

Response of night-migrating songbirds in cloud to colored and flashing light

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Figure 1. 1500W halogen test lights with blue and red filters used to study the impact of light upon migrating birds.

Abstract

Night-migrating birds often accumulate near bright man-made light on nights with low cloud cover or rain. Mass avian mortality events associated with this phenomenon have been documented for more than 150 years. Understanding the mechanism that induces the aggregation of migrants in lighted airspace could lead to a reduction in such mortality. Toward this end, we subjected night-migrating birds flying in dense cloud cover to alternating short periods of different artificial light characteristics. Bird aggregation occurred during periods of white, blue, and green light but not in red light or flashing white light. We discuss these results with respect to visual and magnetoreception-based aggregation theories and the phenomenon of light-induced bird mortality at tall television towers in North America.

Introduction

The nocturnal migration of birds evolved with only starlight and moonlight as consistent photon sources. It is known that some species utilize this subtle light for navigational aid. They use point sources of light in stellar arrays around the North Star for orienta-

tion on clear nights (Sauer 1957, Emlen 1967), and on cloudy nights they can orient by sensing the axial inclination of the earth's magnetic field through a light-dependent mechanism, probably residing in their eye (Wiltchko et al. 1993, Ritz et al. 2000, Ritz et al. 2004, Mouritsen et al. 2004, Möller et al. 2004, Thalau et al. 2005).

The groundswell of artificial lighting associated with modern human habitation has greatly altered the earth's nocturnal photic environment. Little is known about how this light affects migrants on clear nights, but birds have long been observed to aggregate in flight around isolated bright light sources during nights with low cloud ceiling or with light to moderate rain. The phenomenon was widely recognized at coastal lighthouses in western Europe and eastern North America in the nineteenth century. By the mid-twentieth century, artificial lighting was known to be a principal agent for causing large bird kills at airport ceillometers, tall television (TV) towers, smokestacks, and tall buildings in inland eastern North America (for a recent review, see Gauthreaux and Belser 2006).

In North America, aviation obstruction lighting on tall TV towers was documented to

cause bird aggregation behavior by Cochran and Graber (1958) and in a subsequent study by Avery et al. (1976). The towers in these studies had multiple tiers of slow flashing red beacons, each alternating with a tier of non-flashing red beacons in accordance with United States Federal Aviation Administration (FAA) regulations. By the 1970s, bird kills at such towers were widespread in eastern North America (Weir 1976, Avery et al. 1980), with annual mortality of more than 2000 birds per year at some towers (Banks 1979). One long-term study found more than 120,000 bird carcasses under a 300-m TV tower from 1957–1995 (Kemper 1996). This included 24 individual nights when more than 1000 birds were documented killed in the tower's vicinity (Kemper, pers. comm.). Such large nocturnal tower kills appear to be exclusively associated with low cloud cover or rain; under such conditions, a tower's aviation obstruction lights clearly induce aggregations of migrating birds (primarily species in the order Passeriformes). Most of the kills are believed to result when birds collide with a tower's supporting guy wires, the tower itself, or from mid-air collisions with other flying birds.

More than 30 years ago, Avery et al. (1976) called for field studies on the reactions of night-migrating birds to lights of various intensities, wavelengths, and flash rates as a means for increasing our understanding of bird aggregation at tall lighted towers. We report here on the first direct investigation of these artificial light variables for causing bird aggregation.

In October 2005, on five nights with steady bird migration and a cloud layer at ground level, we alternated periods of skyward-facing bright light of known spectrum and irradiance with periods of no light. Acoustic monitoring of avian flight-calls was used to indicate the presence or absence of flying birds during all light and dark periods. Visual observations of birds flying in the lighted space were made to verify bird aggregation during nonflashing light periods.

We concluded that a specific light type induced bird aggregation if periods of that light corresponded with strong acoustic and visual evidence for the presence of birds in at least four consecutive alternating cycles with a period of a different light type and/or a period of no light in which bird presence was not strongly documented. Good correspondence between the acoustic and visual data during nonflashing light periods gave us confidence in relying on the acoustic data for evaluating flashing light tests when we could not verify the presence or absence of birds visually.

We first documented that white light could be used to induce migrant bird aggregation. We then experimented with flashing white light, three different colors, and a combination of red incandescent beacons commonly used for marking aviation hazard on tall TV towers.

Materials and methods

Rationale for study method

To document whether bird aggregation is occurring in a given airspace subject to artificial light alterations, one needs some means to assess the quantity of birds flying in that airspace. Since the visually based studies by Cochran and Graber (1958) and Avery et al. (1976), four studies of bird flight behavior in the vicinity of TV towers with aviation obstruction lighting have been reported, each employing a different method. Larkin and Frase (1988) used tracking radar. Gauthreaux used a thermal imaging device, and Gauthreaux and Belser used an image intensifier (Gauthreaux and Belser 2006). Johnson (2005) used marine radar. The primary focus of these studies was on the flight behavior of birds, and whether it was linear, curved, or hovering. Though some documented passage

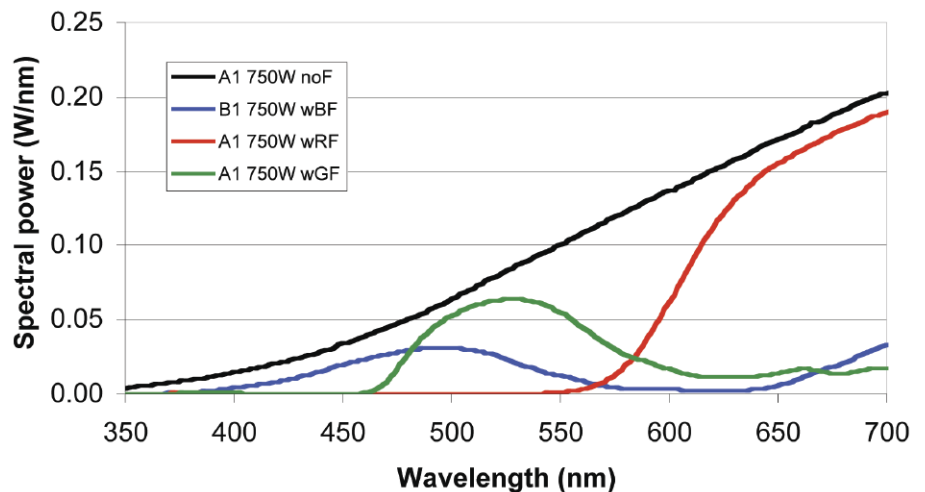


Figure 2. Spectral power distributions of radiation with and without filters used in this study. Measurements are for a single halogen lamp (750W; with UV filter). Filter codes: noF = no filter, wBF = blue filter, wRF = red filter, and wGF = green filter.

rate, quantification of flying birds involved in actual aggregation events was not reported. Because these studies were all carried out at tall TV towers, the lights involved in altering avian flight behavior were well above ground level. The birds studied were generally well above ground level but under a low cloud ceiling, not flying within cloud.

Our investigation aimed to study bird aggregation at a ground-based light source in dense cloud. This scenario presents unique challenges for trying to monitor systematically the quantity of birds in the airspace near the light. Many nocturnal migration studies have used marine radar in the surveillance mode to attempt to quantify a passage rate for targets proceeding directionally in migration. But this technique can have problems with echoes from ground clutter and in detecting very low-flying birds. Quantifying masses of birds in aggregation around artificial lights would be difficult with marine radar in the surveillance mode, and there is a potential problem of validating that the targets are birds. The use of flight speed as a criterion for distinguishing birds from insects may not be reliable during aggregation events.

When marine radar is used in the vertical mode, ground clutter can be eliminated, and low-flying birds can be detected. But in cases where birds are milling around in lighted airspace, quantitative resolution is greatly diminished due to the inability to track individual birds that may repeatedly pass through the radar beam. Counts are reduced to being merely target activity indicators.

Thermal imaging, image intensifier, and visual (in conjunction with a light source) techniques may allow one to distinguish more ac-

curately between birds, bats, and large insects, but operation is impeded by cloud and rain conditions that often accompany aggregation events. Similar to vertical beam radar, target counts during artificial light aggregation events can only be activity indicators due to individual birds flying in and out of the imaging zone.

Acoustic monitoring is notable for being capable of discerning strictly birds—and in many cases the species of birds—in nocturnal flight (Evans and O'Brien 2002), and this method is not impeded significantly by fog and light rain. But birds that do not call, and variable calling rates among individuals and species, confound quantitative estimates. Recent studies indicate that there is at least gross correlation between acoustic data from vocal birds and the density of targets in some locations at some times (Larkin et al. 2002; Evans, in prep). Two previous bird aggregation studies at TV towers found correspondence between flight-calling and the gross number of birds in the vicinity of a tower. Avery et al. (1976) used a ceilometer (spotlight) to count birds visually in aggregation around a tall TV tower in North Dakota. When skies began to clear, they noted that the number of birds seen and heard decreased sharply. In an all-night study of a tower kill phenomenon on 28 September 1960, Ogden and Munro noted gross correlation between flight-calling and birds dropping to the ground (Ogden 1960). They noted that periods when there was relatively low or no flight-calling corresponded with no birds falling to the ground, whereas periods of high calling rate corresponded with a steady rain of birds falling to the ground (Ogden 1960). Simply stated, calling

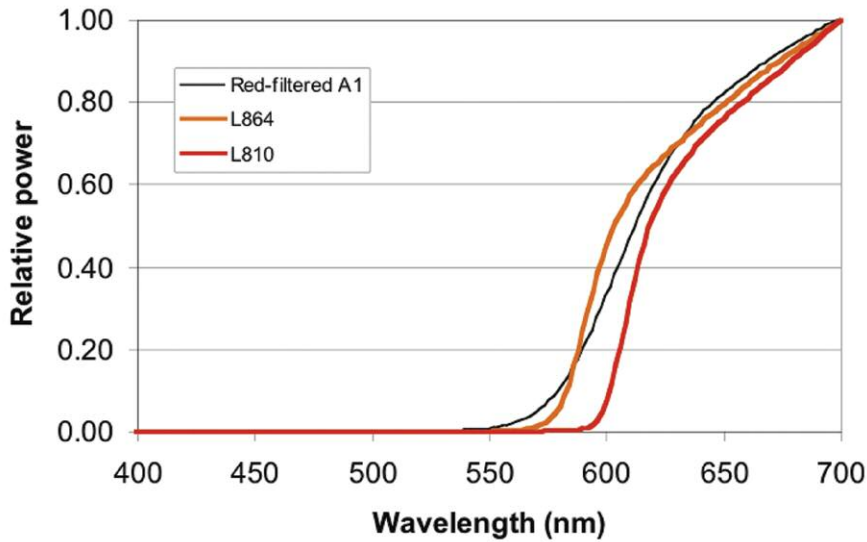


Figure 3. Relative spectral power of a red-filtered halogen luminaire, the large red flashing aviation beacon (L-864), and small red beacon (L-810).

indicates the presence of birds; no calling may or may not indicate the absence of birds. In cases where the species composition of a flight involves many that are known to give regular vocalizations in night flight, then the lack of calling very likely corresponds to a lack of birds given consistent environmental variables. In cases where the species composition is primarily of species that are not known to give regular vocalizations in night flight, then the lack of calling obviously would not correspond with a lack of birds.

There is no demonstrated way to count with accuracy birds flying in cloud or light rain during ground-based aggregation events in artificial light. All the currently practical methods are activity indicators, which provide only an index of abundance.

In this study, we used acoustic and visual methods as coarse activity indicators because of their ability to detect *birds* down to ground level. It was known from previous acoustic monitoring in the region that many species moving through our site during our study time would be vocal during nocturnal migration (Evans and O'Brien 2002; Bull 1998). In addition, both the acoustic and visual monitoring methods are inexpensive, which facilitates duplication and wider experimentation with this study technique.

Study site

Our study site was a lawn outside a rural residence 10 km south of Ithaca, Tompkins County, New York (42.335° N, 76.499° W). The site elevation was 503 m above sea level in hilly terrain near the northern edge of the

Appalachian/Allegheny Plateau. The terrain to the north and northwest was generally at lower elevation for more than 200 km. Terrain to the northeast was roughly the same altitude for 100 km except for several north-south running valleys. These specific geographic characteristics are noted because, with the low cloud ceiling, they could have caused channeling of migration as southbound migrants in the lower atmospheric stratum encountered an increase in terrain elevation (Evans, unpubl. data).

Light from three 60W incandescent lamps within the residence emanated from the residence windows to make a constant, weak light source throughout the study. Within a 5-km radius of the study site, there were several dozen rural residences with various internal lighting emanating from residence windows and some with outdoor lights typical of residences. There were no bright light sources associated with businesses, athletic fields, etc. within 5 km. Our study lights were the brightest source of skyward facing light within this radius. There was extensive brighter lighting associated with the city of Ithaca, 10 km to the north of our study site.

Study period, weather, moon phase, and magnetic environment

The study was carried out on five nights from October 8 through October 14, 2005. This time period corresponded with an "omega-blocking" pattern in the jet stream across eastern North America. Such patterns are characterized by slow-moving frontal systems at the surface. In this case, a cold front had

advanced slowly eastward during the first week of October and stalled as a weak frontal boundary along the Atlantic Coastal region during our study period. This weather pattern slowed bird migration in eastern-central North America in the first week of October, with no northerly winds to facilitate migration. After the slowly moving front passed our study site in central New York State during the day on October 8th, winds became steady from the north to northeast and favorable for migration. For a detailed account of the weather and associated bird migration during our study period, see Dinsmore and Farnsworth (2006) and a subsequent corrigendum (Brinkley 2006).

Accompanying these favorable migration winds was a broad area of low-altitude, solid (100%) cloud cover associated with the weather front and low pressure on the Atlantic coast. Cloud cover observations were made at our study site, and regional weather data, including hourly cloud cover, cloud ceiling height, and wind direction were obtained from the Ithaca airport, 16 km to the north of our study site. These data concurred with our visual observations that 100% cloud cover with a cloud ceiling at or below our study site elevation coincided with most of our study periods. In the five nights of our study, artificial light experimentation was carried out in 29 hourly periods. Twenty-five of these 29 hourly periods had cloud height measurements at the Ithaca airport corresponding to a cloud ceiling height of between 45 and 135 m below our study site. This suggests that birds during most of our study were flying well within the cloud layer.

The moon phase ranged from one day before first quarter (half moon) to three days after first quarter. Light from the moon was not visible to us during our study due to the dense cloud layer. Ambient light at ground level where the study lights were stationed was less than the measurement capability of our light meter (<0.01 lux) in all directions. This measurement included light emanating from the incandescent lamps within the residence, the nearest of which was 20 m away from the site.

Our study site was roughly 5 km west of the center of a 180-km, NNW-SSE running transect of total magnetic field strength measurements made by Lednor (1982). Total magnetic field strength in the region is around 56.0 microTesla with variations 9 km to the north and south of 50-300 nT. No major magnetic anomalies are known from the Ithaca area (C. Walcott, pers. comm.). The K-index to fluctuation in the earth's magnetic field for

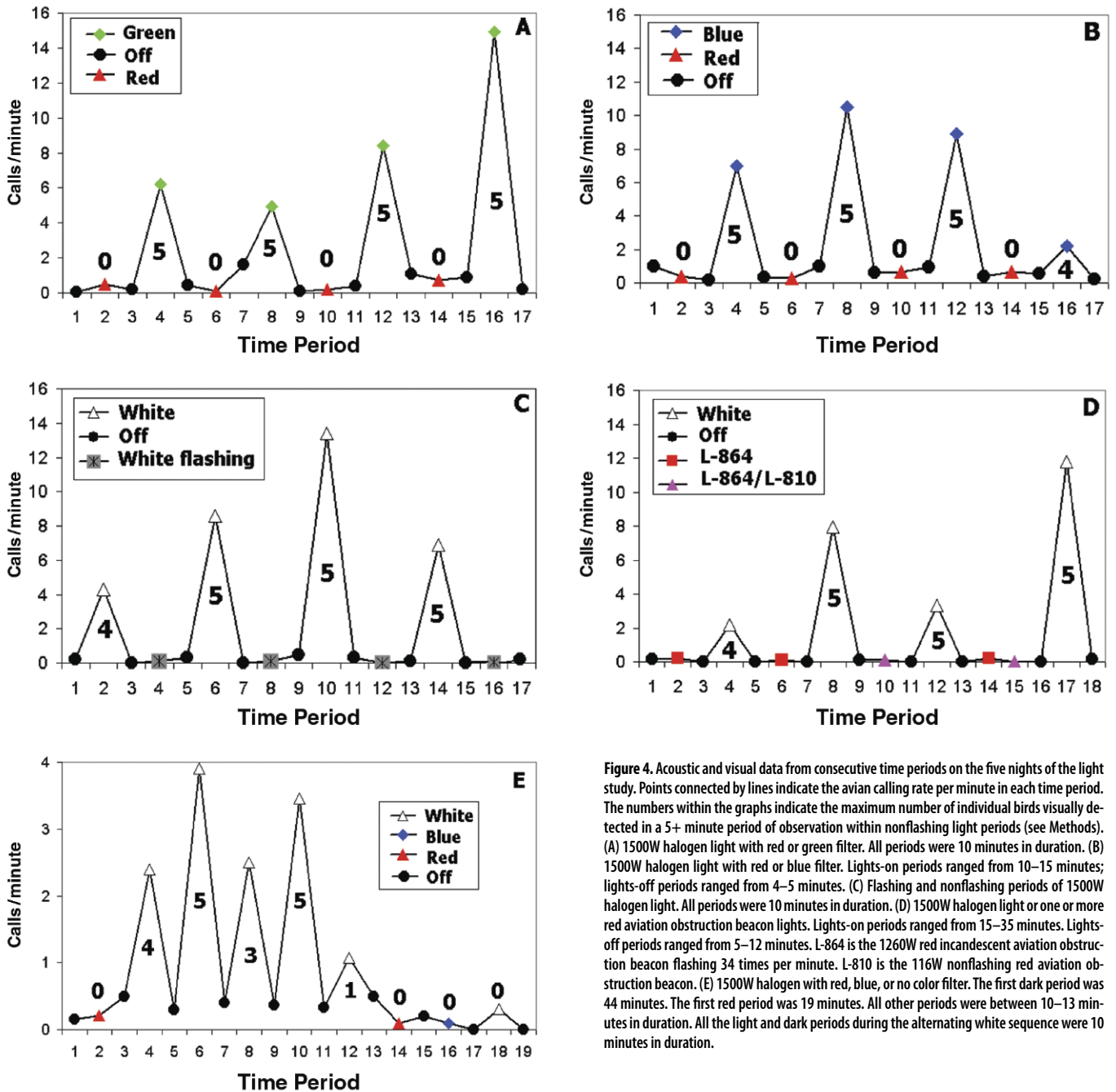


Figure 4. Acoustic and visual data from consecutive time periods on the five nights of the light study. Points connected by lines indicate the avian calling rate per minute in each time period. The numbers within the graphs indicate the maximum number of individual birds visually detected in a 5+ minute period of observation within nonflashing light periods (see Methods). (A) 1500W halogen light with red or green filter. All periods were 10 minutes in duration. (B) 1500W halogen light with red or blue filter. Lights-on periods ranged from 10–15 minutes; lights-off periods ranged from 4–5 minutes. (C) Flashing and nonflashing periods of 1500W halogen light. All periods were 10 minutes in duration. (D) 1500W halogen light or one or more red aviation obstruction beacon lights. Lights-on periods ranged from 15–35 minutes. Lights-off periods ranged from 5–12 minutes. L-864 is the 1260W red incandescent aviation obstruction beacon flashing 34 times per minute. L-810 is the 116W nonflashing red aviation obstruction beacon. (E) 1500W halogen with red, blue, or no color filter. The first dark period was 44 minutes. The first red period was 19 minutes. All other periods were between 10–13 minutes in duration. All the light and dark periods during the alternating white sequence were 10 minutes in duration.

the period October 8-14 (as measured in Ottawa, Canada, 300 km to the north of our study site) was relatively quiet except for October 8—the first night of our light study—when it reached a value of 5 (L. Newitt, Ottawa Magnetic Observatory, pers. comm.). The artificial electromagnetic environment of our study site included most notably the WHCU (870 kHz) AM radio station, which was broadcasting at a power of 1.0 kW in direct line of sight from a series of towers 5 km

to the northeast of our study site. Ritz et al. (2000) and Thalau et al. (2005) allude to the potential importance of documenting such mid-frequency radio wave parameters in nocturnal migration studies.

Study lights and light measurement

Artificial light in this study was created using one pair of work-light luminaires, commercially available in the United States. Each work luminaire was composed of two double-

ended tubular halogen lamps (250W and 500W), a reflector, a metal housing, and a glass pane that filtered out UV light. The pair of luminaires combined to form a 1500W light source. We used two different pairs of luminaires during the study (Figure 1). One of the two pairs was used in the flashing and nonflashing white light tests and with red filters for the red light tests. The other pair was used with blue and green filters for the blue and green light tests. We used Roscolux gel

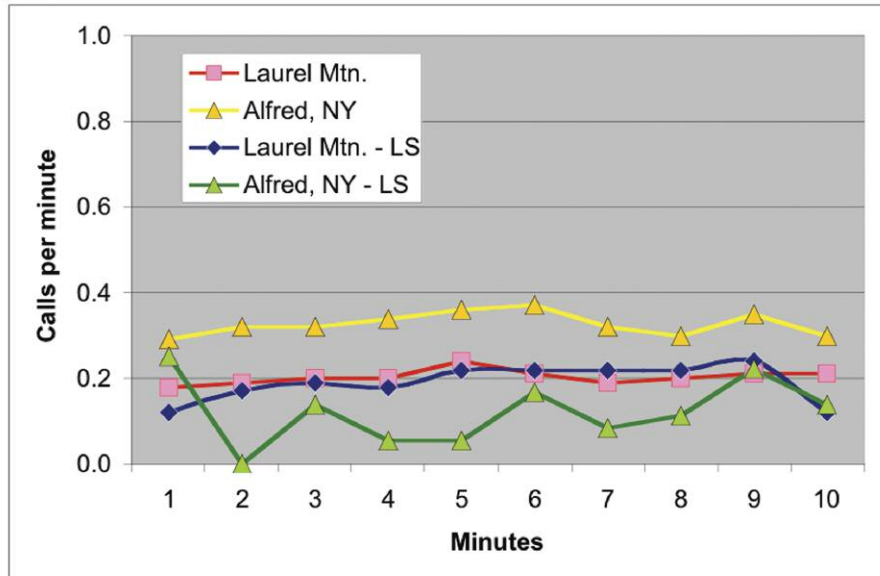


Figure 5A.

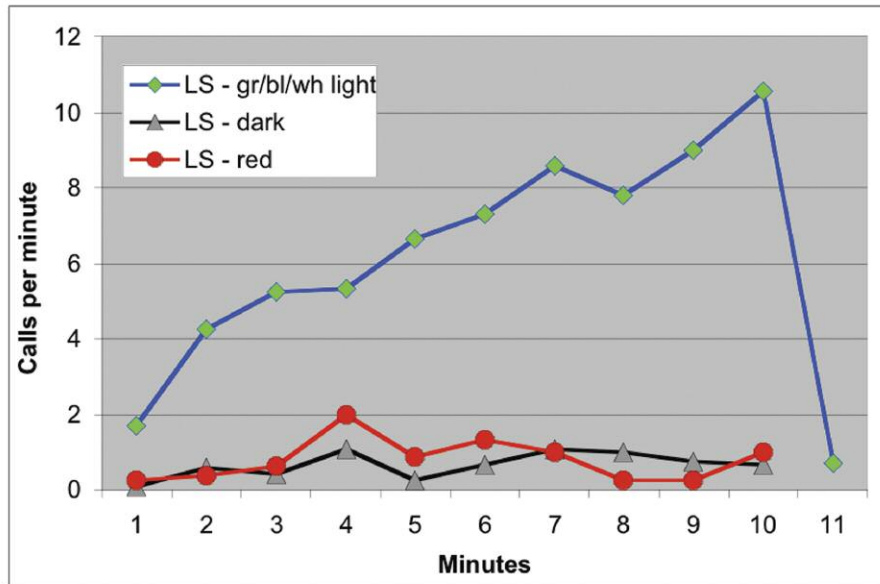


Figure 5B.

Figure 5. This graphic shows the average calling rate for the first, second, third, etc. minute respectively for multiple ten-minute segments at the two reference acoustic stations and in specific light conditions that were precisely ten minutes in duration. (A) Shows such data for all nights from September 1 through October 15 at the control acoustic stations in Alfred, New York, and Laurel Mountain, Pennsylvania, with more than 50 calls detected in nine hours. Each night was broken up into consecutive ten-minute periods. The yellow line (Alfred) and the red line (Laurel Mountain) represent respective minute calling rates for 1080 and 1404 ten-minute periods. The green and blue lines represent respective minute calling rates for 36 ten-minute periods from Alfred and 180 ten-minute periods from Laurel Mountain that occurred during our light study on nights that had more than 50 calls detected in nine hours. (B) Shows respective minute calling rates for each minute in ten-minute periods during specific light periods in our light study (LS). The rising blue line indicates the calling rate detected for each respective minute during the 16 ten-minute periods of aggregation in green, blue, and white light shown in Figure 4A-D. The eleventh minute of the blue line indicates the calling rate in the first minute of lights-off after each of these 16 light periods. The red line indicates the calling rate per respective minute in the 13 ten-minute red light periods during the green and blue light tests (Figure 4A-B). The black line shows the calling rate per respective minute in 16 ten-minute periods of lights-off during the green and white flashing light tests.

filters (Rosco Laboratories, gel filters #19, 69, 389, Stamford, Connecticut).

Variable wattage white light periods were

implemented using a single luminaire with only the 250W, 500W, or both tubular lamps in operation. In the flashing white light test, a

custom-built flash rate controller was used to flash a 1500W halogen luminaire pair with no color filter at 24 times per minute. The on-time per flash was 0.2 second, and the time to peak output appeared nearly instantaneous.

Additional light periods were carried out using a slow-flashing red beacon (FAA type L-864; TWR Lighting, Houston, TX, USA) by itself or in combination with a nonflashing red beacon (FAA type L-810; Galaxy Litebeams, Burbank, California). The L-864 consisted of two 620W incandescent lamps inside a red Fresnel lens, which focused the light on the horizontal plane to produce a peak intensity of about 2000 candela. This beacon was set to produce 34 one-second flashes per minute. Each flash increased in intensity for the first half-second and decreased in intensity for the latter half second. The L-810 contained a single 116W incandescent lamp inside a red Fresnel lens that when mounted upright focused the light on the horizontal plane to produce a peak intensity of about 32 candela.

Each pair of halogen luminaires was mounted approximately 1.5 m above ground level on a tripod. The lamps were angled 20 degrees from the zenith toward the northeast to direct light away from the residence structure and associated trees so as to maximize the transmission of light into the atmosphere. Each lamp pair radiated most light upward within approximately a 75-degree cone (Figure 1).

The red aviation obstruction beacons were laid on their sides and angled approximately 20 degrees from the zenith toward the northeast. This facilitated directing the maximum light intensity from these beacons into the atmosphere.

Spectral power distributions with and without filters were measured at a range of wavelength between 350 nm and 830 nm at 2-nm intervals. These measurements were made using an integrating sphere system, which consisted of a sphere with a diameter of 1.65 m, a computerized double monochromator (Optronic Laboratories, Model 750-M-D, Orlando, Florida), and an enhanced silicone detector (Optronic Laboratories, Model DSM-1D, Orlando, Florida). Each of the four luminaires was first measured with both halogen lamps on (250W+500W=750W). Table 1 summarizes the results of radiant power measurements for the four luminaires derived from the spectral power distribution measurements. These radiant power values were obtained by integrating measured spectral radiant power over a wavelength range visible to birds from 400 nm to 680 nm (Palacios and Goldsmith 1993; Goldsmith and Butler 2005). Since these measurements identified consistency in

Table 1. Results of halogen luminaire radiant power measurements. Each luminaire has an input power of 750W.

Luminaire	Radiant power (W)	
Pair 1	A1	26.9
	A2	26.4
Pair 2	B1	26.6
	B2	25.7
Mean	26.4	

Table 2. Estimated peak irradiances of white and filtered lights at a wavelength range between 400 nm and 680 nm. Column 2 shows radiant power of our white and filtered lights (2 halogen luminaires; 1500W) over the 400–680 nm range as measured with an integrating sphere. Column 3 indicates the calculated irradiance of our filtered lights at 50 m (values do not account for attenuation of irradiance from cloud). See Figure 2 for spectral energy distribution.

Color	Radiant power (400-680 nm)	Peak irradiance at 50m
Blue	7.7 W	< 2.5 mW/m ²
Green	13.6 W	< 4.3 mW/m ²
Red	24.0 W	< 7.6 mW/m ²
White	53.9 W	< 17.1 mW/m ²

radiant power between two luminaires in each pair, only one luminaire from each pair was used for further color-filtered luminaire measurements. Figure 2 shows the results of spectral power distribution measurements with and without the colored filters.

Spectral power distributions of the red aviation beacons were similar to the red-filtered halogen luminaire (Figure 3). Peak irradiance of the red beacons was determined based on the manufacturer specification for those lights. Peak irradiance of the red flashing beacon (L-864) was about one-third that of the red-filtered halogen luminaire.

Most birds in this study were estimated to be 50 m or more from the light source. In order to determine the highest irradiance birds might have encountered at this distance, we measured peak illuminance at 5 m from one of the luminaires (Luminaire A1 in Table 1) in a photometry laboratory at Rensselaer Polytechnic Institute. The peak illuminance was approximately 250 lx. At 50 m, this would be 2.5 lx. Using our previous measurement of luminous flux of 7880 lm for this luminaire, we calculated that in order to get an irradiance of 2.5 lx at 50 m, the solid angle of the beam—or the area projected on the 1-m diameter sphere—should be 1.26 sr, assuming uniform light distribution. This beam distribution is equivalent to a 78.6-degree conical beam. From this, we estimated irradiance of the colored light at 50 m, based on their previously measured spectral power distributions. Table 2 indicates estimated irradiance of the white and filtered lights for two luminaires. These estimated 50-m irradiance values do not account for attenuation from water droplets (cloud; light rain) in the air and, therefore, the actual irradiances during our study would have been substantially lower than those indicated in Table 2.

Acoustic monitoring and flight-call detection
An acoustic transducer (EK-3029cx, Knowles Inc., Chicago, Illinois) was mounted to form a directional microphone with good sensitivity between 3-8 kHz (for microphone design, see <www.oldbird.org/mike_home.htm>).

This microphone was positioned 5 m from the light source and aimed 20 degrees from the zenith toward the northeast. The sensitivity pattern of this microphone was hemispherical, with a region of enhanced sensitivity expanding skyward in roughly a 60-degree cone. The audio signal was digitally recorded for the duration of the study periods. The vertical range of this system for detecting avian flight-calls has been estimated to be greater than 200 m for most small passerine (e.g., Parulidae and Emberizidae) flight-calls and beyond 500 m for mid-sized passerines in the family Turdidae. The precise range is not critical for this study except to note that it covered a much larger volume of space than that covered by the visual observations.

W. Evans listened to the audio recordings using headphones, and calls heard were manually logged by the times of their occurrence. The temporal calling record was then associated with the timing of the light experiments, and call totals were assessed for each light and dark period. For another mode of evaluation, respective minute totals were summed for all ten-minute periods during specific light tests and at two reference acoustic stations on significant migration nights. The calling rate in the first, second, third, etc. minutes were averaged for all ten-minute periods, and any trends in calling rate were assessed.

Spectrographic analysis was carried out on calls that were loud enough to produce a coherent spectrogram. The flight-call reference guide by Evans and O'Brien (2002) was used for species classification. A minimum number of individuals present during each light period was determined by assessing the number of species present through spectrographic analysis.

Visual observations
To corroborate the acoustic data's indication of whether or not bird aggregation was occurring, visual observations of birds flying in the lighted space were made during nonflashing light periods. Precise bird numbers were im-

possible to determine because individuals typically passed in and out of the visibly lighted space. All visual counts represent the maximum number of birds that could be seen in the same field of view. The only exception is when an individual that had not been previously noted was recognized by its profile. This occurred on several occasions when a thrush species was seen during the count period when only smaller warbler- and sparrow-sized passerines had been previously tallied. Visual observations began at least two minutes into the light period and lasted at least five minutes. Once a visual count reached five birds, the observation period was considered sufficient to indicate the presence of birds and was usually discontinued.

All visually observed flying birds were estimated to be within about 50 m of the study lights. Any gross variability in the bird observation capability by a human observer over this range during the different colored-light periods was roughly assessed by whether a tree line approximately 50 m to the east of the study site was visible. Since it was visible in both the short and the long wavelength light periods, no gross differences in the range of human vision were evident during our short and long wavelength light periods. In addition, several species of moths in the family Noctuidae were active and seen clearly at a distance in the red as well as other nonflashing light periods. No bats were seen during our October 2005 study period, but a repeat of this study during two cloud-grounded nights in September 2006 found that bats were distinctly visible in the red light periods. Given that the visual observations in both 2005 and 2006 took place in close proximity to the 1500W bright light source, it is likely that human cone cells were involved in the visual observations and that the lower sensitivity of human rod cells to red light versus blue or green was not a factor in assessing bird presence through visual observation.

Light regimens
One of the following light sequences was repeated at least four times on one of the five study nights:

- White – Lights off
- White – Lights off – White flashing – Lights off
- Red – Lights off – Green – Lights off
- Red – Lights off – Blue – Lights off
- FAA beacon(s) – Lights off – White – Lights off – FAA beacon(s) – Lights off

We separated all experimental light periods

in this study by a period of no light before starting another light period. The purpose with this was to give the birds that had been exposed to a period of artificial light time to move on during the dark period and potentially allow new birds to be in the vicinity before the next light period was imposed. The longer the dark period, the more likely this would be the case. However, this had to be balanced with the fact that as more time passes, weather conditions or the passage rate of migrants necessary to cause aggregation could change. By using conservative estimates for flight speeds (20 km/hr), birds could have been as far as 1400 m from our study site in 4 minutes if they flew straight. Since we could not confirm what birds did, and because we verified that some birds landed in the vicinity of our lights, we could not assume independence between light periods. Analysis of species data within and between nights was our only evidence for different individuals becoming involved in the aggregation events.

Due to the experimental nature of this study, the length of the dark periods we used was somewhat arbitrary. Light and dark periods were typically 10–15 minutes in duration. The alternating red and blue light test had 10–15 minute red and blue light periods but only 4–5 minute dark periods, in order to maximize the number of light study periods on that night. Some light periods with the red flashing beacon were 15–35 minutes in duration, so as to see whether aggregation with that light system might be induced over a longer time period. We carried out the comparison of calling rates between periods of different duration by presenting data in a calls/minute format.

Control sites

Two reference acoustic stations were in operation during this light study. Both were located in rural areas with minor residential lighting in their vicinity. One station was located near Alfred, New York, 107 km to the west of the light study site. The other station was located 107 km to the southwest, 28 km north of Williamsport, Pennsylvania. While the same microphone design and recording equipment were used at these locations, the rates of calling between sites were anticipated to be different because of potentially variable migration patterns and environmental noise at the different sites. The purpose of assessing data from these acoustic stations was to provide a reference for natural variation of flight-calling in the region, at sites without varying artificial light patterns.

Determination of aggregation

Calling rate data were not relied upon to indicate the density levels of migrants. We used acoustic monitoring only as an indicator for a strong or weak presence of birds. Similarly, data from visual observations were not expected to indicate the number of birds present. We used visual observation data only as an indicator of whether or not flying birds were present in the lighted space.

To rule out the possibility of misinterpreting discontinuities in the density of nocturnal bird passage as light-induced bird aggregation, we repeated the varying light regimens and noted consistency in bird presence or absence during specific light conditions. We determined that a specific artificial light condition induced aggregation if that light condition showed strong acoustic and visual evidence for the presence of birds during at least four consecutive cycles with a different light type and/or a dark period in which bird presence was not strongly documented. To further substantiate our light-induced calling patterns, we considered natural calling patterns from two reference acoustic stations in the region.

Good correspondence between the acoustic and visual data gave us confidence in relying solely on the acoustic data for evaluating the aggregation tendency of flashing light tests when we could not verify the presence of birds visually.

In the hypothetical case in which no birds would be present, both the acoustic and visual indices would produce no detections. When a series of repeated light cycles that had been associated with aggregation ceased inducing acoustic and/or visual indication of aggregation, we interpreted this to mean that movements of migratory birds had diminished or ceased in the vicinity of the study site, or that the weather conditions causing the aggregation phenomenon had changed.

Results

Aggregation appeared to be an on-off phenomenon associated with particular light characteristics. Periods of white, blue, and green light had calling rates an order of magnitude higher than dark period calling rates and corresponded with multiple birds seen in the lighted space. No visual observation of birds occurred in the red light periods, and this corresponded with very low overall calling rate during red light. These “no aggregation” red periods occurred repeatedly between alternating periods of green or blue light, in which strong acoustic and visual evidence for aggregation was detected. Figure 4, A and B, shows a sequence of four consecu-

tive light cycles indicating that green and blue light repeatedly induced bird aggregation, whereas the red light did not. The red light had three times greater irradiance than the blue and nearly two times greater irradiance than the green (Table 2). The eight green and blue periods in Figure 4 (A and B) had a mean of 7.2 calls per minute (s.e. 1.7), whereas the eight red periods had a mean of only 0.45 calls per minute (s.e. 0.23) and the 18 dark periods had a mean of 0.48 calls per minute (s.e. 0.35).

Birds were induced to aggregate with all energy levels of white light, the lowest tested being a 250W halogen lamp (in a reflector housing) with a peak irradiance at 50 m of less than 2.7 mW/m². However, when a 1500W white halogen luminaire pair was flashed (24 flashes per minute; 0.2 sec on-time per flash), no acoustic aggregation behavior was documented (Figure 4C).

Over the five nights of study during sequences when bird aggregation was documented, the mean calling rate during dark periods for any specific night never exceeded 0.6 calls per minute (s.e. of 0.14). The calling rate during the flashing red beacon (L-864), the flashing red beacon (L-864) with the constant-on red beacon (L-810), and the flashing white light periods was similar to the dark periods. Figure 4D shows a sequence of four adjacent light cycles in which the flashing red beacon did not induce aggregation by itself or in combination with a low intensity, non-flashing, red beacon. The white light periods in this alternating light cycle had visual confirmation of flying birds and recorded flight-calling an order of magnitude greater than both the dark and red beacon periods.

The proximate calling rate variations shown in Figure 4 are unprecedented based on 19 fall seasons of monitoring natural avian flight-calling rates from more than 10 sites without substantial artificial light in central New York (W. Evans, unpubl. data). Similar patterns of calling rate variation were not found in adjacent ten-minute periods for our control acoustic stations at Alfred, New York, and Laurel Hill, Pennsylvania. We looked at nights with 50 or more flight-calls recorded from September through mid-October (at least 9 hours recording per night). The largest calling rate variation in 1404 adjacent ten-minute periods at Laurel Hill, Pennsylvania was 160%, with a mean of 42%. At Alfred, New York, the largest variation between 1080 adjacent ten-minute periods was 290%, with a mean of 53%. This contrasts with the data in Figure 4, which show eight consecutive variations of 1000% or more in adjacent ten-

Table 3. Species composition of calling during each of the four periods of congregation in the flashing white light test, green light test, and blue light test (see Figure 4A-C). Numbers of flight calls of species or species' complexes with distinctive flight calls are indicated. Many calls in each period could not be classified because they were too weak to identify or could not be placed in a distinctive category. All classification is based on Evans and O'Brien (2002).

SPECIES/ SPECIES COMPLEX	White				Green				Blue			
	1	2	3	4	1	2	3	4	1	2	3	4
Gray-cheeked Thrush <i>Catharus minimus</i>	6	0	0	0	3	1	0	0	0	0	0	0
Swainson's Thrush <i>Catharus ustulatus</i>	5	6	7	3	3	1	0	2	0	0	0	1
Northern Parula <i>Parula americana</i>	9	9	0	1	2	0	0	1	3	0	0	1
Chestnut-sided Warbler <i>Dendroica pensylvanica</i>	0	0	0	2	0	0	0	0	0	0	0	0
Black-throated Blue Warbler* <i>Dendroica caerulescens</i>	29	40	36	2	30	20	36	20	6	2	16	0
Yellow-rumped Warbler <i>Dendroica coronata</i>	0	1	0	3	0	1	1	2	5	3	29	0
Palm Warbler <i>Dendroica palmarum</i>	0	8	0	12	0	0	2	9	2	2	1	1
American Redstart <i>Setophaga ruticilla</i>	0	0	0	0	0	0	0	10	0	0	0	0
Common Yellowthroat <i>Geothlypis trichas</i>	0	12	19	4	2	4	8	18	3	4	0	1
Scarlet Tanager <i>Piranga olivaceus</i>	0	0	2	0	0	0	0	0	0	0	0	0
Savannah Sparrow <i>Passerculus sandwichensis</i>	0	1	11	6	0	0	12	8	4	13	9	1
Swamp/Lincoln's Sparrow <i>Melospiza georgiana/lincolnii</i>	0	0	0	0	0	0	0	1	0	0	0	0
White-throated Sparrow <i>Zonotrichia albicollis</i>	0	0	0	0	0	0	0	3	6	12	5	6
Indigo Bunting <i>Passerina cyanea</i>	0	3	0	0	0	0	0	3	0	0	0	0
Zeep complex**	0	2	6	4	5	4	3	29	1	2	0	0
Species detected acoustically	3	9	6	9	6	6	6	12	8	7	5	6

*Note: An individual Black-throated Blue Warbler often gives two calls in succession, about a half-second apart. In our analysis, we counted such occurrences as two calls.

**In this case, most likely Blackpoll Warbler or Connecticut Warbler; see Evans and O'Brien (2002) for other possibilities.

minute periods on five different nights.

As would be expected, the average calling rate in the first, second, third, etc. minutes of all ten-minute periods on significant migration nights at the two reference stations revealed consistent calling rates per minute (Figure 5A). In other words, in any random ten-minute period during a recording period, one would not expect any specific minute to consistently have more calling than another, and there would be no expected trend of calling increase or decrease over multiple minutes. Data were considered during nights with at least 50 flight-calls per night from September to mid-October (Figure 5A). Such a uniform minute-to-minute calling pattern,

though with greater variance due to a smaller sample size, was documented at the two reference stations during the period of the light study (Figure 5A) and in 16 ten-minute dark periods in the green light and flashing white light tests (Figure 5B).

But in 16 ten-minute light periods when aggregation occurred during the blue, green, and flashing white light tests (nonflashing white light periods), increased calling of birds typically occurred within the first few minutes, and the calling rate tended to increase as a light period progressed. Calling terminated abruptly when lights were turned off (Figure 5B). No trend of increasing calling occurred within 13 ten-minute red light periods em-

bedded within the blue and green light tests (Figure 5B).

At our light study site, visual observations indicated birds were flying in all directions. Some flew past within a few meters of ground level, and some landed nearby. Most birds were seen passing overhead through the lighted space, or were heard calling above the range of our vision in the cloud and/or drizzle. The number of species detected acoustically in most aggregation events was greater than the maximum number of birds documented visually (Table 3; Figure 4). Most birds heard in aggregation events were estimated to be greater than 50 m from the light source. Most birds that were seen did not ap-

pear to give vocalizations while in sight. Species compositions of the aggregation events were typical nocturnal migrant passerines for the region. Table 3 presents the acoustically determined species composition for the aggregation periods shown in Figure 4A-C. Two additional species, not known to give regular nocturnal flight calls, were visually identified when individual birds landed in the vicinity of the light: Gray Catbird (*Dumetella carolinensis*) and the Red-eyed Vireo (*Vireo olivaceus*).

Figure 4E shows the results of the white light test night. A few blue and red light periods were also tested on this night. The sequence of light tests shown here illustrates what was likely a decline in migration passage rate during the course of the night. Toward the end of the night, a period of white and a period of blue light did not indicate either visual or acoustic activity. Careful inspection of the dark period calling rates indicates a drop in calling rate during this time.

Discussion

Avian flight-calling during aggregation periods ceased nearly instantly when lights were turned off. This indicates that the lights played a direct role in causing flight-calling during our aggregation phenomena. It also means that there were numbers of birds in the near vicinity of our light study site that were not calling when the light in the aggregation periods was first turned off. In this respect, the correspondence between calling rate and density of flying birds is shown by our study to be highly variable, making call rate potentially unreliable as an indicator of bird density. But there was strong correspondence between the calling rate and visual observations of flying birds in nonflashing aggregation periods (Figure A-E). This was not just the case in the no-aggregation periods of red light and during the aggregation periods in blue, green, and white light (Figure 4A-E); it was also true in the no-aggregation periods of blue and white light during a time when it appeared that active bird migration had ceased (Figure 4E).

The avian flight-calling rate is influenced by the conjunction of the environmental variables of cloud cover and artificial lighting, but it apparently has elements of consistency when these variables remain constant. This is demonstrated by the shared pattern of increasing calling rate within periods of blue, green, and white light in four different nights of our study (Figure 5B). It is shown by the consistent patterns of calling rate variation in our two control stations (see Results) and by other studies that reveal consistency in calling pat-

terns across broad geographic regions (Evans and Mellinger 1999; Evans and Rosenberg 2000). It is indicated by radar studies that show target passage rate correlation with acoustic data (Larkin et al 2002; Evans, in prep.), as well as by other observations that show gross correspondence between the presence of migrant birds and the flight-calling phenomenon (Odgen 1960; Avery et al. 1976).

Figure 5B indicates unambiguously that, under certain weather conditions, acoustic monitoring can be an indication of whether birds are responding to artificial light. The fact that our visual observations of bird aggregation correspond with the extremes in flight calling during the nonflashing light periods reveals that acoustic monitoring was a reliable index by itself for aggregation phenomenon in those light conditions. The weight of the evidence strongly suggests that the lack of the behavioral response of increased flight calling during the flashing white light periods indicates a lack of bird aggregation. However, there is no substitute for an additional independent means of validating any single-source pattern. Certainly future work with this study method would benefit by the integration of an independent means for continuously assessing bird density during artificial lighting alterations. The challenges of employing such an independent means are considered above, in the Methods section.

Unexpected response to nonflashing red light

Several studies have reported pronounced avian flight-calling in association with apparent bird aggregation at TV towers with red aviation obstruction lighting (Cochran and Graber 1958; Ogden 1960; Taylor and Anderson 1973; Avery et al. 1976). There are many such unpublished accounts, and we have also experienced this phenomenon (W. Evans, unpubl. data). We know without doubt that red lights can induce aggregation and that birds may call during such aggregation events. Yet the irradiance level and spectrum of our lights were very carefully measured, and the data from our study clearly indicate aggregation in blue, green, and white light—but not in red. The possible reasons for this finding are complex and dependent on unknown mechanism(s) for aggregation, which are discussed in more detail in the following sections.

Our finding appears contrary to some prevailing beliefs that bird kills at tall towers with red aviation obstruction lighting are specifically induced by the red nature of the light. But our results may simply indicate that for birds migrating in cloud, blue, green, or white light cause aggregation at lower irradi-

ance levels than red light. Our study is the first to systematically compare avian aggregation tendency in artificial light of different wavelengths.

Mechanism(s) of Aggregation

Theories for why birds aggregate in artificial light have evolved with the paradigm of how birds navigate during nocturnal migration, as well as with progress in understanding avian sensory mechanisms. Current ideas can generally be grouped into two categories. One involves the avian light-dependent geomagnetic sense, with artificial light causing aggregation either due to magnetoreception disruption or because it provides a magnetoreception resource. The other involves avian vision, with artificial light causing aggregation by disrupting a prior vision resource or by enabling a visual refuge. We discuss our study results with respect to these basic ideas and the phenomenon of bird aggregation around tall towers with aviation obstruction lighting.

Magnetoreception disruption theory

After the reported confirmation of light-dependent magnetoreception in captive birds by Wiltschko et al. (1993), the theory emerged that bird aggregation in artificial light might be caused by a “disruption” in the light-dependent magnetoreception mechanism that birds use for orientation (e.g., Gauthreaux and Belser 2006). The Wiltschko et al. (1993) study found that after being kept in the dark, captive birds could not orient in the seasonally appropriate direction when exposed solely to red light, whereas birds could orient well when exposed to constant white, green, or blue light.

Further captive bird studies have revealed the complexity of the mechanism of light-induced magnetoreception. Tests using higher intensity levels of blue and green light showed unique, often seasonally inappropriate, “fixed-direction” responses (Wiltschko et al. 2000; Wiltschko and Wiltschko 2001; Wiltschko et al. 2003). Higher intensity levels of red and yellow light did not produce the fixed-direction responses but caused what appeared to be the same lack of orientation as lower intensity levels of these colored lights (Wiltschko and Wiltschko 2001; Wiltschko et al. 2004b).

An additional study has shown that combinations of monochromatic short and long wavelength light at the lower intensity levels used in the earlier studies also elicit the fixed-direction response (Wiltschko et al. 2004a). This is interesting because white light, which has a broad spectrum of short and long wave-

lengths, enables functional orientation at the low and high intensity levels (Wiltschko and Wiltschko 1972; Möller et al. 2001). It has been theorized, therefore, that the unnatural condition of monochromatic light may cause an imbalance in the magnetoreception mechanism and a dysfunction in the orientation system (Wiltschko et al. 2005).

All the evidence from captive bird studies now suggests that natural magnetoreception is dependent not only on short wavelength light in the blue to green range but also on the intensity of those wavelengths and the composition of other wavelengths that are present. Three types of responses to light have been demonstrated with captive birds: seasonally appropriate orientation, fixed-direction responses, and no orientation. The latter two are generally grouped as disorientation or a disruption in normal magnetic orientation. There are still many questions about light-induced magnetoreception, and this presents a challenge for determining whether disruption of magnetoreception is responsible for bird aggregation in light and, if so, what the specific mechanism is.

With strict respect to the results of captive bird studies, our data do not support the theory that the cause of aggregation in our study was disorientation from a light-induced disruption of magnetoreception. If so, we would not have expected aggregation to occur in the low light levels of our blue and green light, which captive bird studies suggest would enable orientation (Wiltschko et al. 1993; Wiltschko and Wiltschko 1999, 2001). However, we would have expected disorientation-based aggregation with our red light, because red light has not been shown to enable captive birds to orient without a period for adapting (Wiltschko et al. 1993, 2004b).

Similarly, we would rule out the possibility that aggregation in our green and blue light was due to disorientation caused by the fixed-direction response. If this had been the case, then we would not have expected aggregation with our white light, because in captive bird studies white light has not been shown to induce either the fixed-direction response or the “no orientation” mode of disorientation (Wiltschko and Wiltschko 1972; Möller et al. 2001).

A caveat in comparing our data with captive bird studies on light-induced magnetoreception is that there are inherent environmental and contextual differences between field studies and captive studies. These differences include unknowns associated with ambient light in the field studies and the fact that there was no ambient light in the controlled photic en-

vironment of the captive studies. There are also vectorial, spectral, and quantitative differences that may be important variables as well as differences in motivation and behavior prior to light exposure (e.g., flying or not).

Magnetoreception-seeking theory

A more consistent explanation for our results with respect to the findings of captive bird studies arises if we assume that natural light levels during our study were too low to enable magnetoreception. The lower threshold of light levels necessary for magnetoreception in birds is unknown. While moonlight was potentially a factor during our study period, natural light levels would have been very low near ground level due to a persistently thick cloud layer. Aggregation in our white, green, and blue light periods might have occurred because birds found the opportunity for reactivating light-dependent magnetoreception and then tended to remain in, or return to, the lighted area to continue geomagnetic engagement. Since captive bird studies indicate that red light does not readily enable orientation, this suggests it does not readily enable magnetoreception and would explain the lack of aggregation in the red light periods.

The utility of magnetoreception for orientation may be instantly available to birds once activated by light, but there could be a delayed utilization if birds had been previously using another cue such as wind direction. Any delay during the process of cue transfer could be a factor contributing to aggregation.

If such magnetoreception-seeking behavior is the cause for bird aggregation around lights in cloudy conditions, then the question remains why birds congregate around tall communications towers with red aviation obstruction lighting? The red light results from our study do not correspond with the evidence from previous field studies in which red aviation obstruction lighting induced bird aggregation (Cochran and Graber 1958; Avery et al. 1976; Gauthreaux and Belsler 2006).

A possible explanation is that disorientation in red light occurs only if birds are actively using magnetoreception and the red light creates an imbalance in the magnetoreception mechanism as suggested by Wiltschko et al. (2005). The red lights in our study might not have triggered this imbalance if, in fact, the birds were not actively using magnetoreception.

Vision-induced aggregation

As noted by Clarke (1912), the general idea in the early 1900s was that bird aggregation at lights was due to migrant birds that had lost

their way because of weather and “made for the lights in absence of any other direct impulse.” However Clarke’s personal view, based on observations of bird aggregation at two lighthouses, was that migrants were actually “decoyed from or arrested on their course by the influence of the light itself.”

In the USA during the 1960s, vision-based theories arose out of speculation about the cause of mass bird mortality events at TV towers and other lighted structures. Kemper (1964) conveyed the theory that birds that had lost their stellar reference due to cloud cover might be attracted from afar by tower lights in some misguided mechanism related to their stellar navigation system. Herbert (1970) implied that bird aggregation could be due to spatial disorientation caused when artificial light obliterates any previous reference birds have for the horizon. Graber (1968) proposed that birds are not attracted from afar by the lights. Instead, bird aggregation events are composed of birds whose trajectories happen to intersect with the lighted space, which is created by the refraction of the tower lights off small water droplets of cloud or light drizzle. Several later studies concurred with Graber’s idea (Avery et al. 1976; Larkin and Frase 1988).

While there may be mechanisms of aggregation that involve bird attraction to distant light sources or from loss of horizon, our experiments were not geared to study such mechanisms. The aggregation mechanism involved in our study could not have involved bird attraction from afar to point sources of light nor could it have been due to spatial disorientation caused by loss of horizon. Due to the grounded cloud conditions and very limited visibility, birds would not have had any visual reference to the landscape at our study site. Whatever aggregation mechanism was at work involved dark-adapted birds encountering an anisotropically illuminated area.

Why, then, did birds tend to remain in the vicinity of our white, green, and blue lighted space but not the red? One possibility for the lack of aggregation in the red light is that birds’ night (scotopic) vision, relying on rod cells, is much less sensitive to red wavelengths as compared to blue or green. The red light we tested had three times the peak irradiance of the blue light and two times the peak irradiance of the green light. However, when convolved with a spectral sensitivity curve for rhodopsin, avian scotopic sensitivity in the red wavelength range of our test lights was roughly six times less sensitive than the blue and 15 times less sensitive than the green light. Therefore, the red light levels

in our study could simply have been an insufficient visual stimulus or resource for inducing aggregation behavior.

This finding does not concur with the well-documented phenomenon of bird aggregation at tall towers with red aviation obstruction lights. The peak irradiance of our red work light was at least three times greater than that of the medium intensity red beacons typically used for marking tall towers in North America. A difference in our red study light versus such red aviation obstruction lighting on tall towers is that there are more sources of red light on towers. But these individual light sources are separated in space as they mark sequential tiers of a tower. The multiple lights create a larger field of irradiance but not greater irradiance. If the reason birds did not aggregate in our red light was solely due to lower scotopic sensitivity, then more lights should not make a difference.

The only way for birds to encounter greater irradiance from red aviation obstruction beacons than from our red study light is if they fly closer to such tower lights. This is a likely scenario because aviation obstruction beacons are mounted well above ground level on towers, they project their peak intensity horizontally, and some migrant birds would undoubtedly be on a direct course toward the peak intensity vectors of the lights. That such birds would be the ones induced to aggregate is consistent with the theory of aggregation proposed by Graber (1968) and the radar observations of Larkin and Frase (1988).

The horizontal orientation of red obstruction lights on towers versus the perpendicular orientation with our study lights brings up another potential vision aggregation mechanism involving vectorial differences (direction and angular gradient) of light sources discussed by Verheijen (1978, 1985). Vector direction has been demonstrated to be important for sea turtle and amphibian orientation, and it has been shown to be important for birds in horizon glow studies. But the extent to which it impacts birds migrating in cloud is unknown.

Historically, birds migrating in the middle of the night have been accustomed to a dorsal light source. The degree to which they can detect such natural anisotropic light conditions in cloud is unknown, and this would probably depend on cloud layer thickness. We cannot rule out that bird aggregation may have been caused by the ventral nature and/or the unnatural angular gradient of our ground-based light sources.

At intermediate (mesopic) light levels, both cones and rods in the avian retina con-

tribute to visual performance. Since the peak sensitivity of rods is at shorter wavelengths than that of cones, it is expected that the peak sensitivity under such mesopic light conditions would be shifted to longer wavelengths as light levels increase. So as dark-adapted migrants encounter artificial light, at some level of increasing irradiance they would theoretically become more sensitive to red light. The aggregation phenomenon may involve the physiological subtleties of this shift from rod-based to cone-based vision. To further investigate vision-induced aggregation mechanisms, it will be important to identify how avian mesopic vision works as a function of light levels.

No aggregation in flashing light

We found that when flashed, a continuous light source that had just prior been inducing acoustic aggregation behavior now ceased to do so. Night-migrating birds may need a continuous source of light to achieve functional magnetoreception or to use the light as a visual resource. However, the Gauthreaux and Belser (2006) study indicates that white strobes may have some affect on flight behavior of night-migrating birds. Their study showed that birds flying in the vicinity of towers with multiple tiers of white strobe lighting had significantly more nonlinear flight than birds flying at nearby control sites without towers. But since the control sites in their study did not have tower structures, it is not clear in the data presented in their study whether the more nonlinear flight was due to the white strobe lights or from some birds altering their flight path to avoid collision with the tower structure. In this regard, it is noteworthy that their study found that the rates of passage did not vary significantly between the control sites and white-strobed tower sites.

Our study only involved one light source that flashed 24 times per minute, with a longer on-time per flash (0.2 sec) than the typical white strobe light used for aviation obstruction marking. We do not know whether our light had any affect of bird flight behavior. All we know is that it did not lead to an acoustic indication of bird aggregation. Experimentation is needed with faster flash rates and longer duration of individual flashes to see if bird aggregation behavior can be induced with other parameters of flashing light. This is especially important with regard to the pelagic migration of landbirds. Proposals for thousands of offshore wind energy turbines are in preparation for U.S. coastal waters. These structures will have a combination of

flashing obstruction lighting for aviation and boating. For obvious reasons, migratory land-bird response to artificial lights may be different at sea than over land, and any behavioral response to lights at sea has potentially important conservation implications for the species involved.

Conclusion

Our study shows that the color of light and whether it is steady-burning or flashing makes a significant difference in whether night-migrating birds exhibit aggregation behavior. We find no evidence that bird aggregation occurs because a light is red. While red light has been blamed for bird mortality at tall TV towers, our study indicates that for birds migrating within cloud cover, blue, green, or white light would be more likely to induce bird aggregation and associated mortality.

The acoustic data provide strong circumstantial evidence that flashing white light does not induce bird aggregation. Our results in this regard correspond with the circumstantial evidence that no large kills have been documented at tall broadcast towers with white strobe lighting at night (and with no other bright sources of lighting in their vicinity).

While our study showed neither white nor red flashing light to induce bird aggregation, the fact that our nonflashing red also did not induce aggregation suggests that, with equal irradiance, flash on-time, and flash rate, a flashing red light would be less of a stimulus to migrant birds than a flashing white light.

With regard to understanding the mechanism of bird aggregation in artificial light, interpretation of our study results is challenging because we lack information on what orientation cues birds were using prior to intercepting the influence of our study light. There is also a lack of information on the threshold sensitivity for avian vision and for light-induced magnetoreception, and a lack of information on the quantal flux of our light as it dispersed through cloud. We do not know the light levels birds had available before encountering our light. We do not know the light levels birds first encountered that triggered their aggregation behavior, and we do not know how the light level changed for birds as they flew repeatedly through the light field.

Because of these unknowns, our study design and resulting behavioral data do not allow us to distinguish between a visual or magnetobased cause of aggregation. With respect to captive bird studies, our data suggest that magnetoreception disruption was not the aggregation mechanism in our study. However, this could simply be because birds were not relying

on magnetoreception in our study conditions.

It is likely that no matter to what extent birds were using magnetoreception or visual resources, both these light-dependent sensory systems would be impacted by our artificial light sources—at least in the blue, green, and white light periods. Aggregation behavior could be due to adaptations to the new stimuli in both sensory systems.

Sorting out the mechanism(s) of bird aggregation at artificial light sources will require additional laboratory and field studies. While the mechanism of inducing aggregation is still not known, field studies such as ours could lead to practical guidelines to reduce the bird impact of many artificial lighting applications.

With regard to aviation obstruction lighting, two major variables appear to be involved with bird aggregation at such lights in dense cloud conditions: whether such light is flashing or not and light color. Our results suggest that any flashing parameters would cause less bird aggregation than continuous lighting. It is likely that the longer the dark duration between flashes and the shorter the on-time of a flash, the less impact there would be on night migrating birds. With regard to color, night migrating birds migrating in cloud appear to be less responsive to the red spectrum currently specified for use by the FAA in L-864 medium intensity obstruction lighting than light consisting of, or containing, substantial amounts of shorter wavelength light (e.g., white strobe lighting).

Two types of red flashing lights are currently in widespread operation for aviation obstruction marking: the L-864/865 incandescent and xenon flashtube varieties. In two such lights we tested that were purchased from TWR Lighting (Houston, Texas), each had a one-second flash on-time. This contrasts with the more instantaneous type flash of the FAA-approved white strobes. Our study suggests that the red flashing lights have a safer color for birds but a potentially less safe (longer) on-time per cycle. White strobe lighting, on the other hand, has a less safe color for birds but a potentially safer (shorter) flash on-time per cycle. Determining the relative importance of these variables for causing bird aggregation will require additional study. We look forward to further research into the parameters of wavelength and flash rate of lights toward reducing impact to night-migrating birds.

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