## Original Article

# Experimental traffic noise attracts birds during the breeding season

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Understanding how anthropogenic disturbance affects animal behavior is challenging because observational studies often involve co-occurring disturbances (e.g., noise, lighting, and roadways), and laboratory experiments often lack ecological validity. During the 2016 and 2017 avian breeding seasons, we investigated the effects of anthropogenic noise and light on the singing and spatial behavior of wild birds by independently manipulating the presence of each type of disturbance at 89 sites in an otherwise undisturbed boreal forest in Labrador, Canada. Each treatment was surrounded by an eight-channel microphone array that recorded and localized avian vocalizations throughout the manipulation. We analyzed the effects of noise and light on the timing of the first vocalizations of each species at each array during the dawn chorus, and on the proximity of the vocalizing birds to the disturbance when those songs were produced. We analyzed all species combined, and then conducted separate analyses for the six most common species: boreal chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, white-throated sparrow, and yellow-rumped warbler. When all species were analyzed together, we found that traffic noise attracted vocalizing birds. There was some evidence that light repelled birds, but this evidence was inconsistent. In our species-specific analyses, yellow-rumped warbler sang earlier in response to noise; Swainson's thrush was attracted to noise and the combination of noise and light but repelled by light alone. Our study provides some of the first experimental evidence of the independent and combined effects of traffic noise and light on the vocal and spatial behavior of wild birds and suggests that breeding birds may be attracted to noisy roads where they could be exposed to additional forms of disturbance.

*Key words:* **anthropogenic light, anthropogenic noise, bird, birdsong, light pollution, microphone array, noise pollution, passerine, spatial ecology.**

## INTRODUCTION

Urban and industrial developments produce multiple anthropogenic disturbances that negatively impact wildlife (McKinney 2008). Some, such as chemical contamination and anthropogenic structures, can kill animals quickly and directly (Harrison et al. 1997; Bernardino et al. 2018), but others have more subtle and prolonged effects that can be difficult to detect. In the last century, anthropogenic noise and light from cities, roadways, and industry have been recognized as widespread forms of disturbance that affect the physiology, ecology, and behavior of animals (Longcore and Rich 2004; Shannon et al. 2016). Although all animals are at risk, birds may be especially vulnerable because they frequent noisy and illuminated areas and rely heavily on acoustic communication (Longcore and Rich 2004; Slabbekoorn and Ripmeester 2008; Ortega 2012).

Birds exposed to anthropogenic noise can experience several adverse effects. They can incur physical damage, including brain deformities, hearing loss, and deafness (Marler et al. 1973), cognitive impairments, including learning and memory deficits (Potvin et al. 2016), and physiological stress, including rapid heart rate and elevated stress hormones (Kleist et al. 2018). Noise can also alter a bird's behavioral ecology by interfering with acoustic communication (Ortega 2012). For example, noise can interfere with predator avoidance by masking predator cues and conspecific alarm calls (Templeton et al. 2016), and with reproductive behavior by masking or altering sexually selected acoustic displays (Halfwerk et al. 2011a). The effects of noise on song are especially well-documented, with several studies showing that high-energy, low-frequency noise, such as traffic noise, causes birds to shift the timing of song production and to alter the structure of individual songs in ways that are thought to minimize masking (Ortega 2012; Dominoni et al. 2016). For example, birds living in noisy environments can shift song production to quieter parts of the day and increase the amplitude, minimum frequency, tonality, and duration of their songs (Hanna et al. 2011; Ortega 2012). In some cases, birds might avoid noisy, but otherwise ideal, habitats in favor of

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habitats that are suboptimal in other respects (Bayne et al. 2008). It is also possible that birds may not be able to avoid noise because of its pervasiveness in most ecosystems, including in protected areas (Mennitt et al. 2014).

Like noise, anthropogenic light has adverse effects on birds (Longcore and Rich 2004). It can impact sleep and circadian rhythms, which can alter the timing of critical activities (Longcore and Rich 2004; Dominoni et al. 2013; Da Silva et al. 2015). For example, artificial lighting causes birds to initiate reproduction prematurely (Kempenaers et al. 2010; Russ et al. 2017). Light can also affect the spatial ecology of birds. For example, seabirds and migrating songbirds approach artificial lighting, which can increase their risk of predation and collision (Longcore and Rich 2004; Montevecchi 2006; van Doren et al. 2017), and European black-birds (*Turdus merula*) preferentially select artificially illuminated nest sites (Russ et al. 2017).

Understanding the effects of anthropogenic noise and light on birds is challenging because noise, light, and the structures that produce them (e.g., cities, roadways, and industry) often co-occur. Some studies compare disturbed populations living near cities, airports, or highways to populations in areas of minimal disturbance (Dominoni et al. 2013). However, cities, highways, and airports combine habitat alteration, pollution, and altered biological community compositions, which has made ascertaining the independent effects of noise and light, or any other specific form of disturbance, difficult (Summers et al. 2011; Nenninger and Koper 2018). Laboratory experiments on captive animals can disentangle the effects, but often omit important ecological factors and may not translate to the wild. Consequently, there is a need for experimental manipulations on wild birds to fully understand how anthropogenic noise and light affect their behavior.

In this study, we manipulated the presence of anthropogenic noise and light to better understand their independent and combined effects on the singing and spatial behavior of wild birds. We focused on the order Passeriformes because passerines are primarily diurnal and thus vulnerable to the effects of nocturnal lighting. They also rely heavily on vocal communication for attracting mates, repelling rivals, and coordinating activities with offspring and other conspecifics (Bateson and Feenders 2010).

Based on previous, largely correlational, studies, we made several predictions about how birds would respond to experimental noise and light. First, traffic noise should cause birds to distribute their vocalizations more evenly throughout the day (Fuller et al. 2007; Cartwright et al. 2014) and, therefore, to be heard earlier in the morning. European robins (*Erithacus rubecula*) and red-winged blackbirds (*Agelaius phoeniceus*) living in noisier environments both shifted song production from the dawn chorus, which coincides with peak traffic, to quieter times of the day, such as mid-day or night (Fuller et al. 2007; Cartwright et al. 2014). Second, noise should repel birds. Summers et al. (2011) found that species richness increased as the distance from the road increased and the amplitude of the associated traffic noise decreased, suggesting that birds avoid noisy roadways. Third, night lighting should attract birds, since other studies have found that seabirds and migratory songbirds are attracted to artificially lit structures (Montevecchi 2006; van Doren et al. 2017), and that breeding European Blackbirds preferentially select artificially illuminated nest sites (Russ et al. 2017). Fourth, night lighting should cause birds to sing earlier, as has been shown in several songbird species (Kempenaers et al. 2010; Da Silva et al. 2015). Finally, we predicted that birds in the presence of artificial noise and light would be heard even earlier than when only noise

or light were present, and that the repellent effects of noise would offset the attractive effects of light.

## METHODS
### Study area

We conducted 110 trials during the 2016 ($N = 68$) and 2017 ($N = 42$) avian breeding seasons (16 May to 10 July). Trials were distributed across a 50 × 50-km area near Happy Valley-Goose Bay, Labrador, Canada. This area is part of the Boreal Shield Ecozone, which is a large (approximately 1.8 million km$^2$) and relatively undisturbed region that provides substantial habitat for breeding birds. Windspeed at the study site was also known to be low, which is important for detecting and recording acoustic signals. The site was therefore ideal for recording avian responses to experimental noise and light in an otherwise undisturbed forest. Black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) were the dominant tree species, though tamarack (*Larix laricina*), white birch (*Betula papyrifera*), heart-shaped birch (*B. cordifolia*), and trembling aspen (*Populus tremuloides*) were also present. Within the study area, trial locations were selected at random by generating non-repeating UTM coordinates with the website random.org, plotting those points on 1:50 000 scale topographic maps (National Topographic System, Series A771, Edition 4MCE, Map13 F/7 − 13 F/10), and discarding any points that were not within 0.5−1 km of road or trail access, or which were within a swamp, water body, or 0.5 km of another trial location. We separated trials by at least 0.5 km to reduce the risk of birds being detected at multiple sites (Wilson and Mennill 2011), and we excluded locations that were beyond 1 km from road or trail access because carrying our equipment through dense forest over distances greater than 1 km would have been difficult. As part of another study (JP Ethier, unpublished data), 20 locations used in 2016 were re-used in new trials in 2017. We consider these trials as independent replicates because they involved different treatments each year and there was high species turnover at each site between years.

### Microphone arrays

At each trial location, we set up an eight-channel microphone array that allowed us to record and localize avian vocalizations throughout the trial. Each array consisted of four digital audio recorders (Model: SM3; Wildlife Acoustics, Concord, MA) attached to trees, approximately 1.5 m above the ground, at the four corners of a 40 × 40 m square. Each recorder had two microphones: one was built into the recorder (omnidirectional pickup pattern; 50−20 000 Hz [±10 dB] frequency response) and a second, external microphone (model: SMM-A2; omnidirectional pickup pattern; 50−20 000 Hz [±10 dB] frequency response) was positioned in the forest canopy approximately 2 m above the first. Separating microphones in the vertical dimension allowed us to localize birds in three-dimensional space. We elevated the external microphone with a painter's pole and fixed it in place by hooking an attached wire over a tree branch. The microphones were pointed towards the center of the array, and their locations determined with a survey-grade global navigation satellite system (GNSS) with 10-cm accuracy (model: Trimble Geo 7X; Trimble Inc., Sunnyvale, CA). As a requirement for acoustic localization, the clocks of the four audio recorders were synchronized to within 1 ms of each other by connecting them to external GPS units (model: Garmin SM3 GPS) for the duration of the trial (Mennill et al. 2012).

Audio recorders were programmed to record continuously until manually stopped, creating a new stereo audio file every 2 h (WAVE format, 24 kHz sampling rate, 16-bit amplitude encoding, 220 Hz analog high-pass filter, 10 dB analog voltage gain). We had four microphone arrays in 2016, and, on average, were able to set up two arrays at new locations each day. In 2017, we had two microphone arrays, with one being set up each day. Arrays were set up in the afternoon and recorded for a minimum of 48 h. The first 24 h was used as part of another study and involved no manipulations (JP Ethier, unpublished data). The next 24 h served as an experimental period in which we recorded singing behavior during and after experimental disturbance treatments were broadcast.

We set a Kestrel 5500 weather station (Kestrel Meters, Boothwyn, PA) inside each array. Every 20 min, it recorded temperature (±0.1°C), windspeed (±0.1 km/h), relative humidity (±0.1%), and barometric pressure (±0.1 mb). Temperature influences the speed of sound, which is required for the sound localization process. Wind can influence the likelihood of detecting signals on recordings, but windspeed was always low (mean = 0.75 km/h, standard deviation [SD] = 1.65 km/h), and therefore was not considered further. Humidity and barometric pressure were not considered in subsequent analyses because they have negligible effects on the speed of sound (Wölfel and McDonough 2009).

## Disturbance treatments

We returned to the array before 05:00 PM on the day after it was set up and installed one of four disturbance treatments: 1) no light and no noise (control; $N = 39$); 2) light but no noise ($N = 35$); 3) noise but no light ($N = 17$); or 4) noise and light ($N = 19$). Treatments were selected at random, but with the constraint that the speaker used to broadcast noise could only be used every second day due to the time needed to recharge its battery. The sample sizes for treatments involving noise were thus smaller than for other treatments.

Noise was broadcast from an amplified loudspeaker (model: SBT1009BK; speaker diameter: 20.3 cm; The Sharper Image, Farmington Hills, MI) placed facing upwards in the center of the array. The speaker was connected to an external lithium-ion battery (model: Car Rover B019DVZXTE; 26 amp-hour; 12-V; Startwayauto Store, Guangzhou, Guangdong, China) that supplemented its internal battery, and to a digital audio player (model: HS-636-4GBBK MP3 Player; Hipstreet, Markham, ON, Canada) that played the noise stimulus. The entire apparatus was sealed inside a black plastic bag to protect it from rain. The noise stimulus was programmed to begin playing at 05:00 PM (ca. 24 h after the array was set up) and to continue for 15 h (until 08:00 AM the following morning).

The noise treatment included three noise stimuli that were derived from online sources and which, together, represented a range of traffic types. They varied primarily in terms of traffic rate. The first stimulus was recorded from a country highway and was 1 h in length, with approximately seven vehicles passing per minute. The second stimulus was recorded from a two-lane highway, with approximately 10 vehicles passing per minute, and was 8 h in length. The third noise stimulus was recorded from a busy freeway, with approximately 40 vehicles passing per minute, and was 8 h in length. Using Audacity software (version 2.0; Audacity® software is copyright© 1999−2018 Audacity Team; the name Audacity® is a registered trademark of Dominic Mazzoni), each stimulus was normalized to a peak amplitude of −1 dB and then repeated to construct a 15-h playback sequence. The three traffic noise stimuli were assigned at random to trials involving noise (first stimulus

$N = 13$ trials; second stimulus $N = 14$ trials; third stimulus $N = 9$ trials).

During playback in the field, we set the volume on the speaker and the digital audio player to "maximum" to ensure that all stimuli played at approximately the same amplitude in different trials. Using a digital sound level meter (model: 33–2055; C weighting; fast response; 50−126 dB range; ±2 dB accuracy; 0.0002 micro bar reference; RadioShack Corporation, Fort Worth, TX), we measured the peak amplitude of the stimulus over a 5-min period at six predetermined distances from the speaker at the beginning of six different trials, when the speaker's battery was fully charged. Peak amplitudes (mean ± SD) were 84.8 ± 2.8 dB at 1 m, 70.3 ± 9.5 dB at 5 m, 61.5 ± 8.1 dB at 10 m, 54.3 ± 3.9 dB at 15 m, 50.5 ± 1.2 dB at 20 m, and <50 dB at 25 m.

The light treatment was a battery powered light emitting diode (LED; power: 6 W; Super Bright LEDs Inc., St. Louis, MO) that was hung by its power cable from a tree branch at an average height of 4.3 m (SD: 0.8 m; range: 2.6–5.7 m) in the center of the array. At this height, the light's 40° beam angle provided an average area of ground illumination of 7.8 m² (SD: 2.9 m²; range: 2.7−13.5 m²). The light was connected to a light-sensitive switch (model: GLUX-DDS Dusk-to-Dawn Sensor) that activated the light at approximately sunset (78 lux, as measured with a digital light meter; accuracy: 5%; model: 401027; Extech Instruments, Boston, MA) and deactivated it at sunrise (219 lux). At the time and location of our study, the average sunset occurred at 09:22 PM (range: 08:57 to 09:33 PM) and the average sunrise occurred at 04:40 AM (range: 04:33−04:59 AM; www.timeanddate.com, 2018). In trials involving noise and light treatments, we attempted to hang the light directly above the speaker, though vegetation and topography sometimes required them to be separated slightly (mean ± SD horizontal distance: 2.7 ± 2.2 m). We chose LEDs, as opposed to other types of lighting, because LEDs are common, energy-efficient, durable, and available in diverse colors (Mottier 2009).

For each trial involving light, we randomly selected one of five LED colors that are used in exterior lighting and that wild birds might encounter: red ($N = 12$ trials; model: GLUX-RGB18W-S40B-MCL; color: 622 nm), green ($N = 11$ trials; model GLUX-RGB18W-S40B-MCL; color: 528 nm), blue ($N = 9$ trials; model GLUX-RGB18W-S40B-MCL; color: 474 nm), cool white ($N = 13$ trials; model: GLUX-CW6W-S40; correlated color temperature: 5800°K), and warm white ($N = 9$ trials; model: GLUX-WW6W-S40B; correlated color temperature: 3100°K). White lights would be the most frequently encountered by passerine birds, but exposure to other colors is also likely to occur. Including multiple light colors ensured that our stimuli represented diverse forms of light disturbance.

## Acoustic analysis

For each 2-h interval of a trial, we used Audacity software to combine the set of four stereo audio files that had been recorded simultaneously by the array into a single 2-h, eight-channel sound file (WAVE format; 16-bit amplitude encoding; 24 kHz sampling rate). The eight-channel file was named according to the array number, date, and start time of the recording. Using Audacity, we viewed as spectrograms (512-point fast Fourier transformation, 87.5% overlap, Hamming window) all eight-channel audio files recorded between midnight and 08:00 AM on the night when the treatments were deployed. During the data scoring process, we remained blind to the disturbance treatment. Whenever we detected a vocalization from a passerine, we noted its onset and offset and

annotated it according to species, which we defined according to the online Checklist of North and Middle American Birds (Table 1; Chesser et al. 2018). For most species, we annotated their species-specific songs, but, for boreal chickadee, red-breasted nuthatch, and common raven, which do not produce songs, we annotated their species-specific calls (Rodewald 2015). We included vocalizations only if they were visible on the audio channels corresponding to at least three of the four corners of the array since vocalizations can only be localized when they are detected at three or more locations in an array (Mennill et al. 2012; Wilson et al. 2014). Based on our previous experience with this array configuration, vocalizations detected by one or two recorders only originate from at least 40 m away from the center of the array (personal observation; Wilson et al. 2014). Finally, we annotated only the first 10 vocalizations produced after midnight by each species, or all of the vocalizations from a species if it produced fewer than 10.

Vocalizations were localized automatically using a custom program in MATLAB (Version 6.1, The MathWorks, Natick, MA). For each vocalization, the program uses information about its position within the parent file to open the eight-channel clip containing the vocalization. The program applies a species-specific high-pass filter to remove low-frequency background noise (Table 1). It then identifies the channel with the highest signal-to-noise ratio and uses waveform cross-correlation to measure the time-of-arrival differences of the signal between that channel and the other seven channels in the array. The program then simulates a three-dimensional lattice over the study area, and, for each vertex in the lattice, calculates how long it would take for a sound to reach each microphone in the array, as well as the corresponding time-of-arrival differences among the microphones. For each vertex, the sum of the absolute differences between the theoretical and observed time-of-arrival differences are calculated and used as a unitless measure of localization error. Localization error is a measure of model fit, not a measure of geographic distance. The vertex that minimizes localization error is selected as the best estimate of the origin of the sound.

Vocalizations were removed from further analysis if their localization error exceeded 0.02. Previous research involving the playback of sounds from known locations within our arrays (but after our trials were complete) showed that 90% of localizations with an error value of 0.02 or less were within 3.6 m of their true locations, as determined by our GNSS (JP Ethier, unpublished data). For each remaining vocalization, we calculated the distance between its estimated origin and the experimental disturbance using the R packages "sp" (Bivand et al. 2013) and "rgeos" (Bivand and Rundel 2018). If both a light and speaker were present, we calculated the

## Table 1

**Avian vocalizations included in this study**

| Common name | Scientific name | Vocalizations detected | Vocalizations analyzed | Bandpass filter (Hz) |
|---|---|---|---|---|
| Alder flycatcher | *Empidonax alnorum* | 10 (82) | 2 (6) | 2387−6594 |
| American redstart | *Setophaga ruticilla* | 1 (7) | 0 (0) | 3729−9013 |
| American robin | *Turdus migratorius* | 55 (490) | 13 (31) | 1760−4969 |
| Black-throated green warbler | *Setophaga virens* | 37 (296) | 12 (29) | 3042−6470 |
| Blackpoll warbler | *Setophaga striata* | 1 (10) | 1 (1) | 4008−9223 |
| **Boreal chickadee** | ***Poecile hudsonicus*** | **58 (455)** | **20 (64)** | **3348−8336** |
| Brown creeper | *Certhia americana* | 8 (49) | 2 (3) | 3878−7309 |
| Cape May warbler | *Setophaga tigrina* | 15 (122) | 2 (6) | 3545−9291 |
| Common raven | *Corvus corax* | 7 (52) | 1 (1) | 931−1875 |
| Common redpoll | *Acanthis flammea* | 6 (39) | 3 (4) | 2830−6650 |
| Connecticut warbler | *Oporornis agilis* | 1 (10) | 0 (0) | 3090−6040 |
| **Dark-eyed junco** | ***Junco hyemalis*** | **88 (816)** | **36 (139)** | **2975−6839** |
| Fox sparrow | *Passerella iliaca* | 78 (713) | 16 (41) | 2134−5774 |
| Golden-crowned kinglet | *Regulus satrapa* | 1 (1) | 0 (0) | 6840−8250 |
| Hermit thrush | *Catharus guttatus* | 47 (427) | 7 (12) | 2347−5308 |
| Lincoln's sparrow | *Melospiza lincolnii* | 29 (198) | 15 (43) | 1557−7204 |
| Magnolia warbler | *Setophaga magnolia* | 9 (77) | 4 (10) | 2460−8032 |
| Northern waterthrush | *Parkesia noveboracensis* | 15 (110) | 4 (18) | 2196−7672 |
| Orange-crowned warbler | *Oreothlypis celata* | 28 (222) | 11 (26) | 2451−8544 |
| Palm warbler | *Setophaga palmarum* | 1 (10) | 1 (4) | 4500−8000 |
| Philadelphia warbler | *Vireo philadelphicus* | 2 (13) | 0 (0) | 1600−6200 |
| Pine grosbeak | *Pinicola enucleator* | 30 (225) | 8 (20) | 2085−5223 |
| Pine siskin | *Spinus pinus* | 38 (311) | 15 (37) | 3665−6875 |
| Red-breasted nuthatch | *Sitta canadensis* | 15 (92) | 5 (10) | 1046−6844 |
| **Ruby-crowned kinglet** | ***Regulus calendula*** | **79 (713)** | **31 (96)** | **1982−6518** |
| **Swainson's thrush** | ***Catharus ustulatus*** | **71 (702)** | **26 (83)** | **1630−5503** |
| Tennessee warbler | *Oreothlypis peregrina* | 22 (214) | 10 (32) | 2533−9993 |
| **White-throated sparrow** | ***Zonotrichia albicollis*** | **80 (702)** | **20 (43)** | **2235−7130** |
| Winter wren | *Troglodytes hiemalis* | 7 (62) | 3 (8) | 2579−9491 |
| Yellow-bellied flycatcher | *Empidonax flaviventris* | 2 (20) | 1 (5) | 2761−5994 |
| **Yellow-rumped warbler** | ***Setophaga coronata*** | **79 (667)** | **38 (115)** | **2827−6520** |

"Vocalizations detected" shows the number of arrays in which a species was detected, and, in parentheses, the number of vocalizations detected from that species across all arrays. Vocalizations were considered "detected" if they were visible on the spectrograms corresponding to three of the four corners of the array. For our study, we annotated a maximum of 10 vocalizations per species per array. "Vocalizations analyzed" shows the same information, but based on the subset of vocalizations that were localized to within 30 m of the experimental disturbance (or of the center of the array for control trials) with a localization error of 0.02 or less (see text for explanation of this error term). We retained for our analysis a maximum of the first five vocalizations per species per array that met these inclusion criteria. The six species that were present in the greatest number of arrays, as defined by the column "Vocalizations analyzed", were also analyzed individually and are shown in bold.

distance to the midpoint between them, and, if the speaker and light were both absent, we calculated the distance to the center of the array. We excluded from further analysis any vocalizations that were more than 30 m away from the disturbance, or, for control trials, from the center of the array. A 30-m radius around the disturbance ensured that vocalizations originated from locations within or close to the array. Beyond 30 m, we often could not detect noise and light treatments, suggesting that birds may also have been unable to detect them. We excluded 21 trials from the statistical analysis because they contained no detections that met the inclusion criteria.

## Statistical analysis

If birds advance the onset of song in response to noise or light, then that effect should be most evident when birds first start to sing. For each trial, we identified the first five vocalizations produced after midnight by each passerine species. The five vocalizations were derived from the subset of 10 vocalizations that we originally annotated and that met all of the inclusion criteria. Our rationale for including the first five vocalizations, rather than the first vocalization only, was that birds sometimes produce isolated songs at night that do not reflect the general onset of the individual's dawn chorus (Leopold and Eynon 1961). For each of the five songs from each species, we noted the time it was produced (number of minutes after midnight) and its two-dimensional Euclidean distance from the experimental disturbance. If the trial included a light and speaker that were slightly separated, we calculated distances to the midpoint between them. For control trials, distances were calculated relative to the center of the array. Time of production and distance to disturbance for the first five vocalizations from each species were used as dependent variables in subsequent statistical analyses.

We used linear mixed-effects models to test for the effects of noise (present vs. absent), light (present vs. absent), and their two-way interaction on each dependent variable. Noise and light treatments were included as categorical variables with fixed effects, and array number and species identity as categorical variables with random effects to control for nonindependence among data derived from the same location and species. We analyzed all passerines combined, and then conducted species-specific analyses for the six most common species, as determined by the number of arrays in which they were detected (Table 1). These included: boreal chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, white-throated sparrow, and yellow-rumped warbler. Analyses were conducted in R (R Core Team 2019) using the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) packages. Results were considered statistically significant where $P \leq 0.05$.

We included five colors of light to ensure that our stimuli represented the broad category of light disturbance, and to permit a preliminary investigation into the effects of light color on avian responses. Previous research showed that birds respond differently to different colors of light (Poot et al. 2008). It is, therefore, possible that responses to one color could have offset responses to another in our analysis of treatment effects. For example, birds might have been attracted to red lights, but repelled by green lights. We, therefore, conducted additional analyses to determine if either of our two response variables were influenced by light color. For the subset of 73 trials that did not involve a noise playback, we compared each response variable from the passerine dataset among the six light conditions using another linear mixed-effects model. Light color was included as a categorical variable with fixed effects, and array and species were included as categorical variables with

random effects. Note that sample sizes among treatment groups were variable and, for some colors, quite small (no light $\mathcal{N} = 38$ arrays, cool white $\mathcal{N} = 8$, warm white $\mathcal{N} = 6$, red $\mathcal{N} = 9$, green $\mathcal{N} = 7$, blue $\mathcal{N} = 5$). Results should, therefore, be interpreted with caution.

## RESULTS
### Passerine analysis

When all species were analyzed together, the first five vocalizations from each species occurred at 04:50 AM ± 10 min (mean ± SE; determined from a linear mixed-effects model including intercept as a fixed effect and array identity and species as random effects; $\mathcal{N} = 887$ songs from 89 arrays and 27 species; the model used minutes past midnight as the dependent variable, but this was converted to local time here). For reference, sunrise at the time and location of our study occurred at 04:40 AM ± 7.31 min (mean ± SD; range: 04:33−04:59 AM; www.timeanddate.com). Although isolated songs were detected throughout the night (see also Leopold and Eynon 1961), none of the species analyzed are considered to be nocturnal or to sing regularly at night (La 2012). The time of the first five vocalizations was not affected by the presence or absence of experimental noise or light (Table 2).

The average distance to disturbance during the first five vocalizations was 18.4 ± 0.9 m (mean ± SE; determined from a linear mixed-effects model including intercept as a fixed effect and array identity and species as random effects; $\mathcal{N} = 887$ songs from 89 arrays and 27 species; Figure 1). There was a statistically significant effect of treatment on distance, with birds being attracted to noise (Table 2; Figure 1). There was no effect of light or the interaction between noise and light (Table 2; Figure 1).

The color of light did not affect the time of the first five vocalizations or the distance of the vocalizing bird to the disturbance (Table 3).

The results were robust in three important ways. First, the response variables were not derived from a single species that vocalized earlier than all the rest, but, rather, from the vocalizations of 23 different passerine species (Tables 1 and 2). Second, the effect of noise on distance to disturbance was not driven by the very strong effect seen in Swainson's Thrush (see below), since the results remained identical with respect to statistical significance when Swainson's Thrush was removed from the passerine analysis. Third, the findings were not affected by our choice of inclusion criteria (i.e., that vocalizations were localized to within 30 m of the disturbance with a localization error of 0.02 or less). We re-ran the analyses using all combinations of localization error (0.01, 0.02, 0.03, 0.05, 0.1, no limit) and distance (20, 30, and 40 m) and the results with respect to statistical significance remained similar (Supplementary Materials). Specifically, there was a statistically significant attraction to noise in 17 of the 18 models; the only exception was when distance was set to 40 m and localization error to "no limit". For one of 18 combinations (distance = 20 m × error = no limit), there was also a statistically significant interaction between noise and light, such that the attractive effect of noise weakened in the presence of light. Finally, for three combinations (distance = 40 m × error = 0.01, 0.05, 0.1), light significantly repelled birds.

### Single-species analyses

We conducted species-specific analyses on the six most common species (boreal chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, white-throated sparrow, yellow-rumped

**Table 2**

**Effects of light and noise on song production**

| Model | Time of onset | | | Distance to disturbance | | |
|---|---|---|---|---|---|---|
| | Coefficient (±SE) | *t* | *P* | Coefficient (±SE) | *t* | *P* |
| All passerines (*N* = 887 songs from 89 arrays and 27 species) | | | | | | |
| Intercept | **288.1 ± 12.5** | **23.1** | **<0.001** | **20.2 ± 1.0** | **19.3** | **<0.001** |
| Noise | 7.3 ± 15.7 | 0.5 | 0.641 | **−5.6 ± 1.3** | **−4.2** | **<0.001** |
| Light | 6.9 ± 13.7 | 0.5 | 0.618 | −0.2 ± 1.2 | −0.1 | 0.882 |
| Noise × light | −25.6 ± 22.8 | −1.1 | 0.266 | 2.1 ± 2.0 | 1.1 | 0.289 |
| Boreal chickadee (*N* = 64 songs from 20 arrays) | | | | | | |
| Intercept | **304.1 ± 23.1** | **13.2** | **<0.001** | **19.5 ± 2.3** | **8.5** | **<0.001** |
| Noise | 73.2 ± 46.1 | 1.6 | 0.132 | −1.0 ± 4.7 | −0.2 | 0.831 |
| Light | 12.1 ± 46.1 | 0.3 | 0.796 | 0.8 ± 4.6 | 0.2 | 0.855 |
| Noise × light | −85.5 ± 68.4 | −1.3 | 0.229 | −2.7 ± 6.8 | −0.4 | 0.694 |
| Dark-eyed junco (*N* = 139 songs from 36 arrays) | | | | | | |
| Intercept | **260.2 ± 13.3** | **19.6** | **<0.001** | **21.9 ± 1.7** | **13.0** | **<0.001** |
| Noise | −11.1 ± 23.7 | −0.5 | 0.642 | −2.9 ± 3.0 | −1.0 | 0.335 |
| Light | 26.6 ± 21.0 | 1.3 | 0.215 | −4.2 ± 2.7 | −1.6 | 0.126 |
| Noise × light | 10.0 ± 38.5 | 0.3 | 0.797 | −1.6 ± 4.9 | −0.3 | 0.741 |
| Ruby-crowned kinglet (*N* = 96 songs from 31 arrays) | | | | | | |
| Intercept | **307.7 ± 21.1** | **14.6** | **<0.001** | **19.3 ± 1.9** | **10.0** | **<0.001** |
| Noise | −9.5 ± 34.7 | −0.3 | 0.786 | −3.8 ± 3.1 | −1.2 | 0.235 |
| Light | 1.9 ± 36.4 | 0.1 | 0.958 | 3.1 ± 3.3 | 0.9 | 0.357 |
| Noise × light | 5.8 ± 54.4 | 0.1 | 0.916 | 0.4 ± 4.8 | 0.1 | 0.926 |
| Swainson's thrush (*N* = 83 songs from 26 arrays) | | | | | | |
| Intercept | **223.5 ± 6.0** | **37.1** | **<0.001** | **18.4 ± 1.8** | **10.0** | **<0.001** |
| Noise | −5.9 ± 8.8 | −0.7 | 0.506 | **−11.5 ± 2.7** | **−4.2** | **<0.001** |
| Light | 15.5 ± 10.1 | 1.5 | 0.139 | **9.2 ± 3.1** | **3.0** | **0.007** |
| Noise × light | −23.0 ± 15.0 | −1.5 | 0.138 | **−13.3 ± 4.6** | **−2.9** | **0.008** |
| White-throated sparrow (*N* = 43 songs from 20 arrays) | | | | | | |
| Intercept | **264.2 ± 24.1** | **11.0** | **<0.001** | **20.8 ± 3.0** | **6.8** | **<0.001** |
| Noise | −55.0 ± 50.6 | −1.1 | 0.292 | −12.6 ± 6.4 | −2.0 | 0.068 |
| Light | −70.4 ± 35.3 | −2.0 | 0.062 | −4.3 ± 4.5 | −1.0 | 0.355 |
| Noise × light | 68.5 ± 62.8 | 1.1 | 0.291 | 9.0 ± 8.0 | 1.1 | 0.278 |
| Yellow-rumped warbler (*N* = 115 songs from 38 arrays) | | | | | | |
| Intercept | **348.1 ± 15.6** | **22.3** | **<0.001** | **21.4 ± 1.2** | **17.7** | **<0.001** |
| Noise | **−78.5 ± 30.5** | **−2.6** | **0.015** | −1.8 ± 2.3 | −0.8 | 0.448 |
| Light | −30.4 ± 27.6 | −1.1 | 0.279 | 2.0 ± 2.2 | 0.9 | 0.358 |
| Noise × light | 37.2 ± 45.2 | 0.8 | 0.416 | 0.5 ± 3.5 | 0.1 | 0.888 |

Analyses were conducted on all passerine species combined, and separately on the six most common species, as determined by the number of arrays in which they were present. Response variables include the time when each song was produced (minutes past midnight) and the distance between the singer and disturbance during song production for the first five songs per species per array. Responses were modeled using linear mixed-effects models (restricted maximum likelihood) with array identity as a random effect. Estimates for each factor are for the level of the factor where the treatment (noise, light) is present, and *t*-tests are conducted using Satterthwaite's method. SE = standard error. Statistically significant effects (α = 0.05) are in bold.
Random effects for time of song production models (variance ± SD):
All passerines: array = 2287 ± 48; species = 1685 ± 41; residual = 2163 ± 47;
Boreal chickadee: array = 4746 ± 69; residual = 82 ± 9;
Dark-eyed junco: array = 2587 ± 51; residual = 198 ± 14;
Ruby-crowned kinglet: array = 5157 ± 72; residual = 295 ± 17;
Swainson's thrush: array = 326 ± 18; residual = 0 ± 1;
White-throated sparrow: array = 3054 ± 55; residual = 1434 ± 38;
Yellow-rumped warbler: array = 4046 ± 64; residual = 205 ± 14.
Random effects for distance to disturbance models (variance ± SD):
All passerines: array = 13.9 ± 3.7; species = 10.5 ± 3.2; residual = 36.6 ± 6.1;
Boreal chickadee: array = 43.3 ± 6.6; residual = 10.5 ± 3.2;
Dark-eyed junco: array = 40.4 ± 6.4; residual = 6.2 ± 2.5;
Ruby-crowned kinglet: array = 30.8 ± 5.6; residual = 25.8 ± 5.1;
Swainson's thrush: array = 28.8 ± 5.4; residual = 4.1 ± 2.0;
White-throated sparrow: array = 55.3 ± 7.4; residual = 13.5 ± 3.7;
Yellow-rumped warbler: array = 18.2 ± 4.3; residual = 14.2 ± 3.8.

warbler), though we note that sample sizes were smaller than for the passerine analysis (Table 2). We did not apply any adjustments to experiment-wise error because the analysis and conclusions for one species are independent of those for another species.

The time of the first five vocalizations was not affected by noise, light, or the interaction between noise and light for five of the six species, including boreal chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, and white-throated sparrow (Table 2). The only exception was yellow-rumped warbler, which began vocalizing earlier when noise was present versus absent (Table 2; Figure 2). The average distance to disturbance was also not affected by the experimental manipulations for five of the six species,

including boreal chickadee, dark-eyed junco, ruby-crowned kinglet, white-throated sparrow, and yellow-rumped warbler (Table 2). For Swainson's thrush, however, there was a statistically significant effect of the disturbance treatments, with individuals being attracted to noise and repelled by light (Table 2; Figure 3). There was also a significant interaction between noise and light for Swainson's thrush, with individuals being attracted to the combination of light and noise (Table 2; Figure 3). Finally, although many of the analyses were not statistically significant, it is worth noting that, for all six species, birds were, on average, closer to the disturbance when noise was present versus absent (Table 2), which is unlikely to have occurred by chance (binomial test: $P = 0.031$).

## DISCUSSION

We manipulated the presence of anthropogenic noise and light to determine their independent and combined effects on the vocal and spatial behavior of wild birds. When all passerine species were analyzed together, none of the treatments influenced when birds began vocalizing. However, contrary to our predictions, birds were attracted to anthropogenic noise and, depending on the localization settings used, either repelled by or not attracted to anthropogenic light. We found no evidence that birds responded differently to different colors of light. The within-species analyses of six common boreal bird species revealed similar patterns to the passerine analysis, though most of the effects were not statistically significant. There were two exceptions. Swainson's thrush was attracted to noise and the combination of noise and light and was repelled by light when presented in the absence of noise. Yellow-rumped warbler also began singing earlier in the presence of noise.

Traffic noise attracted passerines over spatial scales of 20 to 40 m (Table 2; Figures 1 and 3; Supplementary Materials), which contradicts our prediction and previous studies. Bayne et al. (2008) found that passerine density in the breeding season was lower in areas adjacent to noise-generating compressor stations than in control areas adjacent to quiet, but otherwise similar, oil well pads. Similarly, Blickley et al. (2012) found fewer male Greater Sage-Grouse (*Centrocercus urophasianus*) at leks paired with experimental traffic noise than at silent control leks. Finally, bird densities during the migratory and breeding seasons were lower near real (Reijnen et al. 1995) and simulated (McClure et al. 2016) roads than at sites



**Figure 1**
The effects of noise (noise absent = black; noise present = gray), light, and the interaction between noise and light on the distance to disturbance (or distance to the center of the array for control trials) of the first five vocalizations produced by each species during each trial ($N = 887$ songs from 27 species and 89 trials). Large dots and error bars show mean ± SE, as calculated from a linear mixed-effects model including noise (present vs. absent), light (present vs. absent), and the two-way interaction between noise and light as fixed effects, and array identity and species as random effects (see text for details of models). Marginal $R^2$ (i.e., variance explained by fixed factors) and conditional $R^2$ (i.e., variance explained by fixed and random factors) are calculated according to Nakagawa and Schielzeth (2013) and shown in the lower left of the plot.

**Table 3**
**Effects of light color on song production in passerines**

| Response | Effect | Estimate ± SE | t | P |
|---|---|---|---|---|
| [a]Time | Intercept | 281.1 ± 13.6 | 20.7 | <0.001 |
| | Color (blue) | −36.6 ± 28.1 | −1.3 | 0.198 |
| | Color (cool white) | −0.5 ± 22.0 | 0.0 | 0.981 |
| | Color (green) | 2.0 ± 23.6 | 0.1 | 0.933 |
| | Color (red) | 37.6 ± 23.4 | 1.6 | 0.115 |
| | Color (warm white) | 42.7 ± 30.8 | 1.4 | 0.174 |
| [b]Distance | Intercept | 19.8 ± 0.9 | 21.5 | <0.001 |
| | Color (blue) | −4.6 ± 2.4 | −1.9 | 0.060 |
| | Color (cool white) | 3.7 ± 1.9 | 2.0 | 0.055 |
| | Color (green) | 0.3 ± 2.0 | 0.1 | 0.885 |
| | Color (red) | 1.4 ± 2.0 | 0.7 | 0.486 |
| | Color (warm white) | −4.1 ± 2.6 | −1.6 | 0.119 |

Response variables include the time when each song was produced (minutes past midnight) and the distance between the singer and disturbance during song production for the first five songs of each species. Responses were modeled using linear mixed-effects models (restricted maximum likelihood) with array identity and species as random effects. Estimates are reported for the level of the factor shown in parentheses, relative to the no light condition, and t-tests are conducted using Satterthwaite's method. Only arrays in which the noise treatment was absent were included. $N = 514$ songs from 57 arrays and 24 species. SE = standard error.
[a]Random effects (variance ± SD): array (2357 ± 49); species (2107 ± 46); residual (1942 ± 44).
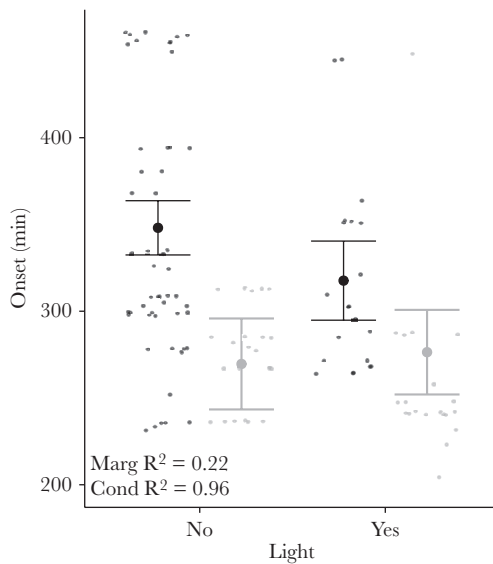[b]Random effects (variance ± SD): array (15 ± 4); species (4 ± 2); residual (30 ± 5).

**Figure 2**
The effects of noise (noise absent = black; noise present = gray), light, and the interaction between noise and light on the time (number of minutes past midnight) of the first five vocalizations produced by yellow-rumped warblers ($N$ = 115 songs from 38 trials). Large dots and error bars show the mean ± SE, as calculated from a linear mixed-effects model including noise (present vs. absent), light (present vs. absent), and the two-way interaction between noise and light as fixed effects, and array identity as a random effect (see text for details of models). Marginal $R^2$ (i.e., variance explained by fixed factors) and conditional $R^2$ (i.e., variance explained by fixed and random factors) are calculated according to Nakagawa and Schielzeth (2013) and shown in the lower left of the plot.

**Figure 3**
The effects of noise (noise absent = black; noise present = gray), light, and the interaction between noise and light on the distance to disturbance (or distance to the center of the array for control trials) of the first five vocalizations produced by Swainson's thrush during each trial ($N$ = 83 songs from 26 trials). Large dots and error bars show the mean ± SE, as calculated from a linear mixed-effects model including noise (present vs. absent), light (present vs. absent), and the two-way interaction between noise and light as fixed effects, and array identity as a random effect (see text for details of models). Marginal $R^2$ (i.e., variance explained by fixed factors) and conditional $R^2$ (i.e., variance explained by fixed and random factors) are calculated according to Nakagawa and Schielzeth (2013) and shown in the lower left of the plot.

away from roads. A possible explanation for our discordant result is that these other studies measured avian densities next to chronic noise that began before birds arrived on the breeding grounds. The density of birds at those sites was likely governed by whether newly arriving migrants (Bayne et al. 2008; McClure et al. 2016) or males establishing leks (Blickley et al. 2012) chose to settle near noisy sites. In contrast, we measured the proximity of breeding birds to a noise source that was introduced into their established breeding territories. It is, therefore, possible that birds avoid noisy sites when choosing where to settle, but approach noise when it occurs within or near their established territories. An alternative explanation is that birds approach novel noise stimuli because they are curious, and then avoid those stimuli after chronic exposure. This seems unlikely because our stimuli typically played for 11.5 h before birds began singing, though it is possible that avoidance occurs only after days or weeks of exposure.

Noise did not affect when birds began singing, as we had hypothesized. Previous studies examining the effects of traffic noise on the timing of the dawn chorus involved natural traffic noise that fluctuated throughout the day (e.g., rush hour). The relatively quiet periods between times of heavy traffic may have provided birds in those studies with predictable periods of relief from acoustic masking, which may have prompted them to shift song production to those times (Fuller et al. 2007; Cartwright et al. 2014). In our study, the simulated traffic occurred at a constant rate throughout the relatively short playback period (05:00 PM until 08:00 AM the following day), thereby providing no predictable cues about when the noise might subside. We also had three different noise stimuli to minimize potential effects of pseudoreplication. All stimuli were of
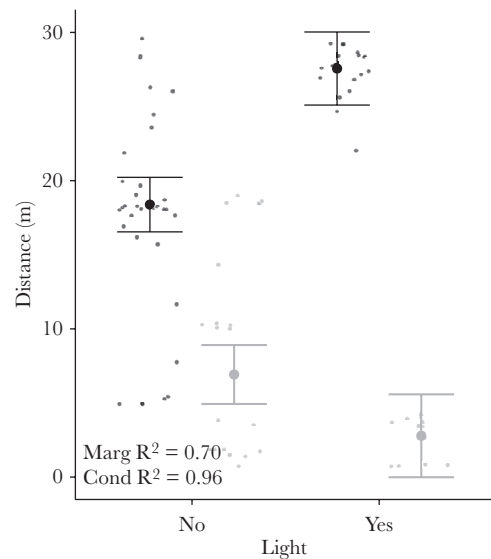
traffic noise, but they included different rates of passing vehicles. It is possible that some species tolerate low levels of noise, and that the onset of singing changes only in response to louder noise or higher rates of traffic. For example, some species may adapt to road noise associated with small, rural road traffic, but not to the constant and intense traffic noise associated with major urban freeways (Reijnen et al. 1995). Another possibility is that these previous studies were correlational in nature and that the reduction in song production during peak traffic times was caused by increased exhaust or light from headlights, rather than by the associated increase in noise (Summers et al. 2011). Additional experimental research is needed to disentangle the effects of noise from the other forms of disturbance that commonly co-occur with noise (e.g., roadways, urban development, vehicles, and exhaust), particularly since the effects of noise on the timing of bird song have been inconsistent in the literature (Ortega 2012; Dominoni et al. 2016).

Vocalizing passerines were not attracted to artificial light when the different colors of light were combined into a single treatment (Figure 1). Depending on the localization settings used, birds may even have been repelled by light. This was surprising because several studies show that birds are attracted to bright lights (Longcore and Rich 2004; Montevecchi 2006; van Doren et al. 2017). However, most of those studies involved birds that were flying during migration or long-distance foraging excursions (Ronconi et al. 2015; van Doren et al. 2017; McLaren et al. 2018). In contrast, our study involved passerines in established breeding territories, suggesting that attraction to light occurs primarily during long-distance flight. Another possibility is that, compared to the lights used in our study,

those used in most previous studies were more visible because they were more powerful and were located in open areas (e.g., oil platforms in the open ocean, light projected skyward, urban glow found above cities; Ronconi et al. 2015; van Doren et al. 2017; McLaren et al. 2018). The lights used in our study were less powerful and were located below the canopy of a dense forest, which likely reduced the light's visibility to birds singing from within the canopy.

Artificial lighting did not cause passerine birds to sing earlier, which contrasts with previous studies (Kempenaers et al. 2010; Dominoni et al. 2013). However, those studies compared birds in brightly lit cities to those living in rural areas with few or no lights. In contrast, our study compared birds' responses to a single dim light versus no light. The intensity of our light treatment was therefore much weaker than in previous studies. Interestingly, Da Silva et al. (2017) also used low-intensity lighting and also failed to detect an effect of light on the onset of dawn song. Together, these studies suggest that the brightness, not just the presence, of artificial lighting may be important in stimulating birds to sing prematurely. This is consistent with Thomas et al. (2002), which showed that species with larger eyes that are more sensitive to dim light begin singing earlier in the morning.

Our species-specific analyses revealed similarities and differences to our overall passerine analysis. First, the species-level analyses supported the finding that passerines are generally attracted to traffic noise. Although the analyses of individual species were generally nonsignificant, birds from all six species were closer, on average, to the noise stimulus than to the silent control, which is unlikely to have occurred by chance. Second, Swainson's thrush was attracted to noise and repelled by light. Passerines were also attracted to noise and, depending on the localization settings, repelled by light, but the effects were much stronger in Swainson's thrush. Of the six species analyzed, Swainson's thrush is the only one classified as an interior forest specialist (Whitaker and Montevecchi 1999). The other five species are categorized as "forest generalists" (boreal chickadee and ruby-crowned kinglet), "open-edge species" (dark-eyed junco, white-throated sparrow), or "ubiquitous species" (yellow-rumped warbler), which all include or tolerate anthropogenic edge habitat in their breeding range. Therefore, habitat specialization and avoidance of disturbed habitat may make Swainson's thrush more sensitive and responsive to noise and light disturbances that occur suddenly within their breeding territories (Bonier et al. 2007). Another possibility is that, because Swainson's thrush forages on the ground (Holmes and Robinson 1988), it may have been more exposed than the canopy-dwelling species to the light and noise stimuli. Third, unlike passerines in general, yellow-rumped warblers sang earlier when noise was present. Yellow-rumped warblers are one of the first warbler species to begin singing in the morning (Morse 1989). It is possible that the forest was quieter, and the traffic noise more obvious, when they began singing, as compared to when most species began singing.

Our approach provided experimental control and passive monitoring of 31 species in a natural context, but it also had several limitations. First, microphone arrays only detect and localize vocalizing animals, which means it is possible that we missed non-vocal responses to experimental treatments. This could not account for the observed attraction to noise but could explain the unexpected finding that birds were not attracted to light. For example, some birds might have approached the light stimulus in silence, whereas others remained distant and singing. A second limitation is that our microphone arrays could only detect and localize birds within 40

m of the disturbance treatments. It is possible that some spatial and vocal responses to experimental treatments occurred beyond this distance, particularly for species with large territories, and that these responses were therefore excluded from our analyses. A third limitation is that our playback equipment needed to be portable, which limited the intensity of our noise and light stimuli. However, all noise and light attenuate with increasing distance from their source, thereby forming intensity gradients. Although our stimuli did not replicate the maximum intensities of light and noise that might be found sporadically in the environment, they undoubtedly simulated intensities experienced by many free-living animals, including those living close to low-intensity disturbances and those living far away from high-intensity disturbances.

Multiple forms of disturbance often co-occur, making it difficult for managers to know which disturbances affect animals and should be mitigated. We found that passerine birds are attracted to traffic noise, but not to light, which often accompanies traffic noise (e.g., streetlights, vehicle headlights). If birds are drawn to traffic noise, then they may experience an increased likelihood of fatal collision with vehicles at roadsides (Kociolek et al. 2011). Although anecdotal, we observed many dead passerines that had been struck by vehicles along the roadways connecting our study sites. Another concern is that attraction to traffic noise may cause birds to reside near roadsides that negatively affect their reproductive success (Halfwerk et al. 2011b) or increase their predation risk (Meillere et al. 2015; Templeton et al. 2016) through the masking of acoustic signals. Being attracted to traffic noise could also increase exposure to air pollution from vehicle exhaust or the risk of poisoning through the consumption of de-icing agents (Kociolek et al. 2011). Our study suggests that conservation biologists and land managers should consider the effects of noise on birds, as well as the use of noise mitigation technologies that reduce noise in vulnerable or ecologically important habitat. Furthermore, given that our trials were conducted in undisturbed areas within the forest, an important future direction would be to repeat our study in disturbed areas to determine whether chronic exposure to noise and light pollution alters the behavioral responses to additional noise observed in the current study.

In conclusion, our study is the first to our knowledge to use microphone arrays to test the independent and combined effects of anthropogenic light and noise on the singing and spatial behavior of wild birds. This promising technology allowed us to passively and accurately quantify the responses of 31 species over a prolonged period of time (8 h per trial) across a broad geographic area (110 sites with blanket coverage over a 30-m radius at each site, or approximately 31 ha). Our results show that birds in the boreal forest are attracted to traffic noise, but not to artificial lighting.

## SUPPLEMENTARY MATERIAL

Supplementary materials are available at *Behavioral Ecology* online.

## FUNDING

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