THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 338–344
DOI: 10.1650/CONDOR-15-136.1

RESEARCH ARTICLE

Anthropogenic light is associated with increased vocal activity by nocturnally migrating birds

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Submitted August 11, 2015; Accepted February 6, 2016; Published April 13, 2016

ABSTRACT

Anthropogenic modifications to the natural environment have profound effects on wild animals, through structural changes to natural ecosystems as well as anthropogenic disturbances such as light and noise. For animals that migrate nocturnally, anthropogenic light can interfere with migration routes, flight altitudes, and social activities that accompany migration, such as acoustic communication. We investigated the effect of anthropogenic light on nocturnal migration of birds through the Great Lakes ecosystem. Specifically, we recorded the vocal activity of migrating birds and compared the number of nocturnal flight calls produced above rural areas with ground-level artificial lights compared to nearby areas without lights. We show that more nocturnal flight calls are detected over artificially lit areas. The median number of nocturnal flight calls recorded at sites with artificial lights (31 per night, interquartile range: 15–135) was 3 times higher than at nearby sites without artificial lights (11 per night, interquartile range: 4–39). By contrast, the number of species detected at lit and unlit sites did not differ significantly (artificially lit sites: 6.5 per night, interquartile range: 5.0–8.8; unlit sites: 4.5 per night, interquartile range: 2.0–7.0). We conclude that artificial lighting changes the behavior of nocturnally migrating birds. The increased detections could be a result of ground-level light sources altering bird behavior during migration. For example, birds might have changed their migratory route to pass over lit areas, flown at lower altitudes over lit areas, increased their calling rate over lit areas, or remained longer over lit areas. Our results for ground-level lights correspond to previous findings demonstrating that migratory birds are influenced by lights on tall structures.

Keywords: anthropogenic light, birds, light pollution, migration, night flight calls, nocturnal flight calls

La luz antropogénica está asociada a un incremento en la actividad vocal de las aves migratorias nocturnas

RESUMEN

Las modificaciones antropogénicas de los ambientes naturales tienen efectos profundos en los animales silvestres, tanto a través de cambios estructurales en los ecosistemas naturales como de disturbios antropogénicos como la luz y el ruido. Para los animales que migran de noche, la luz antropogénica puede interferir con las rutas migratorias, las alturas de vuelo y las actividades sociales que acompañan la migración, como la comunicación acústica. Investigamos el efecto de la luz antropogénica en la migración nocturna de las aves a través del ecosistema de los Grandes Lagos. Específicamente, registramos la actividad vocal de las aves migratorias y comparamos el número de llamados nocturnos en vuelo producidos sobre áreas rurales con luces artificiales a nivel del piso comparado con áreas vecinas sin luces. Mostramos que se detectan más llamados nocturnos en vuelo sobre áreas artificialmente iluminadas. La mediana de llamados nocturnos en vuelo registrada en los sitios con luces artificiales (31 por noche; rango inter-cuartil: 15–135) fue tres veces más alta que en sitios vecinos sin luces artificiales (11 por noche; rango inter-cuartil: 4–39). En contraste, el número de especies detectadas en sitios iluminados y no iluminados no difirió significativamente (sitios iluminados artificialmente: 6.5 por noche; rango inter-cuartil: 5.0–8.8; sitios no iluminados: 4.5 por noche; rango inter-cuartil 2.0–7.0). Concluimos que la iluminación artificial cambia el comportamiento de las aves migratorias nocturnas. El aumento de detecciones podría relacionarse con la presencia de fuentes de iluminación a nivel del piso que alteran el comportamiento de las aves durante la migración. Por ejemplo, las aves pueden haber cambiado su ruta migratoria para pasar sobre áreas iluminadas, volar a menor altitud sobre áreas iluminadas, aumentar su tasa de llamado sobre áreas iluminadas o permanecer por más tiempo sobre áreas iluminadas. Nuestros resultados para las luces a nivel del suelo coinciden con estudios previos que demuestran que las aves migratorias son influenciadas por luces montadas sobre estructuras elevadas.

Palabras clave: aves, llamadas de noche en vuelo, llamadas nocturnas en vuelo, luces antropogénicas, migración, polución lumínica

INTRODUCTION

Anthropogenic light has detrimental effects on diverse animal taxa (Longcore and Rich 2004, Davies et al. 2014). For example, lights mounted atop communication towers, lighthouses, wind turbines, oil platforms, and skyscrapers attract nocturnally migrating birds, resulting in fatal collisions; these collisions contribute to hundreds of millions of birds deaths annually in the United States (Wiese et al. 2001, Hüppop et al. 2006, Gehring et al. 2009, Horváth et al. 2009, Loss et al. 2014). In addition, tall, lit structures disorient birds (Cochran and Graber 1958, Jones and Francis 2003, Longcore and Rich 2004), which can cause them to expend additional energy during migration. Migratory birds rely in part on celestial cues for orientation (Wiltschko and Wiltschko 1996), and birds may become disoriented when anthropogenic light alters the perceived horizon (Herbert 1970). Different types of lights may minimize the effect of artificial lighting (Evans et al. 2007, Poot et al. 2008, Doppler et al. 2015), but such bird-friendly lighting is not widespread.

A growing body of research reveals the disruptive effects that anthropogenic lights atop tall structures have on migratory birds (Wiese et al. 2001, Longcore and Rich 2004, Hüppop et al. 2006, Gehring et al. 2009). Most anthropogenic lights, however, are at ground level, and little research exists on the influence of ground-level lights on migratory birds (although see Evans et al. 2007). Ground-level anthropogenic lights influence other aspects of avian behavior, such as the timing of nest initiation, the timing of the dawn chorus, and the frequency of extra-pair copulations (Kempenaers et al. 2010). Whether widespread ground-level lighting influences migratory behavior of birds has received little attention, even though most migratory birds pass over countless anthropogenic lights during both spring and fall migrations.

By monitoring nocturnally migrating birds, we can evaluate the effects of anthropogenic light on migratory behavior (Evans et al. 2007, Farnsworth and Russell 2007, Hüppop and Hilgerloh 2012). Different technologies can be used to track migrants and study their responses to anthropogenic disturbance. Radar technology facilitates measurements of the size, speed, and orientation of migratory bird flocks (Diehl et al. 2003, Gauthreaux and Belser 2003, Gagnon et al. 2010) but cannot resolve individual birds or the species composition of migratory flocks (Balcomb 1977). Bird banding offers the ability to study individual birds but does not sample migrants during active migration. Acoustic monitoring of the vocalizations produced by migratory birds is a promising technique because it does not suffer from either of these limitations (Farnsworth 2005). Many nocturnally migrating birds produce nocturnal flight calls, which are short, high frequency calls that differ in acoustic structure across species or groups of species (Hamilton 1962, Lanzone et al. 2009). These calls facilitate species-specific research on actively migrating birds (Evans and Mellinger 1999, Evans and O'Brien 2002, Farnsworth 2007). Recent research has demonstrated that nocturnal flight call monitoring is a reliable method for measuring the timing of migration (Sanders and Mennill 2014a), the routes taken by birds (Sanders and Mennill 2014b), and the species composition of flocks (Smith et al. 2014). Although this technique is limited by its ability to detect only vocalizing animals, nocturnal flight call monitoring nevertheless offers an opportunity to explore the effects of anthropogenic disturbances, such as light, on the behavior of actively migrating birds across a wide range of species (Lanzone et al. 2009).

In this study, we assessed the effects of anthropogenic light on nocturnally migrating birds in the Great Lakes region, focusing on ground-level lights such as streetlamps and building lights. We compared the number of nocturnal flight calls produced by birds passing over artificially lit sites vs. nearby dark sites. Because anthropogenic light may attract and disorient migrating birds (Longcore and Rich 2004), we predicted that more nocturnal flight calls and more species of migrants would be detected over artificially lit sites compared to dark sites. Moreover, if the absolute light intensity influences the behavior of nocturnal migrants, we predicted a positive association between number of flight calls recorded and the light intensity across sites.

MATERIALS AND METHODS

We recorded nocturnal flight calls of migratory birds at 16 locations in Essex County, Ontario, Canada, in September and October 2013. Each location contained a "light site," which had a streetlight or building light nearby, and an adjacent "dark site," which had no artificial light nearby (Figure 1; location coordinates in Appendix Table 2). Light sources were broad-spectrum lights with either high pressure sodium (HPS) or light emitting diode (LED) bulbs. To avoid any confounding effects of urban noise, all sites were located in semi-rural areas, including parklands, naturalized areas, low-density residential areas, and small commercial properties. We did not measure background noise, but our recordings showed no evidence of background noise obscuring the birds' calls and no notable

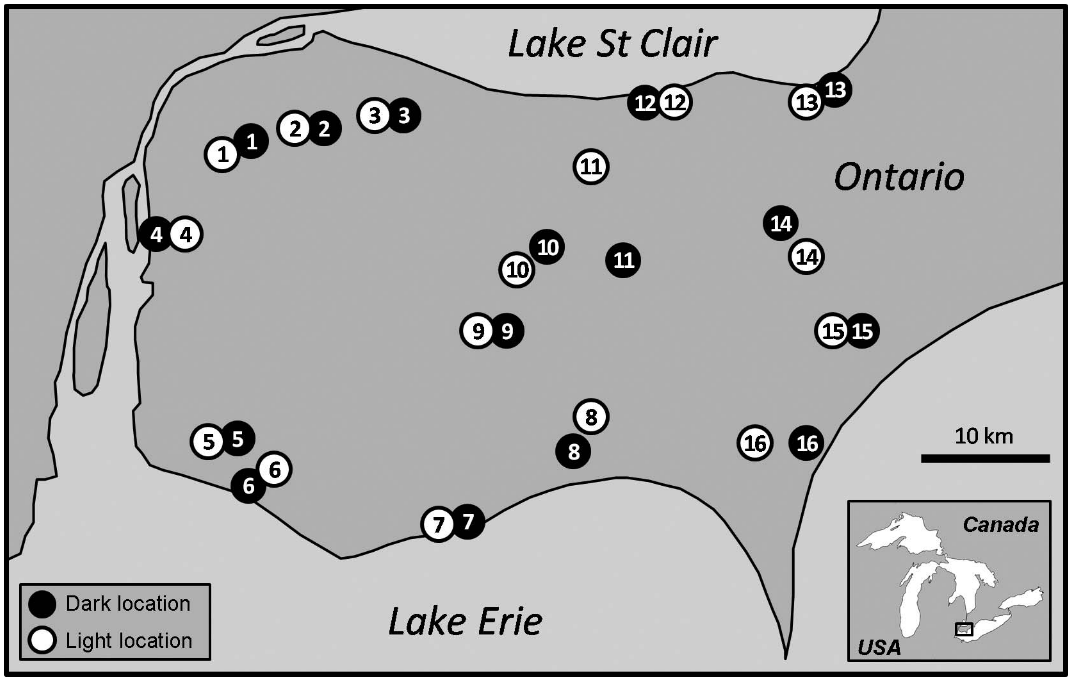

FIGURE 1. Study area with the 16 recording locations, each with an artificially lit site (white circles) and a dark site (black circles) in Essex County, Ontario, Canada. The inset map at lower right shows the location of the recording area within the Great Lakes.

differences in the acoustic profile of light sites vs. dark sites. The light and dark sites at each recording location were separated by 2.3 ± 1.0 km (mean ± SE; range: 0.1–14.9 km; Figure 1), and locations were separated from each other by 27.0 ± 1.1 km (mean ± SE; range: 4.6–54.1 km). Habitat conditions were matched as closely as possible within pairs of sites, and habitat similarity was determined by a visual estimation of canopy cover and the type and

TABLE 1. Nocturnal flight calls detected from different species or species groups at 16 light and 16 dark sites in the southern Great Lakes; the species and species group classification followed Sanders and Mennill (2014a).

	Number of sites		Number of calls	
Species or Species Group*	Light	Dark	Light	Dark
American Redstart (*Setophaga ruticilla*)	3	3	4	18
American Tree Sparrow (*Spizella arborea*)	2	1	9	2
Canada Warbler (*Cardellina canadensis*)	1	1	1	1
Gray-cheeked Thrush (*Catharus minimus*)	6	5	92	43
Hermit Thrush (*Catharus guttatus*)	1	0	1	0
Ovenbird (*Seiurus aurocapilla*)	1	0	1	0
Song Sparrow (Melospiza melodia) / Fox Sparrow (*Passerella iliaca*)*	8	5	76	30
Swainson's Thrush (*Catharus ustulatus*)	10	9	182	76
Veery (*Catharus fuscescens*)	4	2	11	4
White-throated Sparrow (*Zonotrichia albicollis*)	7	7	155	92
Wood Thrush (*Hylocichla mustelina*)	1	1	1	1
Double Downsweep *	14	10	129	133
Single Downsweep *	14	8	130	49
Upsweep *	16	13	285	124
Zeep complex *	15	9	142	88
Unidentified high frequency	3	1	21	2
Unidentified low frequency	1	1	9	1

* Species groups include multiple species that produce nocturnal flight calls with similar spectro-temporal characteristics, ranging from 2 species per category (the Song Sparrow/Fox Sparrow species group) to 9 per group (e.g., the Zeep complex includes 9 species of warbler, and the Upsweep category includes 7 species of warbler and 2 sparrows); details in Appendix 1 in Sanders and Mennill (2014).

density of surrounding vegetation. Light sites were typically on the edge of anthropogenic features such as roads and parking lots, whereas dark sites were often farther away from roads and parking lots.

We measured illumination at each recording site using a light meter (Extech Instruments EA31 Digital Light Meter). We collected illumination measurements within 3 hours after nautical sunset (i.e. when the geometric center of the sun is 12° below the horizon), recording 1 measurement every 30 seconds for 10 minutes and then calculating an average for each site from these measurements. We always measured light levels on the same night for each pair of sites, with only a short delay to travel between sites. We oriented the light meter sensor upward at a height of 1 m, at the exact location where the recording equipment was deployed. These light measurements confirmed that light sites were significantly brighter than dark sites (Wilcoxon signed-rank test: $W = 68$, $p < 0.0001$, $n = 16$ paired sites; site-specific light levels are reported in Appendix Table 2), with a median illuminance of 2.62 lux at our 16 light sites (range: 0.38–8.91 lux) vs. 0.03 lux at our 16 dark sites (range: 0.02 –0.10 lux). The light measurements at our light sites fall within the range of values observed for urban skyglow (0.15 lux), residential side street lights (5 lux), and lit parking lots (10 lux; Gaston et al. 2013).

We recorded nocturnal flight calls from migratory birds using automated digital recorders (Wildlife Acoustics SM2 Song Meters; 44,100 Hz sampling frequency; 16-bit accuracy in wave format; gain settings: 2.5 V bias on, 1,000 Hz high-pass filter on, 60 dB microphone preamplifier on). The weatherproof microphones (Wildlife Acoustics SMX-NFC) were attached by the manufacturer to the middle of a small plexiglass baffle to minimize recording sounds from below the baffle. We mounted microphones at a height of 3.0–4.5 m atop steel poles fastened to trees or posts by nylon straps. At all sites, we positioned the microphones to eliminate obstructions between the microphone and the sky. At the 16 light sites, we mounted our microphones within 1 to 5 m of the light source.

We followed an established protocol for identifying migrants based on recordings of their nocturnal flight calls (Sanders and Mennill 2014a). Recordings were scanned manually for calls and were then compared to spectrograms of calls from known species for identification. In some cases, the calls were distinctive at the species level, and in other cases, they were distinctive at the level of a group of species with similar calls (Sanders and Mennill 2014a,b). The number of species included in each species group varied from 2 (e.g., Song Sparrow [*Melospiza melodia*], and Fox Sparrow [*Passerella iliaca*] produce similar calls) to 9 (e.g., the Zeep complex includes 9 species of warbler, and the Upsweep category includes 7 species of warbler and 2 sparrows; details in Appendix 1 of Sanders and Mennill 2014a). We counted all calls recorded between nautical sunset and nautical sunrise (i.e. when the geometric center of the sun is 12° below the horizon); we chose to analyze this time interval to standardize across recordings the amount of time when natural light might interfere with anthropogenic light. For each pair of sites, we analyzed the same night of recording. We avoided nights when strong winds or rain produced noisy recordings, choosing the night with the lowest levels of background noise for our analysis of each pair of sites. We used 4 Song Meters and 4 microphones to collect the recordings and assigned the equipment at random to light and dark sites so that any variation in microphone sensitivity could not confound our analyses. Although 4 Song Meters were available, we usually recorded only 1 pair of sites on a given night. In one instance we recorded 2 pairs of sites on the same night (i.e. our recordings from the 16 pairs of sites come from 15 different nights).

We used generalized linear mixed models (package glmmADMB; Skaug et al. 2015) in R (R Core Team 2015) to study the relationship between light and migration behavior. Response variables included the number of nocturnal flight calls and the number of species detected, modeled with a negative binomial distribution with a log link function. Fixed effects included site type (artificial light vs. no artificial light) and light intensity (measured in lux). Location (1–16) and recording night (1–15) were included as random effects to control for nonindependence in our data. We present values as median values and interquartile ranges.

RESULTS

Across 16 recording locations, with each location containing an artificially lit site and a nearby dark site, we analyzed 352 hours of recordings (1 night per location), yielding 1913 nocturnal flight calls from 15 different species or species-groups.

We recorded a median of 31.0 calls per night at light sites (interquartile range: 15–135; range: 8–344) compared to a median of 10.5 calls per night at dark sites (interquartile range: 4–39; range: 0–192). Generalized linear mixed models revealed that significantly more nocturnal flight calls were recorded at sites with artificial lights than at sites without artificial lights (Figure 2A; main effect of site type: $z = 3.94$, $p < 0.001$, $n = 16$ locations with 2 sites per location, exp(coefficient [95% confidence interval]) = 3.8 [2.0–7.5]). Within both the light sites and dark sites, the number of calls detected did not covary with light intensity (main effect of light intensity: $z = -1.26$, $p = 0.210$, $n = 16$ locations with 2 sites per location, exp(coefficient) = 0.9 [0.8–1.1]).

We detected a median of 6.5 species or species-groups per night at light sites (interquartile range: 5.0–8.8; range:

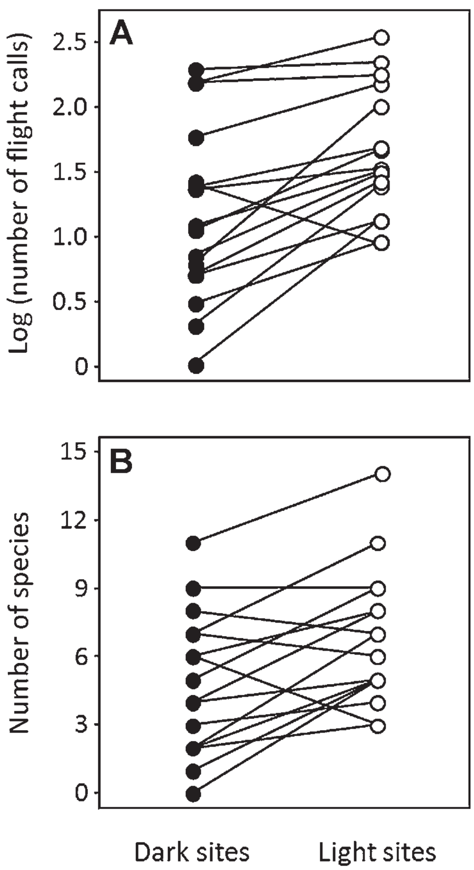

FIGURE 2. Paired comparisons of dark sites with no anthropogenic light (black circles) and nearby sites lit by ground-level anthropogenic lighting (white circles) reveal that **(A)** more nocturnal flight calls were detected over artificially lit sites, but **(B)** the number of species detected over lit and unlit sites did not differ statistically. Values show **(A)** total numbers of calls (values were $\log_{10}$-transformed to decrease clustering in the data) and **(B)** total number of species detected in one night of recording at each of 16 pairs of sites. Points connected by a line represent a light and dark site from the same general location.

3–14) vs. a median of 4.5 species or species-groups at dark sites (interquartile range: 2.0–7.0; range: 0–11). Generalized linear mixed models revealed no statistical difference in the number of species at sites with artificial lights compared to sites without artificial lights (Figure 2B; main effect of site type: $z = 1.60$, $p = 0.110$, $n = 16$ locations with 2 sites per location, exp(coefficient [95% confidence interval]) = 1.4 [0.9–2.1]). Within a given site type, the number of species detected did not covary with light intensity (main effect of light intensity: $z = 0.06$, $p = 0.950$, $n = 16$ locations with 2 sites per location, exp(coefficient) = 1.0 [0.9–1.1]).

A survey of the species and species groups detected at the light vs. dark sites showed that no particular species or species-group was systematically present or absent from dark or light sites (Table 1). Contingency table analysis confirmed that the frequencies of occurrence of each species were independent of site type (2×17 contingency table, Fisher's exact test: $p > 0.999$; Table 1).

DISCUSSION

Along the busy migratory flyway surrounded by the Great Lakes, we detected more nocturnal flight calls from migrating birds passing over sites with street-level anthropogenic lights compared to nearby dark sites. One explanation for our findings is that ground-level anthropogenic light disorients migrating birds, leading to higher calling rates at sites with artificial lights. Nocturnal migrants often move together in flocks (Larkin and Szafoni 2008). Within these flocks, nocturnal flight calls may allow birds to maintain contact with other individuals, or they may aid in orientation by maintaining flock cohesion and flight direction (Hamilton 1962). Given that anthropogenic light has been shown to disorient nocturnal migrants (Herbert 1970, Horváth et al. 2009), the observed increase in calls could reflect the birds' need for more orientation signals when passing over well-lit areas. The disorientation could cause birds to lower their altitude, bringing more birds within the range of our recorders, or it could cause them to remain in the well-lit recording areas for longer periods, leading to an increased rate of detection.

Another possible explanation for our results is that anthropogenic light attracts migrating birds, giving rise to higher calling rates at sites with ground-level anthropogenic lights. Many species of birds are attracted to sources of anthropogenic light on communication towers, lighthouses, and oil platforms, often leading to fatal collisions (Cochran and Graber 1958, Wiese et al. 2001, Jones and Francis 2003). If birds are also attracted to street-level lights, either by changing their course or by lowering their altitude, then this phenomenon could produce the observed increase in the number of calls detected. Both attraction and disorientation due to anthropogenic light may occur in concert to explain our findings. These alternatives could be explored through future studies that combine nocturnal flight call monitoring with radar tracking to evaluate whether birds change course or altitude when passing over sites with street-level anthropogenic lighting.

Although we detected more flight calls above artificially lit vs. dark sites, our analyses did not detect a relationship between light intensity and the number of calls or the number of species detected. This pattern held true within the 16 artificially lit sites but also within the 16 unlit sites. This finding suggests that artificial light has a categorical effect on migrating birds, although we note that our study did not include light intensities intermediate to those found at lit and unlit sites or brighter than 8.9 lux at our brightest site. A future study could use a variable light source, as pioneered by Evans et al. (2007), to monitor the number of calls and the number of species detected at the same site at multiple light intensities, which could range from those intermediate between our light and dark sites to much brighter intensities to mimic passing over a city.

Our results are consistent with the idea that ground-level anthropogenic lights affect nocturnally migrating birds, but do not reveal the underlying mechanism. Artificial lights could drive migratory birds to fly at unusual altitudes, to follow circuitous migration paths, to circle above well-lit areas, or to call at higher rates. Whichever of these explanations is correct, artificial lights seem to lead birds to migrate inefficiently, increasing the energetic demands or time requirements for migration, which in turn may decrease the likelihood of individual birds surviving migration or influence the body condition of individuals arriving at the wintering or breeding grounds. These effects could have a negative impact on migratory birds, underscoring the importance of studying the consequences of anthropogenic modification of the natural environment.

Our results highlight the importance of selecting appropriate recording locations for future research involving nocturnal flight call recordings. Street-level anthropogenic light can substantially increase the number of calls detected through acoustic monitoring; therefore, future studies should avoid environmental biases in detecting migrants by measuring and controlling for anthropogenic light.

ACKNOWLEDGMENTS

We thank D. Ward for field assistance and C. Sanders and P. Pratt for logistical support. For property access, we thank the Essex Region Conservation Authority, Jack Miner Migratory Bird Foundation, Ojibway Prairie Conservation Preserve, Setteringtons Fertilizer, and private landowners M. and M. Phibbs, D. and M. Watson, D. and L. Armstrong, R. and M. Ward, D. and P. Nelner, J. Guyitt, G. and S. Guyitt, and Z. Gray. Two anonymous reviewers and the editors at The Condor: Ornithological Applications helped to improve the manuscript.
Funding statement: For financial support, we thank the Natural Sciences and Engineering Research Council of Canada (NSERC), the University of Windsor, and the Caldwell First Nation.
Author contributions: M.J.W., D.R.W. and D.J.M. conceived the idea, design, and experiment. M.J.W. collected the data. M.J.W., D.R.W. and D.J.M. wrote the paper. M.J.W., D.R.W. and D.J.M. developed or designed methods. M.J.W., D.R.W. and D.J.M. analyzed the data. M.J.W., D.R.W. and D.J.M. contributed substantial materials, resources, or funding.

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APPENDIX TABLE 2. Light levels (in lux) measured at paired light and dark sites in Essex County, Ontario, Canada.

Location	Light Level (lux) at Light Site	Light site (UTM)*	Light level (lux) at Dark Site	Dark site (UTM)*
Big Creek	0.45	0328741 | 4680998	0.03	0328897 | 4681434
Civic Centre	2.16	0336632 | 4680789	0.03	0336715 | 4680885
Comber	7.49	0344735 | 4683395	0.04	0344610 | 4683324
Devonwood	2.70	0326965 | 4673428	0.04	0326792 | 4673421
Hillman	1.10	0327559 | 4658644	0.03	0327643 | 4658585
Holiday Beach	2.54	0331571 | 4655466	0.02	0330718 | 4655312
Homestead	3.25	0346977 | 4650953	0.02	0346872 | 4650964
Lakeshore	0.50	0355155 | 4658547	0.04	0352615 | 4656560
Kingsville	3.44	0349304 | 4669190	0.02	0349371 | 4669107
Maidstone	4.24	0350956 | 4671075	0.02	0352353 | 4675088
McAuliffe	8.07	0358470 | 4682513	0.04	0361417 | 4667827
Ojibway	8.73	0367641 | 4684734	0.06	0367339 | 4684584
Petite Cote	0.47	0374853 | 4685039	0.03	0374674 | 4685003
Ruscom	0.38	0371998 | 4667925	0.03	0369788 | 4673876
Tremblay	1.44	0373432 | 4665667	0.03	0375099 | 4665714
Wheatley	8.91	0371122 | 4654537	0.10	0375051 | 4655286

* All Universal Transverse Mercator (UTM) coordinates are from UTM zone 17, latitude band T.

