

LED lighting increases the ecological impact of light pollution irrespective of color temperature

S. M. PAWSON^{1,3} AND M. K.-F. BADER²

¹Scion, P.O. Box 29-237, Fendalton, Christchurch, New Zealand

²Scion, 49 Sala Street, Rotorua, New Zealand

Abstract. Recognition of the extent and magnitude of night-time light pollution impacts on natural ecosystems is increasing, with pervasive effects observed in both nocturnal and diurnal species. Municipal and industrial lighting is on the cusp of a step change where energy-efficient lighting technology is driving a shift from “yellow” high-pressure sodium vapor lamps (HPS) to new “white” light-emitting diodes (LEDs). We hypothesized that white LEDs would be more attractive and thus have greater ecological impacts than HPS due to the peak UV-green-blue visual sensitivity of nocturnal invertebrates. Our results support this hypothesis; on average LED light traps captured 48% more insects than were captured with light traps fitted with HPS lamps, and this effect was dependent on air temperature (significant light \times air temperature interaction). We found no evidence that manipulating the color temperature of white LEDs would minimize the ecological impacts of the adoption of white LED lights. As such, large-scale adoption of energy-efficient white LED lighting for municipal and industrial use may exacerbate ecological impacts and potentially amplify phytosanitary pest infestations. Our findings highlight the urgent need for collaborative research between ecologists and electrical engineers to ensure that future developments in LED technology minimize their potential ecological effects.

Key words: biodiversity; high-pressure sodium lamp; light pollution; spectra; street lighting; urbanization.

INTRODUCTION

Since the invention of the first practical incandescent light bulb in the late 1870s, night-time light pollution has now become almost ubiquitous in the populated regions of developed countries (Bogard 2013). The extent of artificial light pollution continues to expand swiftly ($\sim 6\%$ annual increase, range 0–20% [Hölker et al. 2010a]), especially in newly industrialized economies. Several aspects of light pollution are clear: (1) there is extensive evidence that artificial lighting that exceeds natural background levels has significant ecological and biological impacts (Longcore and Rich 2004, Rich and Longcore 2005, Hölker et al. 2010b, Davies et al. 2012, Gaston et al. 2013, Le Tallec et al. 2013, Perkin et al. 2014), (2) the spectral composition of light pollution can alter the magnitude of these impacts (van Langevelde et al. 2011, Davies et al. 2013), and (3) the spectral

composition of light pollution has changed, and will continue to change over time with the advent and subsequent adoption of more energy-efficient lighting technologies (Schubert and Kim 2005).

The current trend in global lighting is a shift from “yellow” sodium lamps toward a new generation of broad spectrum, energy-efficient, “white” light-emitting diodes (LEDs) for municipal and industrial lighting (Schubert and Kim 2005, Anonymous 2012). The biological effect of a shift toward a more “white-light night” (sensu Gaston et al. 2012) has not been studied in detail, but direct evidence of biological impacts is mounting (Stone et al. 2012), and comparisons of visual pigment absorbance spectra with the emission spectra of municipal light sources suggests indirectly that such impacts may be widespread among terrestrial animals (Davies et al. 2013).

Gaston et al. (2012) proposed that the ecological consequences of light pollution could potentially be reduced by avoiding critical regions within the spectrum. Currently available municipal and industrial-scale white LED lights are based on monochromatic blue LEDs

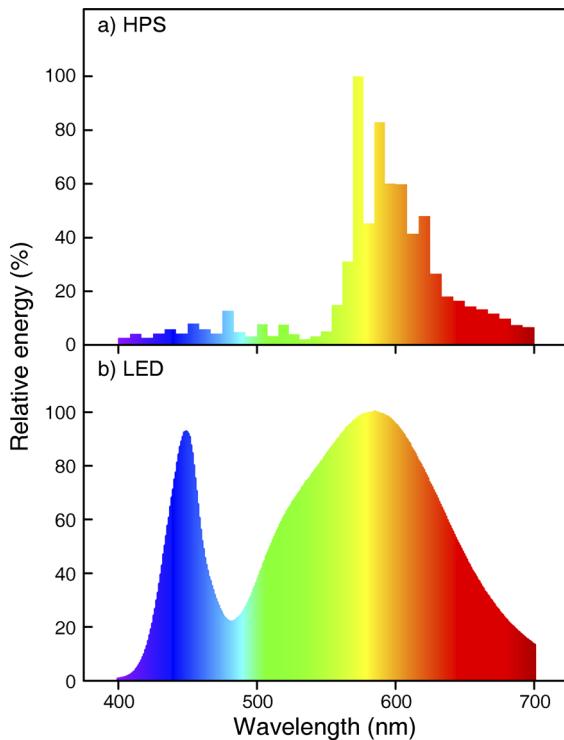


FIG. 1. Relative spectral emission of (a) high-pressure sodium (HPS) lamp (Sunlux ACE, NH-360 FLX; EYE Lighting, Wacol, Queensland, Australia) and (b) light-emitting diode (LED) 4000 K color temperature high bay lamp (LUXEON M, LXR7-SW40; Koninklijke Philips, Amsterdam, The Netherlands). Emission spectra are normalized to the spectrum with the maximum intensity and were kindly provided by each manufacturer.

coated by a single yellow, or multiple yellow-green, phosphor coatings that absorb blue light and reemit longer wavelength emissions (Krames et al. 2007). The phosphor coating can be manipulated to produce a range of white LEDs that differ in the proportion of blue (435–495 nm) wavelengths emitted. This range of white LEDs is normally referred to by their color temperature (degrees Kelvin [K]) with higher temperatures having a greater proportion of emitted blue light. Given the peak UV, blue, and green photoreceptors of many invertebrates (Briscoe and Chittka 2001), we hypothesize that low color temperature LED lights will have less ecological impact than high color temperature LED lights due to the lower intensity blue spectral emissions.

To test this hypothesis we first compared the relative attraction of flying invertebrates to 4000 K white LEDs and high-pressure sodium lamps at a scale equivalent to current industrial/municipal site-lighting practices. This comparison provided an assessment of the potential impact of white LEDs on nocturnal invertebrates if adopted for industrial and municipal lighting. We then compared the relative attraction of flying invertebrates to different color temperature white

LEDs at an experimental scale to identify opportunities for minimizing the ecological impact of white LED lighting. For both experiments we used the attraction of nocturnal flying invertebrates as a proxy measure of ecological impact.

METHODS

Data collection: Comparison of LED and HPS industrial-scale lighting

An industrial-scale lighting comparison of white LEDs and high-pressure sodium (HPS) lamps was conducted using five replicate pairs of 4000 K white LEDs and HPS lamps (see Appendix, Table 1). The key difference in the spectral composition of the LED and HPS lamps was that the LED had greater relative intensity from the blue-green portion of the spectra than the HPS lamp (Fig. 1). An A2-sized sheet of Perspex (Evonik Industries, Darmstadt, Germany) mounted 0.5 m below and directly between each pair of LED and HPS lamps was used to sample flying invertebrates attracted to the lights (see Appendix, Fig. 1). Each night, an A2-sized sheet of Tanglefoot-coated (Contech, Victoria, British Columbia, Canada) Mylar (Fuji Xerox, Connecticut, USA) was attached to both sides of the Perspex pane to snare flying invertebrates. Mylar sheets were identified as “facing” and “away,” depending on their orientation with respect to the location of the lamp that was activated on that particular night. Trapping was conducted between 21:00 and 00:00 on 10 suitable nights from 21 January and 3 February with each sampling location randomly assigned to either LED or HPS lighting on the first night. The active light in each pair was then alternated on subsequent nights. This resulted in a final design of five independent replicates (sampling locations) that compare the two light treatments that were sampled on 10 different nights. The 10 sampling occasions cannot be considered as truly independent, hence tests for the influence of repeated measures were performed (see *Analysis: Comparison of LED and HPS industrial-scale lighting*). Suitable nights were considered to be nights with a forecast air temperature at 21:00 of at least 15°C. Actual air temperature at 22:00 that was recorded at the study site at an elevation of 10 m was used for analyses (see *Analysis: Comparison of LED and HPS industrial-scale lighting*). All LED and HPS comparisons were conducted at the PanPac wood processing facility, Hawkes Bay, New Zealand. Pairs of lights were established on the edge of industrial buildings at the site. The site is bordered by an extensive *Pinus radiata* plantation forest to the west and by coastal grassland to the east with the ocean located <1 km to the east. Insects are known to disperse into the site from the forest as they are attracted by the bright site lighting.

Data collection: Comparison of LED color temperature

The attraction of flying invertebrates to white LEDs with six different color temperatures (see Appendix,

Table 1, Fig. 2) were compared to a control treatment (18-ohm resistor that matched the power consumption and heat output of the tested LEDs) in a completely randomized block design with three replicates (see Plate 1). Each of the three blocks consisted of a linear transect with seven sampling points located at 20-m intervals. Within each block, the six color treatments (and control) were initially assigned at random to one of the seven sampling points. On subsequent nights the individual color treatments were then rotated sequentially to account for any potentially confounding spatial effects that may have occurred due to the location of the sampling point along the transect within the block. LEDs were powered by 12-V DC batteries and the experiment was conducted over four hours each night (20:00 to 00:00) on seven non-consecutive days between 30 January and the 26 February 2013. Delays in sampling were due to periods of unsuitable weather when invertebrate flight activity was minimal.

LEDs were mounted in a heat sink housing (Makers-LED, Aimes, Iowa, USA) and the attraction of flying invertebrates to lights was quantified using A3 Perspex catching panes installed 30 cm in front of each LED. Tanglefoot-coated Mylar sheets were attached to the Perspex to sample flying invertebrates attracted to the light. Unimpeded light was visible to the sides of the Tanglefoot-coated Mylar sheets, however a portion of light emitted during the study did have to pass through the Mylar sheet, potentially altering the spectral composition. To test for this the spectral emission of LEDs with and without a Tanglefoot-coated Mylar sheet were compared (Fig. 2). This showed that there was some absorption of light in the 600+ nm wavelengths (red and infrared), but this change should not have biased our results, as most insects are not sensitive to changes in the far red portion of the spectra (Briscoe and Chittka 2001). In the highly attractive blue-green portion of the spectra, the Tanglefoot coated Mylar sheet did not impact the relative proportion of light emitted.

The input current of individual LEDs was adjusted (via a potentiometer attached to a LuxDrive BuckPuck Driver [LED Dynamics, Randolph, Vermont, USA]) to produce a uniform power output of 12 ± 1 mW (mean \pm SD) for each color temperature (see Appendix, Table 1). To measure power output for calibration the emission from individual LEDs was collimated using a 25.4 mm focal length 1-inch diameter (1 inch = 2.54 cm) lens that was focused on a Coherent J-50MB-HE thermopile sensor (Coherent, Santa Clara, California, USA). Power output was averaged over 10-s intervals, using a Coherent FieldMaxII-TO.

All LED color temperature trials were conducted on the boundary of the Synlait facility, Rakaia, Christchurch, New Zealand. Each of the three independent blocks was established on areas of long grass (intermittently mown) or gravel. The area is surrounded by introduced exotic pastoral grass with shelter belts of *Pinus radiata*. There are

TABLE 1. Results of the optimal linear mixed-effects model results for standardized invertebrates catches at lights equipped with light-emitting diode (LED) or high-pressure sodium (HPS) lamps.

Parameter	Estimate	SE	df	<i>t</i>	<i>P</i>
Intercept	21.65	2.77	50	7.81	<0.001
Light	-8.55	2.55	42	-3.35	0.002
Temp	5.61	0.99	42	5.67	<0.001
Light \times temp	-2.53	1.10	42	-2.30	0.027

Notes: Sample size $n = 5$ blocks. Abbreviations are light, light type; temp, air temperature; and wind, wind speed.

no substantial areas of non-productive ecosystems in the immediate vicinity of the site.

Analysis: Comparison of LED and HPS industrial-scale lighting

Total number of flying invertebrates (pooling panes that were “facing” and “away”) were standardized by the nightly trapping duration to account for the variation in trapping times ranging from 3.7 to 4.2 hours. This standardization procedure changed the scale of the response variables from a discrete to a continuous scale and thus allowed the use of linear mixed effects models (R package nlme [Pinheiro et al. 2014]). The fixed term of the model contained light type, air temperature, wind speed, and their interactions as explanatory variables. Trapping date nested in light type and sampling location were modeled as random terms to account for the hierarchical design and repeated measures. Plots of the standardized residuals vs. fitted values and for each of the explanatory variables were used for graphical model validation. The validation plots indicated heteroscedasticity, which was modeled using a power variance structure that incorporated the fitted values as a variance covariate and light type as grouping variable (i.e., allowing for stratified variance modelling). The significance of the fixed model terms was assessed via backward selection using likelihood ratio tests (Zuur et al. 2009). The final models showed high correlation between the intercept and the slopes of the fixed factors. To overcome this issue the models were refitted using centered air temperature and wind speed values.

Analysis: Comparison of LED color temperature

We applied generalized linear mixed models (GLMM) with Poisson errors and log link fit by Laplace approximation (R package lme4 [Bates et al. 2014]) to analyze the trap catch data. The total number of flying invertebrates caught per trap was compared against color temperature, location (sampling point within transect), and their interaction as fixed terms within the model. Block and trapping date were modeled as random effects. Overdispersion was detected (ratio of residual deviance to residual degrees of freedom > 1) and accounted for by incorporating a per-observation-

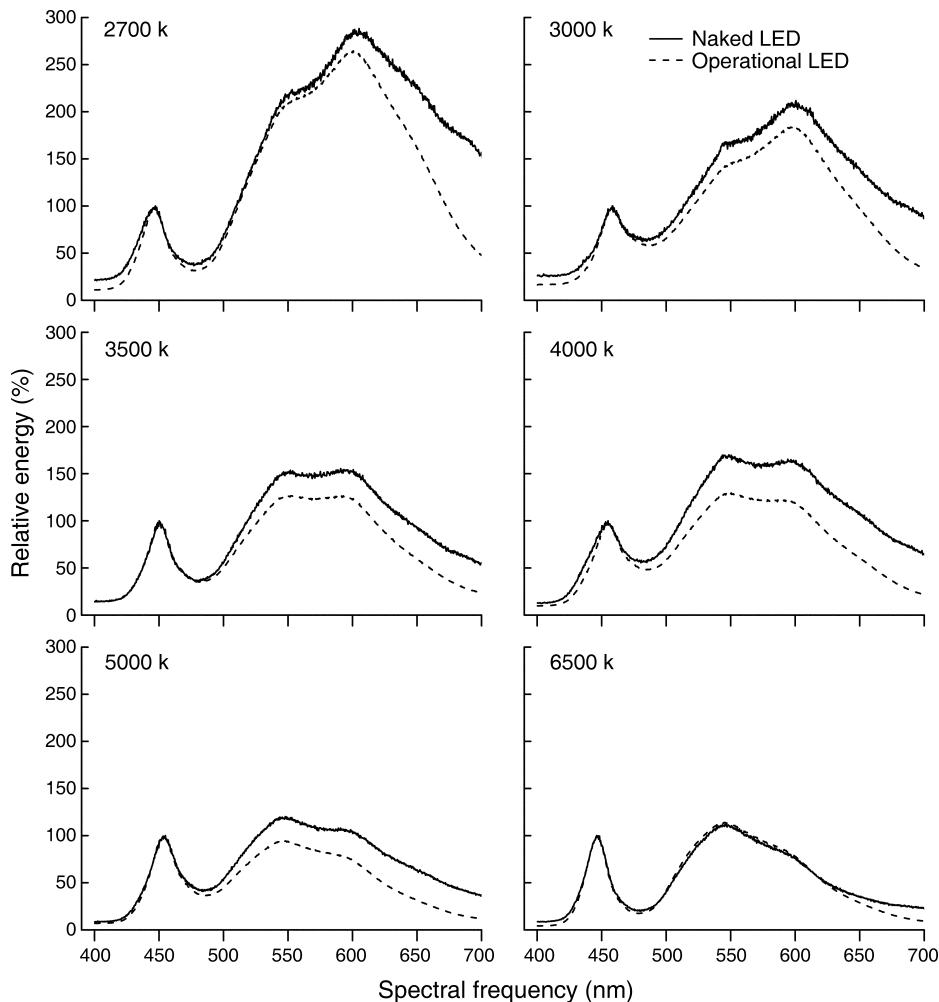


FIG. 2. Relative spectral emission of “white” LED of differing color temperatures. Emission spectra were measured using an OceanOptics USB2000 fiber-coupled spectrometer (Ocean Optics, Dunedin, Florida, USA) with an integration time of 100 ms. Emission spectra are normalized to the maximum spectral intensity in the 400–500 nm range, as insects are most attracted to this portion of the visible spectrum. The shape and form of the curve in the blue-green region is almost identical between naked LEDs and operational LEDs where measurements were taken behind the Perspex and Tanglefoot-coated Mylar.

level random effect. The GLMM was followed by a multiple comparison test using Tukey contrasts to allow pairwise comparisons between color temperatures (R package multcomp [Hothorn et al. 2008]). Plots of the Pearson residuals vs. fitted values and against the response variable(s) were applied for graphical model validation. The significance of the fixed model terms was assessed via backward selection using Akaike’s information criterion (AIC; Zuur et al. 2009). The AIC was favored over the likelihood ratio test, as used for the comparison between LED and HPS lamps (see *Analysis: Comparison of LED and HPS industrial-scale lighting*). Our rationale for using the AIC is that it includes a penalty for the number of parameters, which discourages over-fitting of the model (in this case 36 parameters were associated with the color temperature \times location interaction term). When $\Delta\text{AIC} \leq 2$, we considered the

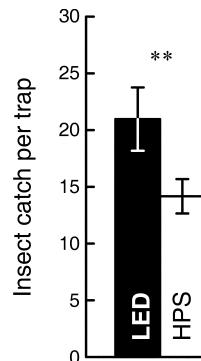


FIG. 3. Number of flying invertebrates (standardized by the 3.7–4.2 h trapping duration) caught in light traps equipped with LED or HPS light. Values are means \pm SE, $n = 5$ replicates. ** $P < 0.01$.



PLATE 1. Image showing one experimental block with five of the six different color temperature LEDs. Note the dark spot between the 4th and 5th light as the location of the just visible control treatment. The 6th color temperature is not visible and is to the left of the image. Individual lights were placed 20 m apart with different blocks placed 200 m apart. Photo credit: S. M. Pawson, Scion.

competitive models to provide similar goodness of fits and opted for the model with fewer parameters. Standardization of trapping times was not required for the comparison of color temperatures as the sample duration varied by less than 10 minutes between treatments. All analyses were conducted in R version 2.15.3 (R Development Core Team 2013).

RESULTS

Comparison of LED and HPS industrial-scale lighting

In total 7300 invertebrates were caught including, 3811 Diptera, 1376 Trichoptera, 994 Coleoptera, 409 Hymenoptera, 308 Hemiptera, 173 Ephemeroptera, 111 Psocidae, and less than 100 Lepidoptera, Neuroptera, Thysanoptera, Araneae, Plecoptera, Isoptera, Orthoptera, and Blattodea. Sampling panes equipped with LED lamps attracted 48% more flying invertebrates on average than HPS lamps (Fig. 3, Table 1). Insect attraction to light was significantly affected by air temperature (Table 1), we observed a precipitous decline in catch numbers during a single night when air temperatures were favorable for flight ($\sim 20^{\circ}\text{C}$). This coincided with a strong easterly wind blowing from the ocean. The prevailing wind directions at the study site were from west and southwest suggesting that flying invertebrates from nearby forested land

would have to fly into a headwind to reach the experimental site.

Comparison of LED color temperatures

In total 12 860 invertebrates were caught, including 8879 Diptera, 1674 Lepidoptera, 1089 Thysanoptera, 450 Coleoptera, 379 Hymenoptera, 144 Neuroptera, and <100 Hemiptera, Psocoptera, Trichoptera, Araneae, Ephemeroptera, Collembola, and Mantodea (in decreasing order of abundance). When considering the pooled catch of all flying invertebrate taxa (removing Araneae, Collembola, and Acarina) LED lamps attracted significantly more flying invertebrates than control traps irrespective of color temperature (Fig. 4, Table 2). However, the difference between control and LED lamps was taxon dependent, strong effects were observed in Diptera and Lepidoptera and no effect observed for Thysanoptera, Hymenoptera, and Coleoptera (Fig. 4). Irrespective of taxa, the LED color temperature had no significant effect on invertebrate attraction (Fig. 4).

DISCUSSION

Light pollution is recognized as a global threat to the conservation of biological diversity that could drive reductions in the quality of provisioning, regulating and

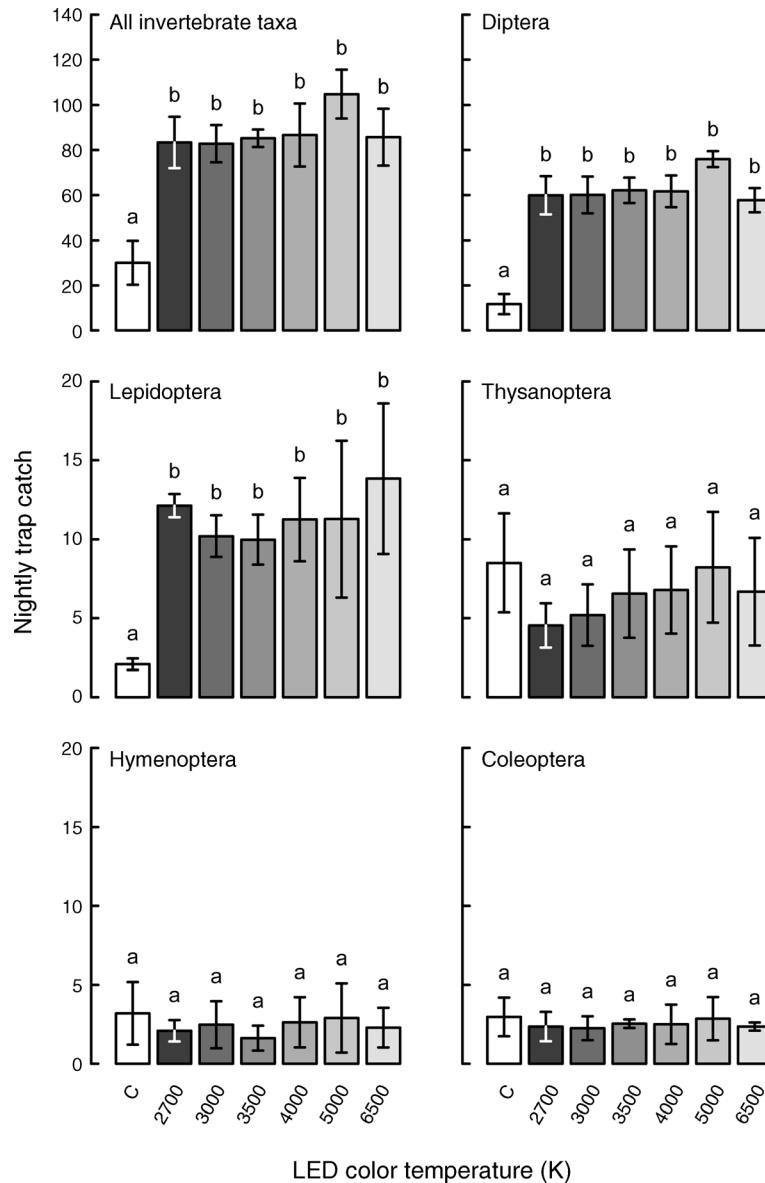


FIG. 4. Effect of LED color temperature on flying invertebrates trap catch over a 4-h sampling period; C is the control trap, values below the bars indicate the color temperature in Kelvin ($n = 3$ blocks, values are means \pm SE). Different lower case letters indicate statistically significant differences at $\alpha = 0.05$ (multiple comparison procedure using Tukey contrasts).

cultural ecosystem services (Hölker et al. 2010b). There is increasing evidence that existing light pollution has significant ecological effects (Rich and Longcore 2005, Gaston et al. 2012, 2013, Perkin et al. 2014). However, the spatial extent, density, and spectral composition of light pollution is predicted to change (Gaston et al. 2012). Continued urban expansion will result in a concomitant encroachment of light pollution into areas that are currently naturally lit, however, spectral changes may alter the type of impacts that these new areas experience, e.g., changed species interactions (Davies et al. 2013).

TABLE 2. Results of a backward selection applied to the generalized linear mixed effects model for LED color temperature and trap position.

Dropped term	AIC
None	608.69
Color temperature \times location	595.11
Color temperature	658.01
Location†	587.52

Notes: AIC stands for Akaike's information criterion.

† The most parsimonious model, which only contained LED color temperature as explanatory variable (i.e., the model with the interaction term and the factor location dropped).

White LED lighting for both municipal and industrial applications is predicted to increase dramatically in the next decade (Anonymous 2012). Gaston et al. (2012) have referred to this anticipated shift from high-pressure sodium (HPS) lights to LEDs, as the formation of a “white-light night.” Our results suggest that a white-light night shift could significantly increase the ecological impacts of light pollution as white LEDs attracted 48% more flying invertebrates than existing HPS lamps. Our study only accounts for the absolute loss of individuals from the population of nocturnal flying invertebrates attracted to LED lights. However, the true extent of white LED light pollution will require an assessment of ecological effects across multiple ecological levels, e.g., species, populations, and communities to address varying complexity in the potential interactions (as suggested by Fox [2013]). In addition further research is required to understand the landscape-scale influence of LED lights at broader spatial scales. As discussed by Davies et al. (2013), light pollution may affect visually guided behaviors of both individuals and of interactions between species or ecological guilds, e.g., predator avoidance and/or prey detection, navigation, pollination, and foraging, may be influenced by light pollution. However, the magnitude of such potential effects may prove to be dependent on both habitat structure (e.g., forest canopy vs. open grassland) and the spatial arrangement of habitat.

Manipulating LED color temperature is one potential intervention that could minimize the ecological impacts of white LEDs as it reduces the intensity of blue spectral emissions that are attractive to invertebrates. However, our results show that the attraction of nocturnal flying invertebrates to currently available phosphor coated white LEDs does not vary with LED color temperature. This effect was strongly observed in Diptera and Lepidoptera as they were the most numerous taxa attracted to the LEDs (Fig. 4). However, there was no observed effect of white LED lights for Hymenoptera, Thysanoptera, and Coleoptera. Given the low sample size for these three taxonomic groups it is difficult to draw absolute conclusions as these individuals may represent accidental by-catch in the hour before dusk that it took to install the sticky sheets, as opposed to actual nocturnal flight activity.

Our general finding for all taxa (Fig. 4) is contrary to our initial hypotheses, and implies that careful selection of currently available off-the-shelf color temperatures is unlikely to mitigate the potential ecological impacts of a broad-scale shift to white LED lighting for municipal and industrial applications. One potential explanation for this is that current low color temperature white LEDs still emit a proportion of blue-green spectra (Fig. 2). It may be possible to overcome this issue using longpass optical filters, or alternatively by selecting specific monochromatic LEDs (with narrow spectral wavelengths) that avoid the highly attractive blue-green spectra, however this has yet to be tested.

In addition to their direct ecological impacts light pollution from white LEDs is likely to exacerbate existing domestic, e.g., midge swarms and industrial infestations of sanitary and phytosanitary pests that are known to be highly attractive to white lighting (Pawson et al. 2009, Goretti et al. 2011). The potential nuisance impact of such unwanted domestic pest species is an additional factor that should be considered in the selection of municipal lighting. However, more important is the potential for white LED lighting to increase phytosanitary and biosecurity risks that could lead to additional indirect ecological impacts. For example, white light is more attractive than light emitted from HPS lamps to gypsy moth (*Lymantria dispar*); an invasive, polyphagous, forest pest (Walliner et al. 1995). The potential ecological impacts from the establishment of gypsy moth in new regions are severe, e.g., defoliation affecting productivity (Sharov et al. 2002) and local extinction of other Lepidoptera (Wagner and Van Driesche 2010), and ships infested with egg masses are a known pathway that is actively monitored by a number of countries, including Australia and New Zealand (MacLellan 2011). Thus a transition to white LEDs at, or near, ports may elevate the risk of egg masses moving on a transoceanic pathway, which potentially increases the risk of establishment in new regions.

Although we have shown that the color temperature of existing yellow phosphor white LEDs cannot be used to reduce their ecological impact on flying invertebrates, other options may reduce the effects of white LEDs in the future. Gaston et al. (2012) highlight the potential of white LEDs derived from a combination of monochromatic LED light sources, e.g., red, blue, and green, that together would form a white light. This may provide greater ability to avoid certain spectral emissions to reduce the effects of light pollution. However, before multiple primary LEDs (e.g., RGB emitters) can become a reality for large-scale illumination there are significant technological breakthroughs required for both green and red LEDs (Krames et al. 2007). Alternatively, longpass filters could be used to remove specific spectral emissions as was previously suggested to reduce the attractiveness of mercury vapor and high-pressure sodium lamps to particular pest species (e.g., gypsy moth; Walliner et al. 1995). Practically such filters may have limitations as they would significantly alter color rendering and may increase per unit costs and energy consumption per unit of light emitted.

CONCLUSION

Phosphor-coated white LED lamps have the potential to increase the impacts of light pollution dramatically. Given the strong impetus for their adoption in municipal and industrial applications, it is imperative to fully understand the potential long-term impacts of white LED lights on ecological communities, populations, and species. A comprehensive assessment of overall impacts and knowledge about the influence of each region of the visible spectrum will allow technologists to work with

ecologists to focus future developments in lighting technology that balance the needs of illumination with reduced ecological impact.

ACKNOWLEDGMENTS

The authors acknowledge Paul Fielder and Zachary Tremer from LED Dynamics for advice on LED binning and the supply of specific LED components. Rob Eagle of PanPac and Simon Causer of Synlait milk products for access to their respective facilities to conduct experiments. Sebastian Horvath for the analysis of LED spectral frequencies and the calibration of power output from different color temperature LEDs. Jess Kerr, Brooke O'Connor, Liam Wright, Tia Uaea, Thornton Campbell, Krystal Jansen, and Arild Roberts for the establishment of field trial sites and Sarah Cross for assistance in identifying and counting insect samples.

LITERATURE CITED

- Anonymous. 2012. Lighting the way: perspectives on the global lighting market. Second edition. McKinsey and Company, New York, New York, USA.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Bogard, P. 2013. The end of night: searching for natural darkness in an age of artificial light. Little, Brown and Company, New York, New York, USA.
- Briscoe, A. D., and L. Chittka. 2001. The evolution of color vision in insects. *Annual Review of Entomology* 46:471–510.
- Davies, T. W., J. Bennie, and K. J. Gaston. 2012. Street lighting changes the composition of invertebrate communities. *Biology Letters* 8:764–767.
- Davies, T. W., J. Bennie, R. Inger, N. H. de Ibarra, and K. J. Gaston. 2013. Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? *Global Change Biology* 19:1417–1423.
- Fox, R. 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* 6:5–19.
- Gaston, K. J., J. Bennie, T. W. Davies, and J. Hopkins. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological Reviews* 88(4):912–927.
- Gaston, K. J., T. W. Davies, J. Bennie, and J. Hopkins. 2012. Review: reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology* 49:1256–1266.
- Goretto, E., A. Coletti, A. Di Veroli, A. M. Di Giulio, and E. Gaino. 2011. Artificial light device for attracting pestiferous chironomids (Diptera): a case study at Lake Trasimeno (Central Italy). *Italian Journal of Zoology* 78:336–342.
- Hölker, F., et al. 2010a. The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society* 15(4):13.
- Hölker, F., C. Wolter, E. K. Perkin, and K. Tockner. 2010b. Light pollution as a biodiversity threat. *Trends in Ecology and Evolution* 25:681–682.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50(3):346–363.
- Krames, M. R., O. B. Shchekin, R. Mueller-Mach, G. O. Mueller, L. Zhou, G. Harbers, and M. G. Craford. 2007. Status and future of high-power light-emitting diodes for solid-state lighting. *IEEE/OSA Journal of Display Technology* 3:160–175.
- Le Tallec, T., M. Perret, and M. Théry. 2013. Light pollution modifies the expression of daily rhythms and behavior patterns in a nocturnal primate. *PLoS ONE* 8:e79250.
- Longcore, T., and C. Rich. 2004. Ecological light pollution. *Frontiers in Ecology and the Environment* 2:191–198.
- MacLellan, R. 2011. Gypsy moth surveillance in New Zealand. *Surveillance* 38:49–50.
- Pawson, S. M., M. S. Watt, and E. G. Brockerhoff. 2009. Using differential responses to light spectra as a monitoring and control tool for *Arhopalus ferus* (Coleoptera: Cerambycidae) and other exotic wood boring pests. *Journal of Economic Entomology* 102:79–85.
- Perkin, E. K., F. Hölker, and K. Tockner. 2014. The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshwater Biology* 59:368–377.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-117. <http://CRAN.R-project.org/package=nlme>
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rich, C., and T. Longcore, editors. 2005. Ecological consequences of artificial night lighting. Island Press, Washington, D.C., USA.
- Schubert, E. F., and J. K. Kim. 2005. Solid-state light sources getting smart. *Science* 308:1274–1278.
- Sharov, A. A., D. Leonard, A. M. Liebhold, E. A. Roberts, and W. Dickerson. 2002. “Slow the Spread”: a national program to contain the gypsy moth. *Journal of Forestry* 100:30–35.
- Stone, E. L., G. Jones, and S. Harris. 2012. Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology* 18:2458–2465.
- van Langevelde, F., J. A. Ettema, M. Donners, M. F. Wallis-DeVries, and D. Groenendijk. 2011. Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation* 144:2274–2281.
- Wagner, D. L., and R. G. Van Driesche. 2010. Threats posed to rare or endangered insects by invasions of nonnative species. *Annual Review of Entomology* 55:547–568.
- Walliner, W. E., L. M. Humble, R. E. Levin, Y. N. Baranchikov, and R. T. Carde. 1995. Response of adult lymantriid moths to illumination devices in the Russian far east. *Journal of Economic Entomology* 88:337–342.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Appendix

Photos of experimental setup and specifications of light-emitting diode (LED) and high-pressure sodium vapor (HPS) lamps used for all studies (*Ecological Archives* A024-191-A1).

Supplement

Raw invertebrate data of LED color comparison and LED vs. HPS comparison (*Ecological Archives* A024-191-S1).