

Colors of attraction: Modeling insect flight to light behavior

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Abstract

Light sources attract nocturnal flying insects, but some lamps attract more insects than others. The relation between the properties of a light source and the number of attracted insects is, however, poorly understood. We developed a model to quantify the attractiveness of light sources based on the spectral output. This model is fitted using data from field experiments that compare a large number of different light sources. We validated this model using two additional datasets, one for all insects and one excluding the numerous Diptera. Our model facilitates the development and application of light sources that attract fewer insects without the need for extensive field tests and it can be used to correct for spectral composition when formulating hypotheses on the ecological impact of artificial light. In addition, we present a tool allowing the conversion of the spectral output of light sources to their relative insect attraction based on this model.

KEYWORDS

artificial light at night, Diptera, Lepidoptera, light pollution, phototaxis, spectral sensitivity

1 | INTRODUCTION

Over the last 150 years the use of artificial illumination has dramatically changed the nightscape (Garstang, 2004). Insect attraction to light is a well-known phenomenon, which was already reported shortly after the introduction of outdoor lighting (Claypole, 1885; Douglas, 1856). Although there are a number of nonexcluding underlying mechanisms (e.g. Hsiao, 1973; Robinson & Robinson, 1950) by which insects come to light sources, we broadly interpret positive phototaxis as insects arriving at light sources for the purpose of this study. The large-scale use of artificial light at night has been identified as a significant threat for many organisms and ecosystem services (Hölker, Wolter, Perkin, & Tockner, 2010; Longcore & Rich, 2004). For moths (Lepidoptera), effects have been reported at individual (Truxa & Fiedler, 2012; van Geffen, van Grunsven, van Ruijven, Berendse, & Veenendaal, 2014; van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011; van Langevelde, van Grunsven, Veenendaal, &

Fijen, 2017) and population levels (Eisenbeis, 2006; van Langevelde et al., 2018) and artificial light is thought to contribute to the decline of moth populations in Western Europe (Fox, 2013; Frank, 1988; Groenendijk & Ellis, 2011). Attraction of insects to artificial light sources can indirectly negatively affect pollination in plants that depend partly or completely on nocturnal pollination (Knop et al., 2017; Macgregor, Evans, Fox, & Pocock, 2017). Less well studied is the role of artificial light in attracting disease vectors (Erazo & Cordovez, 2016; Longcore et al., 2015). Some of these groups of insects are positively phototactic, such as the vectors of Chagas disease (e.g. *Triatoma* spp.) (Erazo & Cordovez, 2016; Minoli & Lazzari, 2006), leishmaniasis (e.g. *Lutzomyia intermedia* and *L. whitmani*) (Erazo & Cordovez, 2016), malaria (*Anopheles* spp.) (Barghini & De Medeiros, 2010), and West Nile virus (*Culex* spp.) (Bentley, Kaufman, Kline, & Ja, 2009).

The spectral composition of a light source directly influences the degree to which it attracts insects. Many nocturnal insects are attracted to light sources rich in UV (Barghini & De Medeiros,

2012; van Langevelde et al., 2011) and short wavelength (visible) light is in general more attractive than long wavelength light (Longcore et al., 2015; Somers-Yeates, Hodgson, McGregor, Spalding, & Ffrench-Constant, 2013; van Langevelde et al., 2011). Many studies have compared attractiveness of different light sources to nocturnal flying insects, specifically moths (Barghini & De Medeiros, 2012; Eisenbeis, 2006; Eisenbeis & Eick, 2010; Pawson & Bader, 2014; Somers-Yeates et al., 2013; van Grunsven et al., 2014; van Langevelde et al., 2011). Nevertheless, despite this body of theory we still cannot predict insect flight to light based on the spectral output of a light source (van Grunsven et al., 2014).

The current technological shift from high-intensity discharge lights to UV-poor but broad spectrum LEDs is changing the spectral composition of nocturnal illumination worldwide (Davies, Bennie, Inger, Ibarra, & Gaston, 2013). This could result in less or more attraction of insects depending on the spectral composition of the LEDs (Longcore et al., 2015) and the light sources they replace (van Grunsven et al., 2014). A model to assess the contribution of different parts of the spectral composition of modern light sources to insect attraction is urgently needed and could greatly influence the development and application of light sources with reduced attractiveness to flying insects. We developed such a model by parametrizing a theoretical model of the insect eye with field experiments on the attractiveness of a variety of different light sources for a wide range of flying insects. This model consists of two parts, the first weighs the parts of the emission spectrum, giving a value for the attractiveness of a spectrum expressed in the proposed new unit Insect Light Attraction (ILA) and the second quantifies the relationship between ILA and insect attraction for a given radiant flux.

2 | MATERIALS AND METHODS

2.1 | Model construction

The spectral response model presented here contains an action spectrum that gives the relative attractiveness for insects per nanometer wavelength so that the products of emitted power per nanometer and its relative attractiveness summed over the entire spectrum (the so-called sum product) gives the signal strength as experienced by the attracted insects (Laughlin, 1981). This action spectrum is composed as a linear combination of the absorption bands of the common photoreceptors in insect eyes. Most insects share a UV (U) and a short wavelength or blue receptor (S) and many insects additionally have a middle wavelength or green receptor (M). A fourth receptor, for red light, and even a fifth receptor can be found in some insects, but this is rare and mostly found in diurnal species (Briscoe & Chittka, 2003; Peitsch et al., 1992). In an earlier version of the model, a fourth receptor was included but this did not improve the model and therefore we chose not to include it in our final model (data not presented). We fitted the sensitivity curves using data from three field experiments described below. The spectral sensitivity curve of each photoreceptor class could be described by a skewed Gaussian curve with four independent parameters as proposed by Stavenga, Smits, and Hoenders (1993). This curve

has a single peak wavelength (λ_{max}), peak height (A), width (a_0), and skew (a_1) as described by the equation:

$$\alpha_i = A_i \exp \left[-a_0 x_i^2 \left(1 + a_{1,i} x_i + a_{2,i} x_i^2 \right) \right],$$

where $x_i = 10 \log \left(\frac{\lambda}{\lambda_{max,i}} \right)$ and restricting the parameterization by setting:

$$a_{2,i} = \frac{3a_{1,i}^2}{8}$$

Adding the UV (U), blue (S), and green (M) bands together, we could construct the reaction spectrum as follows:

$$\varepsilon(\lambda) = \sum \alpha_i(\lambda) = U(\lambda) + S(\lambda) + M(\lambda).$$

2.2 | Parameter ranges based on known sensitivity curves

The ranges for the parameters defining these templates (Table 1) were a priori determined from published sensitivity curves for different groups of insects (Beier & Menzel, 1972; Eguchi, Watanabe, Hariyama, & Yamamoto, 1982; Hu & Stark, 1980; Johnsen et al., 2006; Poiani, Dietrich, Barroso, & Costa-Leonardo, 2014; White, Xu, Münch, Bennett, & Grable, 2003; Yamaguchi, Desplan, & Heisenberg, 2010; Zufall, Schmitt, & Menzel, 1989). Peak height was set at 1 for the U absorption band and was free for the other two bands. The ranges used are limited to primary or α bands. The higher-order bands of the different receptors overlap completely with the primary band of the UV and blue receptors. They have been incorporated in the UV and blue band by fitting their shape so that the fitted curve reflects the sum of the primary band and overlapping higher order curves of the other receptors. The individual curves therefore are dominated by the primary band of the respective receptors but does not exactly describe this, as it can include higher order bands of other receptors. However, the overall model does describe the sum of all primary and higher order bands.

2.3 | Fitting the model using field data

The parameters of the spectral response curves were determined by modeling the numbers of insects attracted by the different lamps caught per unit time in three field experiments. In these field experiments, 18 spectrally different light sources were tested (six by van Langevelde et al., 2011, six by van Grunsven et al., 2014, and 6 by Smit & Groenendijk, 2011, see Supporting Information 1 for details on the field experiments), 97,746 insects, spread over 14 orders, were caught and identified, with Diptera being the most numerous group (74,121 individuals).

We fitted the log of the sum product of the spectral distribution of the photon flux, $q_{n,p}$ (in mol photons $\text{nm}^{-1} \text{s}^{-1}$), with the spectral attraction model, ε , versus the observed attraction, N_s , using a logistic function

$$\log_{10} (N_s) = \log_{10} \frac{L}{1 + e^{-k(x-x_0)}},$$

TABLE 1 The ranges for the different parameters used to define the templates for the UV, blue, and green band and the final fitted values

	Peak wavelength (λ_{max})			Width (a_0)			Skew (a_1)			Peak Height (A)	
	Minimum	Maximum	Fitted	Minimum	Maximum	Fitted	Minimum	Maximum	Fitted	A priori	Fitted
UV	320	400	352	74	483	74	4	36	36	1	1
Blue	400	472	400	206	403	363	0	12	12	No limit	1
Green	490	570	520	228	401	232	1	9	5	No limit	0.3

where $x = \log_{10}(\int q_{n,p}(\lambda)\epsilon(\lambda)d\lambda)$, (\log_{10} of sum product), $x_0 = 0.83$ (midpoint of the s-curve), $k = 1.90$ (steepness of the curve) and $L =$ local asymptotic maximum of the curve.

The factor L allows for differences in conditions or local insect densities between experiments, L thus has a single value per field study. This corresponds with an asymptotic maximum of the logistic function for each experiment and ranged from 600 to 4000. We used a generalized reduced gradient method of iteration to achieve the highest Pearson correlation coefficient between the left-hand side (observed attraction) and the right-hand side (modeled attraction) of the logistic equation given above by adjusting values of λ_{max} (peak wavelength), A (peak height), a_0 (width), and a_1 (skew) for the three photoreceptor bands, and L , x_0 , and k to fit the logistic function. The peak height parameter of the U band was fixed at $A = 1$ and the other peak heights calculated relative to this (Figure 2).

2.4 | Relation output and attraction

The fitting procedure gave the attractiveness for each wavelength relative to the peak height of the U band. We chose to subsequently scale the model so that the most attractive wavelength has an attractiveness of 1 summed over all bands. The sum product of the spectral output and this response curve has an exponential relationship with insect attraction. Most parameters were fitted as described above but the local asymptotical maximum (L) depends on the local insect density and therefore has no universal value; it varied from 113 to 3074 insects per 1000 s in our datasets. However, this value has a linear relation with the predictive attraction and therefore does not present a problem when comparing light sources. For the calculations presented in Supporting Information 3 we chose an L of 1000, arbitrary but well within the range we observed. Some examples of light sources with output in lumen, calculated attractions and measured attraction are given in Supporting Information 2.

2.5 | Marginal means as measure of attractiveness

Using the model, the marginal means of the log counts of the lamps were estimated. We used these marginal means as measure of attractiveness, i.e., the $\log_{10}(N_s)$ in the logistic equation above. The adjusted 95% confidence intervals constructed for the marginal means take into account that in the model calibration, a factor for the counts was fitted for each of the experiments (L), so that only the differences between the lamps are relevant. Such a factor translates to an addition on the log-count scale, meaning that during the calibration the average log-count of a test can be fitted perfectly. This can be interpreted as allowing for differences in insect densities or environmental variables

between experiments. The 95% confidence intervals for all lamps are quite similar. This is important when considering the calibration: if the estimated attractiveness of some lamps would be much more uncertain, the fit criterion should reflect that extra uncertainty. In our case, the adjusted confidence intervals were similar and thus the fit criterion does not need adjustment. The correlation coefficient for the relation between the spectral response model and the data used to fit the model was $r = 0.993$ with $RMSE = 0.097$ (Figure 2a) indicating that the model fits the empirical data very well, especially considering the large diversity of light types in this data set. Our data contain a large number of individuals from the order Diptera, which made up 43% of the individual insects in the data used to fit the model. Therefore, a good fit for Diptera can result in a good fit overall without a good fit for other insects. We assessed whether the spectral response model as fitted on the complete data sets is also accurate for non-Diptera by using the data sets excluding Diptera. The correlation between the model predictions and the non-Dipteran data sets is high ($r = 0.996$, $RMSE = 0.10$) as well.

As the goal of the model is to predict the total number of flying insects, and not the number for lower taxonomical levels, we did not assess the fit at order level.

2.6 | Model interpretation

The sum product of the spectral output of a light source per unit wavelength and its action spectrum (Figure 1) gives the output weighted for insect attraction; we propose to call this new unit Insect Light Attraction (ILA). The light output in ILA has a logistic relationship with the number of insects attracted. ILA can be calculated by multiplying the lamps' spectral output with the ILA spectral response curve, which gives a dimensionless value for the relative attraction of a light source. This can easily be done using Supporting Information 3.

2.7 | Model validation

We validated our model with data from two experiments not used for fitting the model. The first experiment was performed in the Netherlands, using Robinson traps with light sources mounted above, and the second in California, USA, using pan traps with shielded lights directed at the pan trap (Longcore et al., 2015). The Dutch dataset was collected using six light traps with different light sources over 18 nights catching a total of 3809 insects. From the Californian dataset, five traps with different light sources were included that caught 4911 insects in total over 19 nights (for details see Supporting Information 2). A negative binomial regression model with a log-link function was used to correct for the effects of night and location, and the estimated marginal means

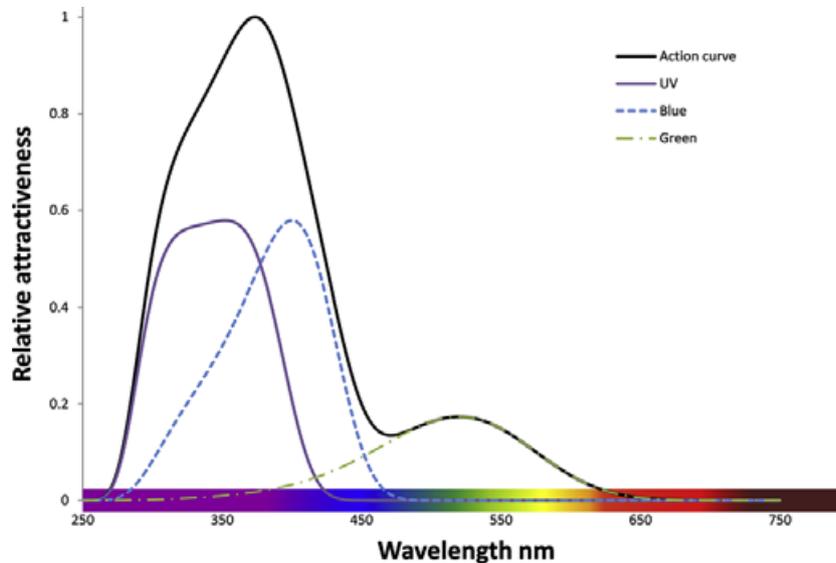


FIGURE 1 The action curve for the relation between spectral output (in photons $\text{nm}^{-1} \text{s}^{-1}$) and attraction of insects is the sum of the curves for the UV, blue, and green photoreceptors [Color figure can be viewed at wileyonlinelibrary.com]

for the different lamps were used as was done for the other datasets. We then compared the predictions based on the spectral output with the measured attraction.

The data used for validation contain a large number of individuals from the order Diptera, therefore, we assessed whether the spectral response model as fitted on the complete datasets is also accurate for non-Diptera by using the datasets excluding Diptera. As the goal of the model is to predict the total number of flying insects, and not the number for lower taxonomical levels we did not perform a validation at order level.

3 | RESULTS

3.1 | Model description

The spectral response curve is the sum of three Gaussian curves with the parameters given in Table 1, these parameters are the peak wavelength (λ_{max}), peak height (A), width (a_0), and skew (a_1) for each band resulting in the action spectrum shown in Figure 1. The sum product of the spectral output of a light source and this spectral response curve has a logistic relationship with the number of insects attracted following the function $N_s = 1000 / (1 + e^{-1.9(\text{Log}(10)x - 0.83)})$ with N_s being attraction and x being the aforementioned sum product. Using the tool provided as Supporting Information 3, both the ILA, i.e., the sum product, and the relative attractiveness of light sources can be calculated from the spectral output of light sources.

3.2 | Validation of the model

For the validation of the model, we used a Dutch and a Californian dataset not used for model fitting. We found strong correlations between the model predictions based on the spectral composition of the lamps used and the data for the Dutch ($r = 0.941$, $\text{RMSE} = 0.15$)

and for the California dataset ($r = 0.967$, $\text{RMSE} = 0.12$) (Figure 2b; Supporting Information 2).

In both datasets, Diptera formed a large proportion of the insects caught (87% for the Dutch and 58% for the Californian dataset). Therefore, a good prediction might be caused by a good prediction of the response of only the Diptera, while being a poor predictor for other insect groups. To assess whether the spectral response model is also accurate for non-Diptera, we tested the spectral response model excluding Diptera from the data using the same method. The correlation between the model predictions and attraction for the validation datasets excluding Diptera is relatively strong as well ($r = 0.829$, $\text{RMSE} = 0.23$ for the Dutch and $r = 0.825$, $\text{RMSE} = 0.22$ for the Californian data set). The correlation between predicted and measured attractiveness is less strong than when the complete data sets were used, but reasonable given the large reduction in the data and therefore reliability of the estimates of attractiveness remains high.

4 | DISCUSSION

Our model accurately assesses insect attraction to light sources based on their spectral output by combining current knowledge on insect eye physiology and large field datasets on the attractiveness of different light sources for a wide range of insect groups. This is especially relevant given the current world-wide trend to replace older lighting with LED technology. Our model allows a priori comparison of light sources for their insect attraction. Hence, it is a crucial tool for the application and development of light sources and can facilitate the application of light sources that attract fewer insects, with benefits for conservation and reduction of pest and disease vectors.

Although the model is based on data from the Netherlands, the validation with data from California indicates that the insects occurring in this region do not substantially differ in their spectral sensitivity. For the California dataset, the model ranks the lights correctly but

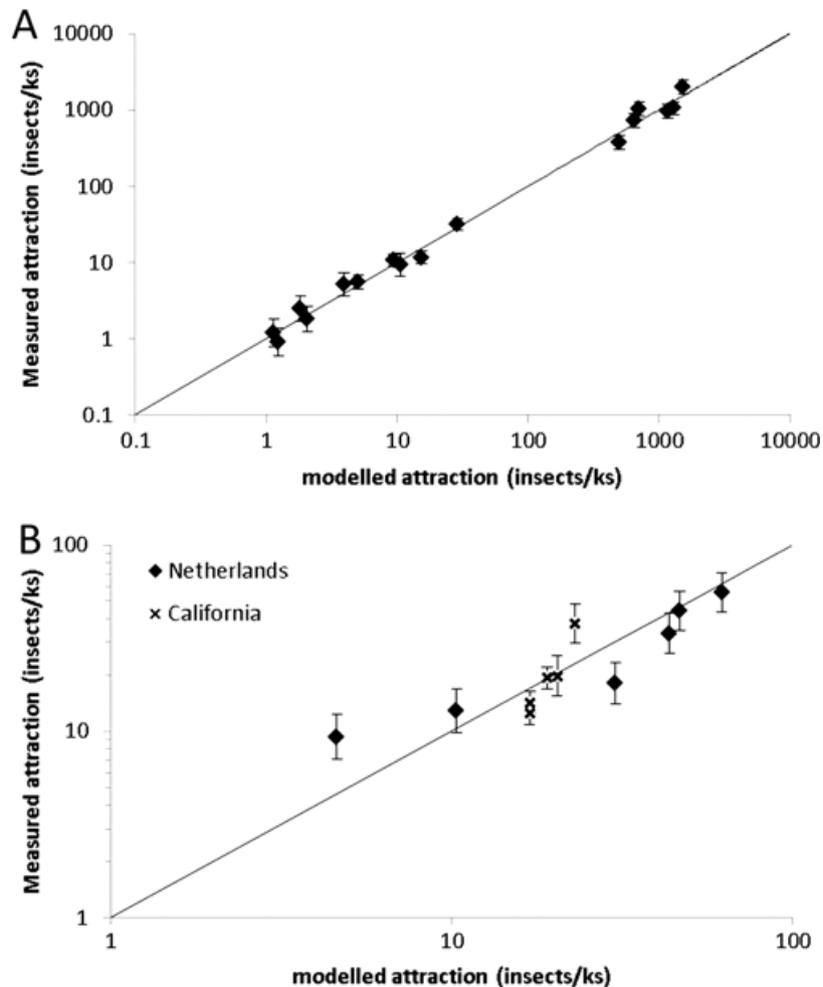


FIGURE 2 The model predictions are highly correlated with the empirical data, both for the experiments used to fit the model (a; $r = 0.993$) as well as for the validation test (b; $r = 0.941$ for the Dutch and $r = 0.967$ for the California data; ks is kilosecond). The empirical data is corrected to only include the effects attributed to the lamp types and to exclude effects caused by differences in locations and nights. The values are marginal means with estimated 95% confidence intervals. The line $X = Y$, reflecting a perfect model, is included as a reference

the ratio between the light sources in attracted number of insects is larger than predicted. The light was projected downward in this experiment (Longcore et al., 2015), in contrast to the spherical projection in the other experiments. Therefore, the light intensity of the trap as perceived by insects is different. The light intensity will be low when perceived outside of the projection and much higher for insects within this beam. As the relationship between ILA and attraction is not linear but described by a logistic function, this causes the model to underestimate the differences between light sources (Figure 2b). That the traps are ranked correctly and there seems to be a near linear relationship between modeled and measured attraction indicating that the ILA is estimated well.

Even when the datasets are strongly reduced after removal of the Diptera, the model still gives a good prediction of the number of insects attracted. The lower correlation coefficients and higher RMSE for the data without Diptera can be explained by the drastic reduction of the number of individual insects included in the analysis. Our spectral response model is thus not limited to Diptera but valid for nocturnal positively phototactic insects in general. As there

is a huge diversity in insect visual systems and spectral response can differ strongly between species (Briscoe & Chittka, 2003), the proposed model may not be valid for lower taxonomic levels or individual species (Somers-Yeates et al., 2013; van Grunsven et al., 2014). We did not model attraction for lower taxonomic levels, such as separate orders, as we were interested to provide a tool for assessment of current light sources or the development of new ones for nocturnal flying insects as a group. However, as we demonstrate here the wide variation between species apparently does not preclude the formulation of a validated model to predict the general pattern in the response of nocturnal flying insects.

Light level is currently expressed in photons $m^{-2} s^{-1}$, Watt $m^{-2} s^{-1}$, or lux (Cinzano, Falchi, & Elvidge, 2001; Longcore & Rich, 2004). Such units, quantifying particles, energy, and illuminance, respectively, are unsuitable for the assessment of the impact of irradiance on insects as light sources with a similar luminous or radiant flux can differ in attractiveness to insects depending on the spectral composition. We present here a new unit for the attractiveness of light to insects, namely the Insect Light Attraction (ILA), that weighs the spectral output for the

differences in attraction effect for each wavelength. This allows for a qualitative comparison of light sources thereby allowing light designers to develop a light source that attracts fewer insects. Insight in potential insect attraction of light sources can be the key to mitigate and minimize ecological impact of nocturnal illumination or in locations where the attraction of nuisance insects and disease vectors are an issue. This model creates the possibility for, e.g., policy makers to lay down demands on light sources with less impact on insect populations without the need for field tests. This is highly relevant as, e.g., different white LEDs that are perceived as similar by the human eye can substantially differ in their attraction of nocturnal insects (Longcore et al., 2015).

Furthermore, our model can give insight in the impact of the current change in spectral composition of the nightscape (Davies et al., 2013). For spatially explicit studies the model presented here can be combined with remote sensing data, such as from VIRRS or photos from ISS (Kyba et al., 2014). This makes it possible to quantitatively compare the exposure to artificial light for different areas or the same area at different moments in time, for instance before and after a change in lighting, taking the spectral composition into account. The impact of artificial light at night on a larger spatial scale is currently unknown. The model presented here allows for the formulation of testable hypotheses on the impact of artificial light on populations of nocturnal insects and allows us to correct light levels for spectral composition when assessing the impact on insects.

Artificial light at night affects insects in more ways than mere attraction. It has been shown to interfere with pollination (Macgregor et al., 2017), feeding (van Langevelde et al., 2017), chemical communication (van Geffen et al., 2015b), mating behavior (van Geffen et al., 2015a), and disrupt initiation of diapause (van Geffen et al., 2014). It is currently unknown to what extent the model presented here is applicable for other impacts of artificial light on insects, besides attraction. The latter four studies were shown to be affected more by short than long wavelength light reflecting the general pattern found for flight to light behavior here. This suggests that other impacts of artificial light on insects might have a similar spectral sensitivity as attraction. If this is true mitigation to reduce attraction would also reduce the other impacts.

In conclusion, the model presented here allows comparing light sources for better informed choices, is valuable for the development of more insect friendly lighting, helps to formulate quantitative hypotheses on the impact of nocturnal artificial light and allows for a quantitative comparison of light pollution from areas with different spectral composition.

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REFERENCES

- Barghini, A., & De Medeiros, B. A. (2010). Artificial lighting as a vector attractant and cause of disease diffusion. *Environmental Health Perspectives*, 118, 1503–1506.
- Barghini, A., & De Medeiros, B. A. S. (2012). UV radiation as an attractor for insects. *LEUKOS - Journal of Illuminating Engineering Society of North America*, 9, 47–56.
- Beier, W., & Menzel, R. (1972). Untersuchungen über den Farbesinn der deutschen Wespe (*Paravespula germanica* f., Hymenoptera, Vespidae): Verhaltensphysiologischer Nachweis des Farbesehens. *Zool Jd Physiol Bd*, 76, 441–454.
- Bentley, M. T., Kaufman, P. E., Kline, D. L., & Ja, Hogsette (2009). Response of adult mosquitoes to light-emitting diodes placed in resting boxes and in the field. *Journal of American Mosquito Control Association*, 25, 285–291.
- Briscoe, A. D., & Chittka, L. (2003). The evolution of color vision in insects. *Annual Review of Entomology*, 46, 471–510.
- Cinzano, P., Falchi, F., & Elvidge, C. D. (2001). The first world atlas of the artificial night sky brightness. *MNRAS*, 328, 689–707.
- Claypole, E. (1885). Entomology by the electric lamp. *The Canadian Entomologist*, 17, 117–119.
- David, A. 2017. Sora® bluefree™ led white light: A new paradigm in circadian-friendly lighting.
- Davies, T. W., Bennie, J., Inger, R., Ibarra, N. H., & Gaston, K. J. (2013). Artificial light pollution: Are shifting spectral signatures changing the balance of species interactions? *Global Change Biol*, 19, 1417–1423.
- Douglas, J. W. (1856). *The world of insects: A guide to its wonders*. London, England: J. Van Voorst.
- Eguchi, E., Watanabe, K., Hariyama, T., & Yamamoto, K. (1982). A comparison of electrophysiologically determined spectral responses in 35 species of lepidoptera. *Journal of Insect Physiology*, 28, 675–682.
- Eisenbeis, G. (2006). Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. In C. Rich & T. Longcore (Eds.), *Ecological consequences of artificial night lighting* (pp. 281–304). Washington DC: Island Press.
- Eisenbeis, G., & Eick, K. (2010). Attraction of nocturnal insects to street lights with special regard to LEDs: Abstracts of the Society for Conservation Biology, 24th Annual Meeting, Edmonton, Alberta, Canada, 3–7 July 2010: 64.
- Erazo, D., & Cordovez, J. (2016). The role of light in Chagas disease infection risk in Colombia. *Parasites & Vectors*, 9, 1–10.
- Fox, R. (2013). The decline of moths in Great Britain: A review of possible causes. *Insect Conservation and Diversity*, 6, 5–19.
- Frank, K. (1988). Impact of outdoor lighting on moths: An assessment. *Journal of Lepidopterists' Society*, 42, 63–93.
- Garstang, R. H. (2004). Mount Wilson Observatory: The sad story of light pollution. *Observatory*, 124, 14–21.
- Groenendijk, D., & Ellis, W. N. (2011). The state of the Dutch larger moth fauna. *Journal of Insect Conservation*, 15, 95–101.
- Hölker, F., Wolter, C., Perkin, E. K., & Tockner, K. (2010). Light pollution as a biodiversity threat. *Trends in Ecology and Evolution*, 25, 681–682.
- Hsiao, H. S. (1973). Flight paths of night-flying moths to light. *Journal of Insect Physiology*, 19, 1971–1976.

- Hu, K. G., & Stark, W. S. (1980). The roles of drosophila ocelli and compound eyes in phototaxis. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 135, 85–95.
- Johnsen, S., Kelber, A., Warrant, E., Sweeney, A. M., Widder, E. A., Lee Jr, R. L., & Hernández-Andrés, J. (2006). Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. *Journal of Experimental Biology*, 209, 789–800.
- Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature (London, United Kingdom)*, 548, 206–209.
- Kyba, C., Garz, S., Kuechly, H., de Miguel, A. S., Zamorano, J., Fischer, J., & Hölker, F. (2014). High-resolution imagery of earth at night: New sources, opportunities and challenges. *Remote sensing*, 7, 1–23.
- Laughlin, S. (1981). Neural principles in the peripheral visual systems of invertebrates. In H. Autrum (Ed.), *Handbook of sensory physiology* (Vol. vii/6b, pp. 133–280). Berlin, Germany: Springer.
- Longcore, T., Aldern, H. L., Eggers, J. F., Flores, S., Franco, L., Hirshfield-Yamanishi, E., ... Barroso, A. M. (2015). Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. *Philosophical Transactions of the Royal Society B*, 370, 20140125.
- Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, 2, 191–198.
- Macgregor, C. J., Evans, D. M., Fox, R., & Pocock, M. J. (2017). The dark side of street lighting: Impacts on moths and evidence for the disruption of nocturnal pollen transport. *Global Change Biology*, 23, 697–707.
- Minoli, S. A., & Lazzari, C. R. (2006). Take-off activity and orientation of triatomines (heteroptera: Reduviidae) in relation to the presence of artificial lights. *Acta Tropica*, 97, 324–330.
- Pawson, P. M., & Bader, M. K.-F. (2014). Led lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications*, 24, 1561–1568.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F., & Menzel, R. (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A*, 170, 23–40.
- Poiani, S., Dietrich, C., Barroso, A., & Costa-Leonardo, A. (2014). Effects of residential energy-saving lamps on the attraction of nocturnal insects. *Lighting Research and Technology*, 47, 1477153514526880.
- Robinson, H. S., & Robinson, P. J. M. (1950). Some notes on the observed behaviour of lepidoptera in the vicinity of light-sources together with a description of a light-trap designed to take entomological samples. *Entomology Gazette*, 1, 121–132.
- Smit, M., & Groenendijk, D. (2011). *In light of conservation. Effects of different lamp types on the attraction of night-flying insects*. Wageningen, the Netherlands: Dutch Butterfly Conservation.
- Somers-Yeates, R., Hodgson, D., McGregor, P. K., Spalding, A., & French-Constant, R. H. (2013). Shedding light on moths: Shorter wavelengths attract noctuids more than geometrids. *Biology Letters*, 9, 20130376.
- Stavenga, D. G., Smits, R. P., & Hoenders, B. J. (1993). Simple exponential functions describing the absorbance bands of visual pigment spectra. *Vision Research*, 33, 1011–1017.
- Truxa, C., & Fiedler, K. (2012). Attraction to light-from how far do moths (Lepidoptera) return to weak artificial sources of light? *European Journal of Entomology*, 109, 77–84.
- van Geffen, K. G., Eck, E., Boer, R. A., van Grunsven, R. H. A., Salis, L., Berendse, F., & Veenendaal, E. M. (2015a). Artificial light at night inhibits mating in a geometrid moth. *Insect Conservation and Diversity*, 8, 282–287.
- van Geffen, K. G., Groot, A. T., van Grunsven, R. H. A., Donners, M., Berendse, F., & Veenendaal, E. M. (2015b). Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecology & Entomology*, 40, 401–408.
- van Geffen, K. G., van Grunsven, R. H. A., van Ruijven, J., Berendse, F., & Veenendaal, E. M. (2014). Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution*, 4, 2082–2089.
- van Grunsven, R. H. A., Donners, M., Boeke, K., Tichelaar, I., van Geffen, K. G., Groenendijk, D., ... Veenendaal, E. M. (2014). Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. *Journal of Insect Conservation*, 18, 225–231.
- van Langevelde, F., Braamburg-Annegarn, M., Huigens, M. E., Groenendijk, R., Poitevin, O., van Deijk, J. R., ... WallisDeVries, M. F. (2018). Declines in moth populations stress the need for conserving dark nights. *Global Change Biology*, 24, 925–932.
- van Langevelde, F., Ettema, J. A., Donners, M., WallisDeVries, M. F., & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144, 2274–2281.
- van Langevelde, F., van Grunsven, R. H. A., Veenendaal, E. M., & Fijen, T. P. M. (2017). Artificial night lighting inhibits feeding in moths. *Biology Letters*, 13, 20160874.
- White, R. H., Xu, H., Münch, T. A., Bennett, R. R., & Grable, E. A. (2003). The retina of *manduca sexta*: Rhodopsin expression, the mosaic of green-, blue- and UV-sensitive photoreceptors, and regional specialization. *Journal of Experimental Biology*, 206, 3337–3348.
- Yamaguchi, S., Desplan, C., & Heisenberg, M. (2010). Contribution of photoreceptor subtypes to spectral wavelength preference in drosophila. *Proceedings of the National Academy of Science of the United States of America*, 107, 5634–5639.
- Zufall, F., Schmitt, M., & Menzel, R. (1989). Spectral and polarized light sensitivity of photoreceptors in the compound eye of the cricket (*Gryllus bimaculatus*). *Journal of Comparative Physiology A*, 164, 597–608.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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