures. This indicates that the intense stray-light close to the diffuse lights negatively affects the target-focused echolocation, likely by visually deterring or momentarily blinding the bats.

Limitations of our approach are related to the very small, localized study site. Given that all our samples are spatially highly correlated, our results are only valid within the restriction that the three replicates (Fig. 1) are considered pseudo-replicates. Nevertheless, our results suggest a trend that represents an important step toward more sustainable outdoor lighting.

We conclude that both LED color temperature and luminaire design are important drivers for impacts of light pollution on insect abundance. In particular, the interactions between the neutral-white LED (4000 K) and luminaire shapes amplify the negative effects of light emitted in the environment as we caught on average 16% more insects at neutral-white LEDs with diffusors that emitted light into the surroundings and were thus strongly visible. Therefore, focused lighting, i.e., lighting that limits stray light into the environment appears ecologically more beneficial. It is therefore imperative that steps towards sustainable outdoor lighting include aspects of luminaire design as an important driver of light pollution reduction.

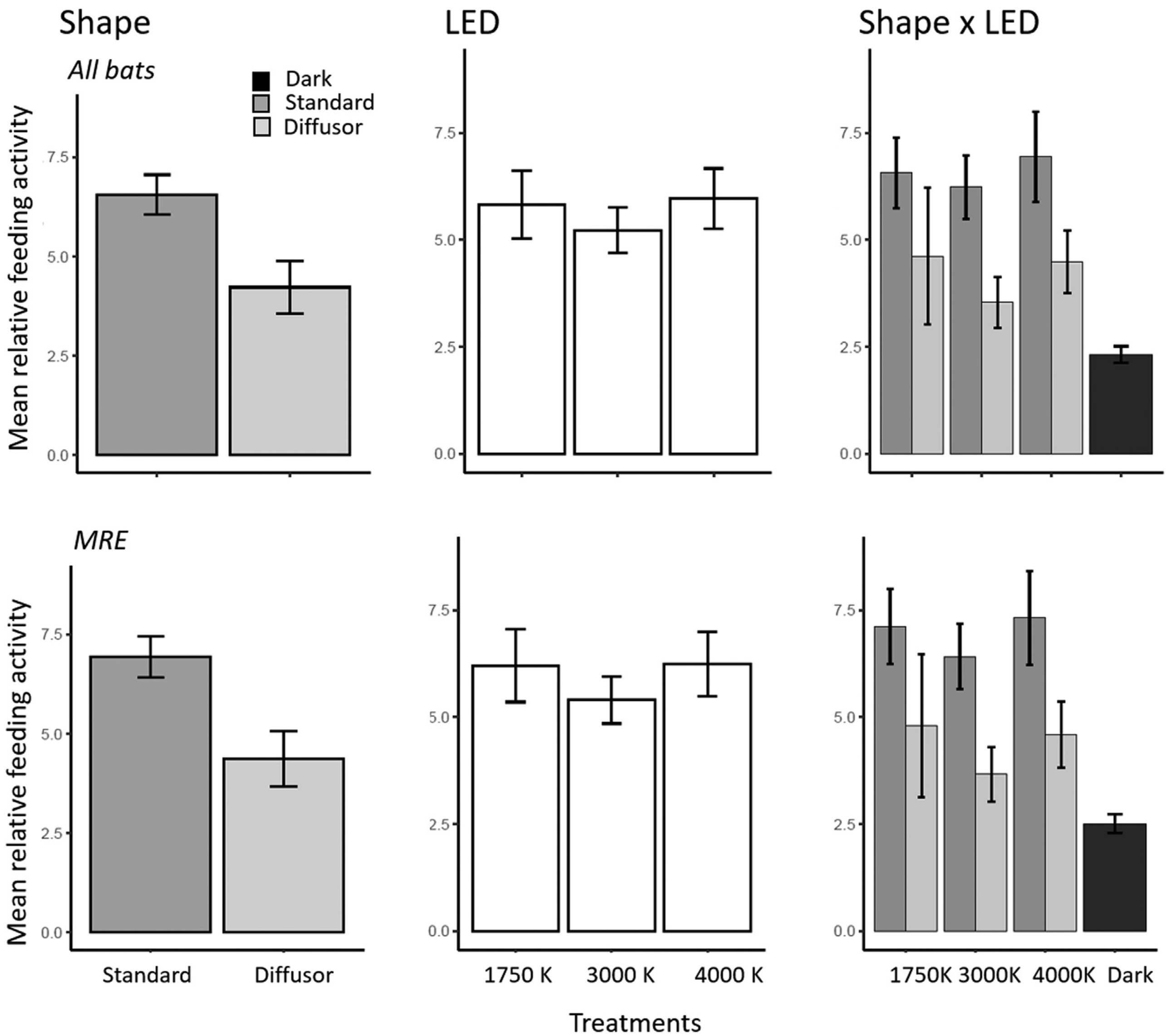

Fig. 5. Mean relative feeding activity of bats (± standard error) as a function of luminaire shape (luminaire with diffusor (Diffusor) and standard luminaires (Standard)) and three LED color temperatures (1750 K, 3000 K, 4000 K). MRE: mid-range echolocator. The left and the middle columns show GLMM results for impact of light treatments luminaire shape (luminaires with diffusor (Diffusor) and standard luminaires (Standard)) + three LED color temperatures (1750 K, 3000 K, 4000 K). The right column shows results for combined impacts for luminaire shapes:color temperatures. Indicated are only statistically significant comparisons. Please note that dark sites are shown for visual comparison only and did not enter the statistical analyses. Statistical levels of significance: *** < 0.001 ** < 0.01, * < 0.05. Regression tables and contrasts are reported in Appendix I).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.07.002.

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