







SYMPOSIUM

Potential Effect of Low-Rise, Downcast Artificial Lights on Nocturnally Migrating Land Birds

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Synopsis Artificial light at night (ALAN) on tall or upward-pointed lighting installations affects the flight behavior of night-migrating birds. We hypothesized that common low-rise lights pointing downward also affect the movement of nocturnal migrants. We predicted that birds in flight will react close to low-rise lights, and be attracted and grounded near light sources, with a stronger effect on juveniles during their autumn migration. We conducted a controlled longitudinal experiment with light-emitting diode floodlights and considered nearby structures that turn on lights at night. We analyzed 1501 high-resolution 3D nocturnal flight paths of free-flying migrants and diurnally captured 758–2009 birds around experimental lights during spring and autumn 2016, and spring 2017. We identified change points along flight paths where birds turned horizontally or vertically, and we considered these indicative of reactions. Flight paths with and without reactions were generally closer to our experimental site in spring than in autumn when the lights were on. Reactions were up to 40% more likely to occur in autumn than in spring depending on the threshold magnitude of turning angle. Reactions in spring were up to ~60% more likely to occur at ~35 m from the lights than at >1.5 km. In autumn, some vertical reactions were ~40% more likely to occur at ~50 m from the lights than at >2.2 km. Interactions between distance to lights and visibility or cloud cover were consistent with known effects of ALAN on nocturnal migrants. Under poor visibility, reactions were up to 50% more likely to occur farthest from structures in spring, but up to 60% more likely to occur closest to lights in autumn. Thus, the effects of ALAN on night-migrating land birds are not limited to bright lights pointing upward or lights on tall structures in urban areas. Diurnal capture rates of birds were not different when lights were on or off for either season. To our knowledge, this is the first study to show that low-rise lights pointing downward affect night-migrating birds. Although the interpreted reactions constitute subtle modifications in the linearity of flight paths, we discuss future work that could verify whether the protection of nocturnal migrants with lights-out programs would have greater impact if implemented beyond urban areas and include management of low-rise lights.

Introduction

Human-made structures such as roads, border walls, and rows of wind turbines are examples of physical human-made obstacles that can interrupt or block the local and migratory movement of animals (Forman and

Alexander 1998; Cabrera-Cruz and Villegas-Patracá 2016; Liu et al. 2020). However, less tangible anthropogenic factors such as sensory pollution (i.e., the negative impact that anthropogenic stimuli have on the sensory systems of organisms) can also affect the

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movement of animals through different mechanisms (Dominoni et al. 2020). One type of sensory pollution widely spread across the world derives from the excessive and misdirected use of artificial light at night (ALAN; Cinzano et al. 2001; Elvidge et al. 2001; Falchi et al. 2016). The environmental effects of ALAN stem from the disruption to the natural cycle of diel brightness levels that life evolved with, affecting a wide range of biological groups and ecological processes (Longcore and Rich 2004; Hölker et al. 2010), including nocturnal bird migration (reviewed in Gauthreaux and Belser 2006).

Perhaps the best-known effect of ALAN on night-migrating birds relates to their positive phototaxis. Most local-scale studies on the relationship between ALAN and the movement of nocturnal migrants use lights on tall structures, such as communication towers, light-houses, and high-rise buildings, or rely on exceptionally bright lights that shine skyward (Saunders 1930; Johnston and Haines 1957; Verheijen 1981; Dutcher 1884; Larkin and Frase 1988; Jones and Francis 2003; Gehring et al. 2009; Longcore et al. 2012; Parkins et al. 2015; Van Doren et al. 2017; Lao et al. 2020). However, these sources of ALAN are relatively uncommon. Luminaries on communication towers in the United States only account for ~0.1% of public outdoor lighting, while parking lot, street, and roadway lights account for nearly 50% (Buccitelli et al. 2017). By comparison, the number of luminaries in private residences accounts for ~70% of all the lights installed in the United States, with exterior lighting accounting for the highest consumption of electricity. Furthermore, >90% of all single-family housing built in the United States between 2009 and 2019, as well as ~60% of all new multifamily housing built between 1994 and 2019, have one to two floors only (US Census Bureau 2020a), but less than 10% are within urban clusters (US Census Bureau 2020b). Therefore, nocturnal migrants are more likely to encounter low-rise outdoor illumination equally used in rural, semirural, and urban areas, and we need to understand its effects.

Bird orientation is affected by light in a variety of spectra (i.e., colors). Wiltschko et al. (1993) found that silvereyes (*Zosterops lateralis*) in migratory restlessness are disoriented by red lights. This color is related to greater bird mortality at wind turbines (Gehring et al. 2009), as well as to higher numbers of birds and to non-linear flight paths near TV towers (Larkin and Frase 1988; Gauthreaux and Belser 2006). Wiltschko and Wiltschko (1999) found that European robins (*Erithacus rubecula*) are disoriented by yellow but not by blue or green lights; accordingly, Poot et al. (2008) reported greater attraction to red than to green and blue lights. Interestingly, however, artificial light in the green to blue spectrum generally has strong effects on different

groups of wildlife, including seabirds (Longcore et al. 2018). Studies of the effects of ALAN on nocturnal migrants using low-rise lights with brightness similar to those used for outdoor illumination have found that lights in the low end of the spectrum (e.g., blue) attract more birds than light with high wavelengths (i.e., red; Evans et al. 2007; Rebke et al. 2019; Zhao et al. 2020). These studies, however, enhanced the effect of their lights by pointing them upward and/or by setting them close to mist-nets facing the expected direction of migration to analyze what other factors relate to the attraction.

Light-emitting diode (LED) lights with strong emission in the blue spectrum (Falchi et al. 2011) are being used to replace older yellow/orange (sodium vapor) lamps throughout the world (Kyba et al. 2017). Here we used LED lights in the blue to green spectrum to emulate lighting settings similar to those used for low-rise outdoor illumination in a dark, sparsely lit rural landscape to analyze the potential influence of downcast ALAN on nocturnal land bird migrants. Our objectives were to experimentally examine whether this type of lighting elicits behavioral reactions of birds actively migrating at night, and to assess whether it attracts and grounds birds near sources of downcast light.

Exposure to ALAN during nocturnal migratory flights affects different aspects of the flight behavior of individual birds. At a fine scale (<1 km), night-migrating birds fly within 1° or 2° of a straight line (Larkin et al. 1975). However, changes in flight direction, speed, and altitude have been related to ALAN (Larkin and Frase 1988; Bruderer et al. 1999). Reactions of night-migrating birds, such as passerines, to ALAN suggest that visual cues from the ground might influence their flight (Martin 1990, 2017). Hence, we hypothesized that low-rise lights pointing downward also affect the flight behavior of migrating birds. Specifically, we predicted that birds exhibit a greater probability of turning with greater proximity to lights.

ALAN also affects where birds stop over during the day between nocturnal flights (McLaren et al. 2018; Cabrera-Cruz et al. 2020). While stopover densities of birds indicate broad-scale attraction to lights from long distances, presumably by migrating birds during flight, there is also fine-scale (~1 km) avoidance of bright areas, which indicates that migrants may land away from bright ALAN or relocate away from ALAN sources after landfall (McLaren et al. 2018). Evidence that low-rise lights attract and ground night-migrating land birds supports the latter scenario (see Zhao et al. 2014, 2020). This effect may be stronger on juvenile birds during their first autumn migration, as they have stronger attraction to city sky glow (light scattered in the atmosphere) than adults (Gauthreaux 1982), and a greater proportion of light-averse individuals may migrate

during spring (Cabrera-Cruz et al. 2020). Thus, we hypothesized that low-rise, downward-pointing lights also attract migrants during the night, grounding them near the lights, perhaps with a stronger effect on juveniles. We predicted more captures of nocturnal migrants in nets during mornings following nights when experimental lights were on than when the lights were off. We also predicted a greater capture rate for juveniles relative to adult birds during the autumn, but not in spring.

This work sheds some light on the unexplored potential effect that widespread low-rise downcast lights have on the flight behavior and grounding of nocturnally migrating land birds.

Methods

Study area

We conducted our study at one experimental site for the tracking radar and mist-netting methods, and two control sites for mist-netting only. All sites are located within 20 km from the coast of the northeastern corner of the Chesapeake Bay, eastern Maryland (United States; Fig. 1). One of the highest densities of night-migrating birds in the northeastern United States has been registered with the weather radar station closest to our study site in autumn (KDOX, bird density = 151.25 cm²/km²; Farnsworth et al. 2016). Furthermore, habitats around the Chesapeake Bay are consistently used during stopover (Buler and Dawson 2014) as birds negotiate a highly light-polluted landscape (Cabrera-Cruz et al. 2018).

Our experimental site was located at Foreman's Branch Bird Observatory (FBBO), east of the Chesapeake Bay coast (39.227044°, -75.984489°, 0 m above the ground level [AGL]). FBBO is a long-term bird-banding station part of Washington College's River and Field Campus, previously known as "Chino Farms," an Important Bird Area designated due to the presence of Northern Bobwhite (Small and Long 2019; BirdLife International 2020). It is located in Queen Anne's County near the border with Kent County defined by the Chester River (Fig. 1), approximately 8 km east of Chestertown. Next to the bird-banding laboratory lies a mowed area of approximately 15 m x 15 m, where we installed our experimental lights (hereafter experimental plot). At the regional scale, FBBO is located ~45 km south of a major highway (Interstate-95) that connects Baltimore and Philadelphia, two large and highly light-polluted cities within the northeastern US region. However, FBBO is part of a local landscape dominated by agricultural fields with interspersed patches of other habitats such as grasslands, deciduous woods, creeks, and rivers (Gimpel et al. 2010, 2014; Small 2017) and scattered agricultural facilities such as barns, silos, and households. Thus, the extent and

brightness of ALAN in the local landscape is lower than at the regional scale (Fig. 1; Supplementary Fig. 1), making our lights one of the few isolated sources of ALAN in the immediate surroundings.

Our two control sites for mist-netting were in woodlots of the North Bay Adventure Camp and the Harford Glen Environmental Education Center, hereafter North Bay and Harford Glen, respectively. Forest type at North Bay is mixed and Harford Glen is deciduous (Homer et al. 2012). North Bay is in northeast, MD, approximately 29 km north of FBBO (39.491,840°, -75.981,131°), while Harford Glen is approximately 42 km and 315° from FBBO, in Bel Air, MD (39.487,849°, -76.342,280°). At these sites, we did not install nor manipulate sources of ALAN. However, the degree of ALAN intensity around the sites differs. North Bay is within the Elk Neck State Park, with no large housing developments within 5 km, making it largely free of light pollution (Supplementary Fig. 1). Harford Glen is within a state park with the same name, but the mist-netting array is adjacent to a housing development and hence surrounded by more sources of ALAN compared to our other sites.

Experimental lights and design

We installed three unshielded LED floodlights (LE 34000032-DW) on top of two telephone poles located in the periphery of the experimental plot, approximately 15 m apart from each other and facing outward from the experimental plot. We mounted the floodlights ~5 m from the ground, orienting them ~45° downward from the horizontal, thus illuminating the vegetation next to the array of mist-nets around the plot. Each floodlight emitted continuous "daylight" white light through a 120° beam with wavelengths concentrated between 400 and 600 nm (Supplementary Fig. 2), a correlated color temperature (CCT) between 5000 and 6000 K, and a luminosity of 22,000–23,800 lumens. We repeatedly turned our experimental lights on all night for three consecutive days, then off for five days, throughout three bird migration seasons: spring 2016 and 2017 (April 1–May 31), and autumn 2016 (September 1–October 31).

Flight behavior: tracking flight paths with radar

We recorded high-resolution flight paths of individual birds migrating at night near the experimental plot using an Enterprise Electronics Corp tracking radar (X-band) model WF-100 (Enterprise, Alabama, United States). This radar tracks with a minimum range resolution of 2 m and within an elevation range from -2° to 89°. For further details of this unit, see Larkin (2010).

Radar does not identify the objects it detects; hence, we refer to them as targets. However, wing-beat

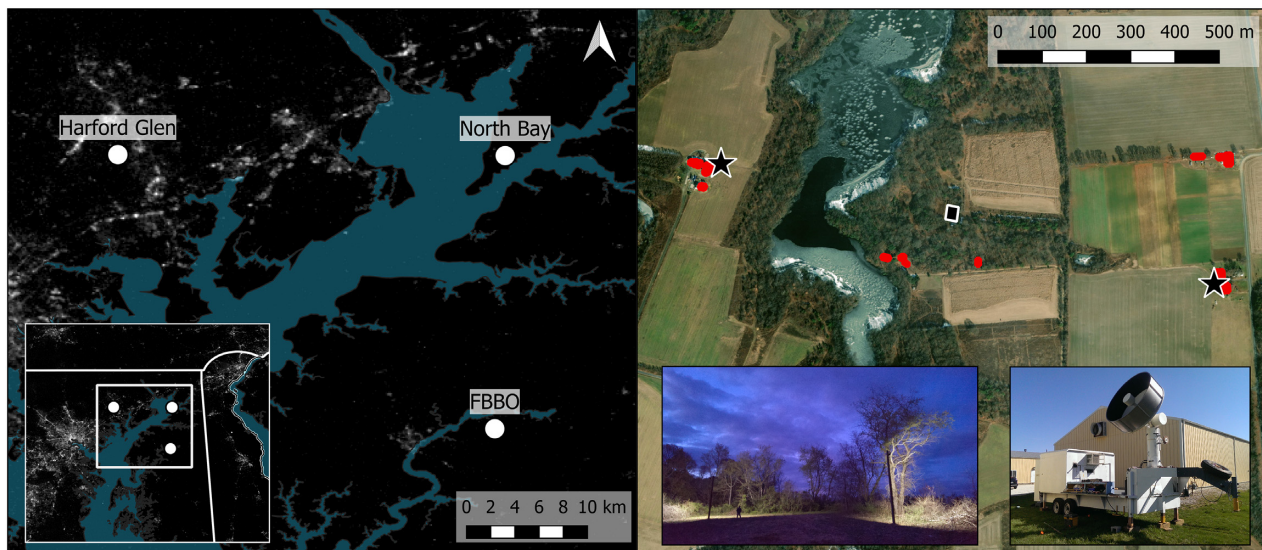


Fig. 1 Location of experimental and control sites (white dots) around the Chesapeake Bay (dark blue) over a nightlight satellite image; white square in the inset shows the same area in relation to the state of Maryland straight-line boundaries. Right: location of our experimental plot at FBBO (black square) and locations of tracking radar in spring and autumn (black stars) with human-made structures in red. Bottom left: experimental lights; bottom right: tracking-radar unit (lights and radar photos: S.A.C.-C.). Color version is available online.

patterns of birds are distinct from insects and are useful for classifying tracking radar targets (Zaugg et al. 2008). We used an oscilloscope to visually inspect the wing-beat patterns of targets in real time (Larkin and Diehl 2012) and stopped tracking targets whose wing beats were not bird like. Wing-beat patterns and flight speeds of bats overlap those of birds (Bruderer and Popalisseanu 2005; Zaugg et al. 2008) but can also perform meandering flights that are uncharacteristic of migrating birds. Custom software produced Cartesian plots of the flight paths as targets were being tracked, and we stopped tracking those that looked highly sinuous (i.e., likely bats). Two-dimensional (2D) plots are, however, a limited representation of 3D movement; hence, before analysis, we created and visually screened 3D plots of each path and discarded those paths with meandering movements (i.e., likely bats) that were not apparent during data collection. Furthermore, to minimize the contamination of our data with nonbird paths or with targets in local movements, we evaluated the straightness of each path, and the airspeeds of the targets, and discarded from analysis those that did not meet specific criteria (see the “Analysis” section below).

We manually controlled the antenna to scan the surrounding airspace within an ~ 5 – 10 km radius around the radar, continually searching for targets flying in a general direction toward the experimental plot. When we detected a target, we switched the radar to automatic mode of operation in which the radar “locked” onto the target and tracked its movement, recording between 0.3 (2017) and 1 (2016) target locations per second, as well

as the time of each detection down to 1 ms. Spherical coordinates of targets were recorded in relation to radar location: radial distance (m), azimuthal angle (0 – 359°), and polar or inclination angle (degrees). Tracking of individual targets stopped when the radar lost the target’s signal or when the radar operator intervened.

To maximize the detection of birds with the narrow beam of the radar, we sampled flight paths only during nights dominated by bird migration assessed by examining real-time patterns of reflectivity from a nearby weather radar (Nilsson et al. 2018). Furthermore, we began sampling 3–4 h before sunrise to increase the likelihood that we would capture potential landfall events of migrating birds. To enhance the tracking radar’s field of view in relation to the seasonal direction of bird migration, we sampled flight paths from two different sites in spring and autumn located within 650 m to the east and west of the experimental plot, respectively (Fig. 1).

Attraction to ALAN: mist-netting and bird capture rates

We captured, banded, and released migratory land birds at our experimental site during the bird migration seasons defined above. The North Bay site did not operate during autumn 2016, and the Harford Glen site only operated in spring 2017. We operated mist-nets daily at all sites except during rain. At the control sites, we operated 10–15 nylon Japanese mist-nets (6 m long, 2.6 m high, 4-shelf, 30-mm mesh). At FBBO, we dedicated to this study a subset of similar mist-nets ($n = 11$) adjacent to the experimental plot and closest to the banding lab.

At each site, we took captured birds to a central banding station/laboratory, where they were banded with standard numbered aluminum bands from the United States Geological Survey (USGS) Bird Banding Laboratory (see the Ethical statement). Before each bird was released, we sexed and aged them to the extent possible following Pyle (1997), and we collected standard biometric data, including wing chord, fat, and mass.

Analysis

Flight behavior: tracking flight with radar

We transformed polar coordinates from the time series of tracking radar measures for each target into a series (hereafter “paths”) of latitude, longitude, and altitude coordinates at a high temporal resolution (~ 0.3 –1 Hz). We edited paths to eliminate erroneous locations and to separate paths of multiple targets sampled in the same radar track. These situations occurred either when the target flew near a structure on the ground and the radar switched to tracking it (condition reflected by a sudden and drastic drop in the recorded altitude) or when the radar beam switched to tracking another target aloft (Larkin and Szafoni 2008).

Not all paths suggested a linear movement, as expected from a migrating bird (Larkin et al. 1975). Straightness index (SI) is a measure of linearity with values ranging between 0 and 1, where 1 indicates a straight line. We estimated SI of each path with the function “TrajStraightness” from the R package “trajr” (McLean and Volponi 2018) and removed from analysis all paths with $SI < 0.85$ assuming that these represented local, nonmigratory movements. We visually inspected and verified that this SI threshold did not remove linear paths with irregularities that may reflect in-flight behavioral reactions.

We estimated the vector of each path relative to the air by subtracting the wind vector from the ground vector (see below). We then estimated the target’s horizontal airspeed by taking the square root of the sum of the vectors and then averaging across the locations in the path. We discarded paths with an average airspeed < 6 m/s because they were likely not migrating birds (Cabrera-Cruz et al. 2013).

Path annotation

Measuring and recording the magnitude of external factors such as environmental conditions co-occurring at every location of an animal along its path of movement is known as annotation (Obringer et al. 2017). Cloudy skies, poor visibility, and low cloud ceiling height exacerbate the attraction of nocturnal migrants to ALAN (Larkin and Frase 1988; Evans et al. 2007; Rebke et al. 2019). Similarly, bird collisions with lighthouses oc-

cur more frequently on nights with little moonlight (Verheijen 1981), indicating a potential effect of moon illumination on the response of birds to lights. Furthermore, wind is the main factor affecting bird flight (Liechti 2006).

We used the Environmental-Data Automated Track Annotation tool (EnvDATA; Dodge et al. 2013) to annotate our flight paths with cloud cover (%), visibility at the surface (m), terrain elevation (m), temperature at the surface (K), dew point temperature (K), and the U and V components of the wind (m/s) (Supplementary Table 1). We used elevation and temperatures to estimate the cloud base height (km) following FAA (2016), and U and V winds to estimate wind speeds for the air-speed calculations described above (m/s), but also to estimate wind support and cross wind. Following Safi et al. (2013), we calculated wind support as the length of the wind vector in the direction of the birds’ flight, where positive values represent tailwind and negative values headwind, while crosswind represents the speed of the wind vector perpendicular to the travel direction irrespective of which side it came from. We first obtained U and V wind data from the 3D (multilevel) NCEP NARR dataset, which EnvDATA’s algorithms interpolated to the locations along each path in all XYZ dimensions. We noticed, however, that not all paths under 255 m AGL ($n = 272$) were annotated fully. (The lower the flight height, the fewer the annotated steps or locations along the path.) Hence, we annotated all paths < 300 m AGL with U and V wind data from 30 m above the surface, also obtained through EnvDATA. Further details of the datasets accessed by EnvDATA for annotation are available in Supplementary Table 1. We used the function “getMoonIllumination” from the R package “suncalc” (Thieurmél and Elmarhraoui 2019) to estimate the fraction of the moon that was illuminated during the nights when flight paths were collected.

Our study site is immersed in a matrix of agricultural lands with scattered buildings, many of which turn on lights at night. Because these local structures may also affect the flight behavior of migrating birds at night and elicit a reaction, we included distance to structures as a predictor variable. We obtained 1-m resolution 2013–2014 land-cover data spanning the geographic extent of all our flight paths from the Chesapeake Conservancy (<https://chesapeakeconservancy.org>). We annotated every path with the Euclidean distance from each location along the path to structures, defined as “human-constructed objects made of impervious materials that are greater than approximately 2 meters in height” (Chesapeake Conservancy, 2016). A visual examination of high-resolution satellite imagery available through the ArcGIS map server (ESRI et al. 2020) confirmed that these structures correspond with buildings

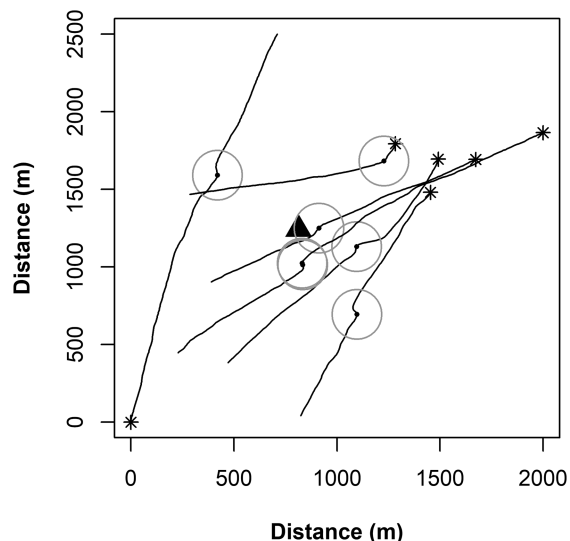


Fig. 2 Selected examples of flight paths near our experimental plot and lights (black triangle) with starting points of paths identified with black stars. Change points of the 99% quantile indicated by black dots along the path, with gray circles showing the potential behavioral reaction.

in the area. We could not corroborate which structures were illuminated because there are no datasets with the geographic resolution needed to resolve lights from buildings that are public and georeferenced (Levin et al. 2020) at the time of this study with the frequency at which we collected flight paths.

Identifying behavioral reactions

Change points are specific locations along a movement path where an animal does something different compared to a series of previous steps with homogeneous characteristics, suggesting a behavioral change or adjustment (Gurarie et al. 2009). Directional change, the angular change between any two successive steps in a path in relation to the speed of such change, provides a measure of nonlinearity (Kitamura and Imafuku 2015). We used the function “TrajDirectionalChange” from the R package “trajr” (McLean and Volponi 2018) to estimate directional changes (in degrees) along each path in the horizontal and vertical planes of movement. For each plane of movement, we pooled the directional changes of all steps of all paths and estimated their 10, 25, 50, 75, 90, 95, and 99% quantiles. We then identified steps along each path with directional changes greater than those thresholds. Thus, change points represent discrete locations where the target’s heading changed to a greater degree than a certain threshold and do not necessarily represent a behavioral reaction. However, change points do indicate the general location along the path where a behavioral reaction occurred (Fig. 2), and the magnitude of the reaction (or magnitude of turn)

relates the threshold level: The higher the quantile or threshold, the stronger the reaction.

We removed any change points identified within the first and last 10 steps of each path because those could be artifacts from the radar switching to or from another target that we might have overlooked during the path-editing process. In order to minimize the probability of identifying spurious change points derived from instrumental error (Bradshaw et al. 2007), we first smoothed the paths using the function “TrajSmoothSG” from the R package “trajr” using polynomial orders 3 and 1, and filter lengths 5 and 11, for paths collected in 2016 and 2017, respectively. The difference in the degree of smoothing obeys to the different resolutions of paths between years, and it did not modify the apparent sinuosity of the paths, nor removed deviations from linearity that may indicate behavioral reactions (Supplementary Fig. 3).

We characterized the potential type of reaction of all change points identified in each plane of movement. For the horizontal and vertical planes, respectively, we measured the horizontal distance and the altitude of the identified change point and of two neighboring locations three steps away. For change points and neighboring locations in the horizontal plane, we estimated their slant range to our lights and categorized the potential reaction of change point by comparing its slant range to that of its neighbors. For example, if the slant range of the change point was shorter than the range of its neighbors, then we categorized it as a reaction toward the location of the lights; if, on the contrary, the slant range of the change point was longer compared to its neighbors, then it was classified as a reaction away. We used five different categories of reactions: toward, away, descend, ascend, and neutral (Supplementary Fig. 4). However, we did not categorize reactions when the location of our lights was within 80° to the front or back of the change point in relation to the main direction of movement of the path (Supplementary Fig. 5). We did this because reactions may have been mischaracterized as toward or away the lights if lights were ahead or behind the target when the reaction occurred. For change points and neighboring locations in the vertical plane, we categorized three potential reactions: ascend, descend, and neutral, and also comparing the altitude of the change point to its neighbors.

Statistical analysis

We tested whether change points occurred in paths that were generally closer to our lights with separate analyses of variance for spring and autumn migration seasons to compare the minimum distances of paths with and without change points to our lights when they were on and when they were off. Here we included as predictors

the main effect of light treatment (on/off) and a binary identifier for change and nonchange points, as well as their two-way interaction.

For each path with at least one change point, we randomly selected one nonchange point >20 locations from each change point to minimize the risk of using environmental information highly correlated between them (Northrup et al. 2013). To analyze whether the distance of change- and nonchange points to our experimental plot varied with season and light treatment, we first estimated their difference by subtracting the distance of nonchange points to lights from the distance of change points, so that a negative value indicated that change points occurred closer to our lights. We then used a separate analysis of variance by plane of movement (horizontal and vertical), specifying the differences in distances as a response variable, as well as the main effect and the two-way interaction of season (spring/autumn) and light treatment (on/off) as predictor variables.

We estimated the probability of change point occurrence each season with the light treatment using seasonal binomial generalized linear models fitted with the “stan_glm” function of the R package “rstanarm” (Gabry et al. 2020). Here we specified the change points and nonchange points identified with each threshold quantile as response variables, and as predictor variables the main effects and interaction of lights (on and off) and season (spring and autumn).

We estimated the probability of each type of change point reaction in the horizontal and vertical planes of movement when the lights were on and off with multinomial regressions for each quantile and season using the function “multinom” from the R package “nnet” (Venables and Ripley 2002; Ripley and Venables 2020). For each regression, we specified the categorized reactions as response, and as predictors the lights’ treatment (on/off), and its interaction with slant range from change points to lights’ location in the case of reactions in the horizontal plane, or with flight altitude of change points for reactions in the vertical plane. For the multinomial models of horizontal reactions, we used reactions “toward” as the baseline to compare all other reactions to; for vertical reactions, we chose “neutral” reactions (i.e., no apparent changes in altitude between the sampled change point and the neighboring locations three steps away). The “multinom” package does not estimate significance values for the model coefficients; hence, we estimated *P*-values using *z*-tests following Hilbe (2020).

We analyzed the potential effect of the environment on flight behavior separately for each season and plane of movement (horizontal and vertical) by modeling the relationship of selected predictors to both change points

and nonchange points from paths sampled when the lights were on. In an exploratory analysis, we fitted binomial generalized linear mixed models to estimate the probability of behavioral reactions, including day of year as random intercepts to account for potential differences in the response of birds to lights throughout the season due to potential taxonomic relatedness of birds migrating during similar moments of each season (Horton et al. 2018). Because the relationship between probabilities of change points and environmental predictors did not vary by date, we fitted simpler (more parsimonious) models. For each season, we fitted binomial generalized linear models where the response variables were the change points and nonchange points identified with each threshold quantile, using the “stan_glm” function of “rstanarm.” In each quantile model, the predictors included the horizontal distance of change- and nonchange points to our lights and to structures, as well as cloud cover, cloud base height, wind support, cross-wind, visibility, illuminated fraction of the moon, and height AGL (m). Because we sampled paths in the second part of the night when birds stop migrating for the night (Bolshakov et al. 2003; Michalik et al. 2020), we also included as predictors time to sunrise, and the difference in flight altitude between the last and first step of the paths, so that negative and positive values indicate descending and ascending flights, respectively. We also included the two-way interactions between distance-to-lights and visibility, distance-to-lights and total cloud cover, and distance-to-lights and cloud base height, as well as the interaction between visibility and distance-to-structures. However, we first tested for a correlation among our predictors with a Pearson’s correlation test and discarded predictors with $r > |0.6|$ (Dormann et al. 2013). For each model, we used three independent Markov chains to estimate posterior distributions with 10,000 iterations each, the first half of which were discarded as warm-up, and we saved every other of the not-discarded iterations as model output. To facilitate model convergence (Kéry 2010), we standardized all predictors to have a mean 0 and standard deviation 1.

We used the default priors set in “rstanarm,” intended to be weakly informative and to provide information on the relative plausibility of parameter values. We used the R package “bayesplot” (Gabry and Mahr 2018) to generate trace plots and assess model convergence by visually inspecting chain mixing. We also inspected Rhat values (i.e., the potential scale reduction factor; Sturtz et al. 2005), making sure that all of the model parameters had a value close to 1.0, indicating good chain mixing and convergence (Sturtz et al. 2005). However, model convergence is no proof of model fitting (Conn et al. 2018). To provide a measure of variance explained by our models, we estimated the R^2 of each model with

a method defined specifically for the Bayesian context (Gelman et al. 2019) following an implementation for binomial models by Gelman et al. (2020).

Furthermore, because the main concern in a Bayesian framework is to obtain a satisfactory posterior distribution (Gelman 2013), we considered an acceptable model to have a posterior distribution consistent with the observed data. We estimated Bayesian *P*-values, which represent probabilities revealing discrepancies between the model and the observed data. For a true model, the Bayesian *P*-value lies near 0.5, while discrepancies are indicated by values close to 0 or 1 (Gelman 2013). The *P*-value is then a measure of discrepancy or similarity between the observed data and the representation that the model makes of it and does not evaluate the significance of a particular predictor variable. We assumed that a predictor had a positive or negative effect on the response if the 80% credible interval of the posterior probability of change point occurrence did not overlap zero, visualized with the graphical representation of the standardized model parameters not overlapping the vertical zero line of a forest plot.

Mist-netting

Because each season and at all sites the majority of captured birds were Passeriformes, we limited our analysis to this order and only considered new daily captures of night-migrating species (Schreckengost 2017). We estimated daily capture rates of migrants (those species listed in the Neotropical Migratory Bird Conservation Act; USFWS 2000) at each site by estimating the total daily number of captures and then dividing by net hours operated in the corresponding day. We calculated age-specific daily capture rates after removing all undetermined-age birds from both seasons.

For each mist-netting day during all seasons, we identified the treatment (lights on/off) applied the previous night at the experimental plot. For all sites, we defined a trial as a consecutive sequence of three days with the lights on and five days with the lights off at our study site. Similarly, for analysis of data from all sites, we considered capture rates from the three days when the lights were on at our experimental plot and from the three days in the middle of the 5-day sequence when the lights were off. That is, we removed from analysis those days with the lights off that were immediately before and after the 3-day lights-on treatment to allow for a 1-day separation between treatments. We then estimated the average capture rates of each treatment (i.e., lights on or off) but only for treatments with at least two days of mist-netting. Finally, we calculated the difference of capture rates within trials by subtracting the average capture rates in the lights-off treatment to those in the lights-on treatment, where a positive value indi-

cates higher captures when the lights were on the previous night.

To compare capture rates between mornings following nights with the lights on and off at our experimental plot, we used an analysis of variance with the difference in capture rates within trials as a response predictor (where a positive value indicated higher capture rates when the lights were on), and season as a single predictor. To compare capture rates between age groups, we first categorized second-year and after-second-year birds in spring as young and adult of the season, respectively; for autumn, we assigned hatch-year and after-hatch-year birds to those same categories. We then estimated the difference in mean capture rates of birds by age group within treatment, so that a positive value indicated higher capture rates for birds of the given age group when the lights were on. We compared age classes with a two-way analysis of variance with differences as the response and the main effect as well as the two-way interaction of age group and season as predictors. To compare among sites, we estimated the difference in mean capture rates per trial for each site, so that a positive value indicates higher capture rates when the lights were on. We then averaged the mean capture rates at the control sites by trial, and compared those to the mean capture rates at the experimental plot with a two-way analysis of variance where difference between sites was the response, and the main effect and two-way interactions of site and season were the predictors.

Results

Tracking radar

In total, we tracked 1501 targets between 3 am and sunrise with a mean path duration of 100 s (range = 7–592). Of those, 16.6% had fewer than 50 steps or locations, 0.9% had an average airspeed < 6 m/s, and 2.4% had an SI < 0.85. Of the 1203 remaining paths, 9.5% had severe irregularities in the horizontal plane, which persisted after applying the smoothing filter, and 28.4% had clear patterned up-and-down oscillations in the vertical plane derived from a damaged antenna mount and difficulty tracking over radar “clutter” from tall trees (Supplementary Fig. 6). After excluding all these, we analyzed 1089 and 861 paths for change points in the horizontal and vertical planes of movement, respectively, with 209, 582, and 298 paths for horizontal analysis and 148, 511, and 202 paths for vertical analysis from spring 2016, autumn 2016, and spring 2017, respectively. The median flight altitudes of paths analyzed in the horizontal and vertical planes were 367.8 and 347.8 m AGL (range 35.9–1324.2 m AGL).

Magnitude of behavioral reactions

The 10, 25, 50, 75, 90, 95 and 99% quantiles of directional changes in the horizontal plane and vertical plane were 0.12, 0.37, 0.99, 2.4, 4.8, 7.1, and 14.8° (range = 0–90°) and 0, 0.84, 2.79, 5.65, 13.28, 19.80, and 40.57° (range 0–81.2°), respectively. Directional changes in the bottom three and four quantiles of each dataset are within or very close to the linearity expected in the fine-scale movement of a migrating bird (Larkin et al. 1975), and, hence, they are probably not behavioral reactions. Therefore, we present results for only the top three quantiles ($\geq 90\%$), where the highest quantile represents the highest magnitude of turn and the strongest behavioral reaction. The interpreted behavioral reactions, however, constitute subtle modifications in the linearity of flight paths, where birds turned but then resumed their linear trajectory in the same general direction of flight (Fig. 2); we did not witness circular paths. Supplementary Table 2 shows details of the number of paths with change points by season and light treatment for each of the top three quantiles.

Proximity of behavioral reactions to experimental lights

Considering a minimum distance to our experimental lights in the horizontal plane in spring, paths with the mildest behavioral reactions (i.e., with change points of the 90% quantile) were nearly significantly closer to the experimental lights than paths without reactions (Supplementary Table 3). There were no differences, however, in the distance of paths with and without the two strongest behavioral reactions (i.e., with change points of the 95% and 99% quantiles) to experimental lights. Nevertheless, paths in spring were consistently and significantly closer to our experimental plot when the lights were on. In autumn, there were no differences in the minimum distances of paths with and without reactions of the two mildest intensity to our lights (Supplementary Table 4), but paths with the strongest behavioral reactions were significantly farther away from our lights; contrary to spring, there were no differences in relation to light treatment. The interaction between behavioral reactions in the horizontal plane and light treatment was not significant at explaining the minimum distance of paths to our experimental lights for any magnitude of reaction and season. For the vertical plane in spring, paths with behavioral reactions of the mildest magnitude were nearly significantly closer to experimental lights than paths without reactions (Supplementary Table 5); paths with any magnitude of reaction, however, were significantly closer to experimental lights when lights were on. In autumn, there were no differences in the minimum distance of paths with and

without change points of any magnitude, or in relation to light treatment, to experimental lights (Supplementary Table 6).

Considering the difference in distance of change- and nonchange points in the horizontal plane to our experimental lights, behavioral reactions of the two mildest magnitudes were nearly significantly closer to experimental lights in spring (Supplementary Table 7), but there were no differences in relation to light treatment or to its interaction with season. For the vertical plane, neither light treatment, nor season, nor their interaction affected distances of behavioral reactions of any magnitude (Supplementary Table 8).

Probability of behavioral reactions

Results from the analyses of variance above suggest that change points occur randomly with respect to whether experimental lights were on or off. Nevertheless, the probability of change points in both planes was significantly different by season (Supplementary Tables 9 and 10; Fig. 3), with change points in both planes more likely to occur in autumn than in spring (Supplementary Figs. 7 and 8).

Types of behavioral reactions

In the horizontal plane and when the lights were on, ascending was the most common reaction, with a 48–63% probability, while the probability of descending varied between 26 and 29% (Supplementary Table 11). Reactions away or toward the lights have consistently $< 10\%$ probability, except for reactions away for turns of the highest magnitude. Neutral reactions were less than 1% likely to be reactions of the mildest magnitude but nonexistent for the strongest. In both seasons, the probability of ascending increased with slant range or proximity of the reaction to our experimental lights, while the probability of descending decreased (Supplementary Fig. 9). Similarly, the probability of reactions toward the lights was slightly higher closer to the lights in autumn and highest for reactions of the highest magnitude, but not in spring. Reactions away from the lights were the lowest overall and did not vary much with proximity to lights or slant range. Except for reactions of the mildest magnitude in autumn (Supplementary Table 12), light treatment had a nonsignificant effect on the probability of reactions in the horizontal plane (Supplementary Tables 12 and 13).

In the vertical plane, the probabilities of ascending and descending reactions were very similar in both seasons, ranging between 44 and 56% when the lights were on in spring and between 44 and 54% with the lights off; in autumn, probabilities ranged between 44 and 54% with the lights off and between 47 and 51%

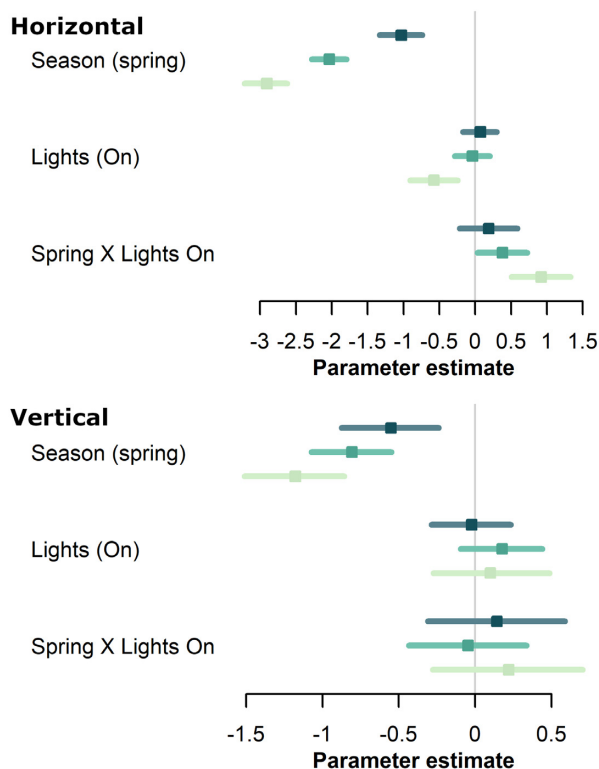


Fig. 3 Credible intervals (80%) from binomial Bayesian generalized linear models of change-point occurrence in the horizontal (top panel) and vertical (bottom panel) planes of movement of night-migrating birds in relation to season and light treatment, for three quantiles of directional change. Each line represents the credible intervals of each quantile regression, with shades of colors within each variable indicating the level of quantile (i.e., light green = 90% quantile, cyan = 95%, darker = 99% quantile; color version available online).

with the lights off (Supplementary Table 14). Neutral reactions (i.e., no apparent change in altitude between change point and neighboring locations) consistently had a probability equal to or lower than 4% during both seasons and light treatment. Flight altitude was not a significant predictor of reactions in the vertical plane of movement in any season (Supplementary Tables 15 and 16); light treatment was significant only for reactions of the 99% quantile in spring.

Predicted probabilities of reactions in the horizontal and vertical planes of movement in relation with slant range and flight altitude, respectively, co-vary with the light treatment (Supplementary Figs. 9 and 10). These results further suggest that reactions occurred independently of our experimental lights.

Modeling of factors influencing behavioral reactions

Our binomial generalized linear models of change-point occurrence in the horizontal plane explained be-

Table 1 Percentage of variance (R^2) explained by and Bayesian P -value (P) of our seasonal models of probability of change points occurring in the horizontal and vertical planes of movement in relation to multiple environmental predictors, for the top three quantiles of directional changes

Quantile	Horizontal				Vertical			
	Spring		Autumn		Spring		Autumn	
	R^2	P	R^2	P	R^2	P	R^2	P
99%	14	0.52	18	0.53	17	0.52	24	0.53
95%	6	0.50	10	0.51	7	0.52	9	0.52
90%	7	0.51	7	0.52	6	0.51	6	0.51

See main text for a definition of P .

tween 7 and 18% of the variance (Table 1; Supplementary Fig. 11), while our models of change points in the vertical plane explained between 6 and 24%. In both cases, the variance explained increase in magnitude of behavioral reactions (or magnitude of turn), and was higher in the autumn models. However, the Bayesian P -values of all our models (Supplementary Tables 17–20) ranged between 0.50 and 0.53, indicating good consistency between the observed data and models' posterior distributions.

Horizontal plane, spring

Change points of the highest magnitude with lights on were not related to proximity to our lights (Fig. 4). Change points of the second and third levels of magnitude, however, are approximately 60% likely to occur close to our lights compared to 30% at the farthest distance measured (Fig. 5). Interestingly, change points of the highest magnitude were also ~60% closest to other structures and only ~35% farthest away. Change points of three top magnitudes are 60–70% likely to occur in relation to strong crosswinds and 25–35% in weak crosswinds. Furthermore, the interaction between distance to structures and visibility was significantly related to change points of the third level of magnitude (90%), such that under poor visibility change points were ~30 and ~80% likely to occur closest and farthest from our lights, respectively, but ~50 and ~35% under good visibility.

Horizontal plane, autumn

Change points of neither magnitude were neither related to distance to lights nor related to crosswinds (Fig. 4), contrary to spring. The interaction between distance to lights and cloud cover, however, was related to the probability of change points of the second magnitude (95%), with change points being more likely to occur far from the lights when the cloud cover was lowest. Specifically, change points farthest from our lights

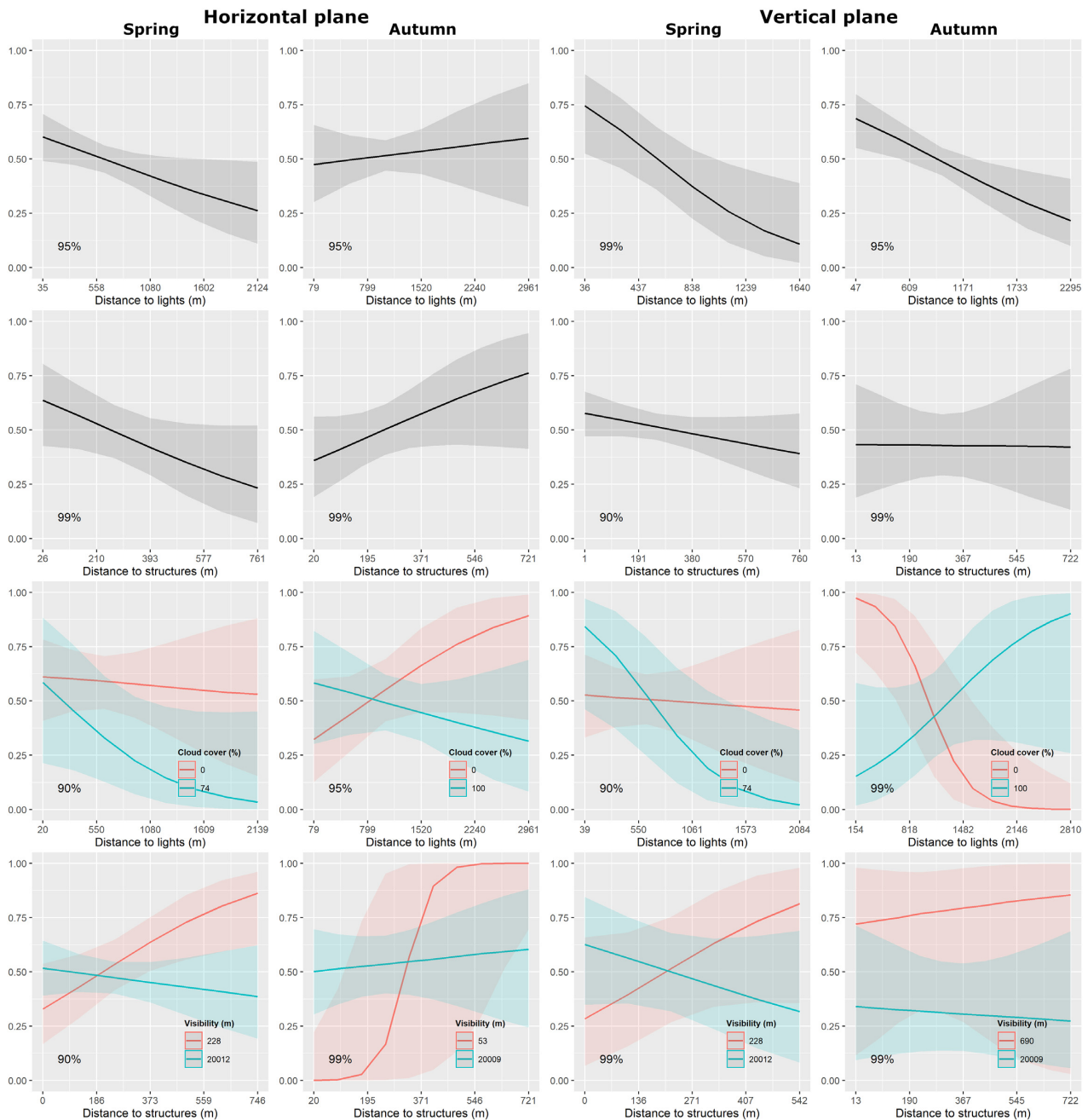


Fig. 4 Probability (Y-axes) of change points or behavioral reactions of night-migrating birds in relation to multiple predictors in the horizontal and vertical planes of movement in spring and autumn (columns 1–2 and 3–4, respectively). From the top to bottom row: distance to experimental lights, distance to structures, interaction of distance to lights with cloud cover, and interaction of distances to structures with visibility. Quantile of change point (see text) is shown at the bottom left of each panel. Legends in the bottom two rows show the minimum (red) and maximum (blue) values of the predictor interacting with that in the X-axis; color version is available online. Similar plots for all predictors and interactions for the 99% quantile included in each model are available in Supplementary Figs. 12–19.

were ~85% likely to occur under a low cloud cover, but ~30% likely under a high cloud cover; conversely, change points closest to our lights were ~60 and ~30% likely to occur under a high and low cloud cover, respectively (Fig. 5). Interestingly, the probability of change points of the highest magnitude was related to the interaction between distance to structures and visibility,

such that they were ~50% likely to occur close to structures under good visibility but ~0% likely under poor visibility; conversely, far from structures, change points were ~100% likely to occur under poor visibility and ~60% likely under good visibility. Change points of the highest magnitude were ~75% likely to occur far from structures but ~30% near to them, opposite to spring.

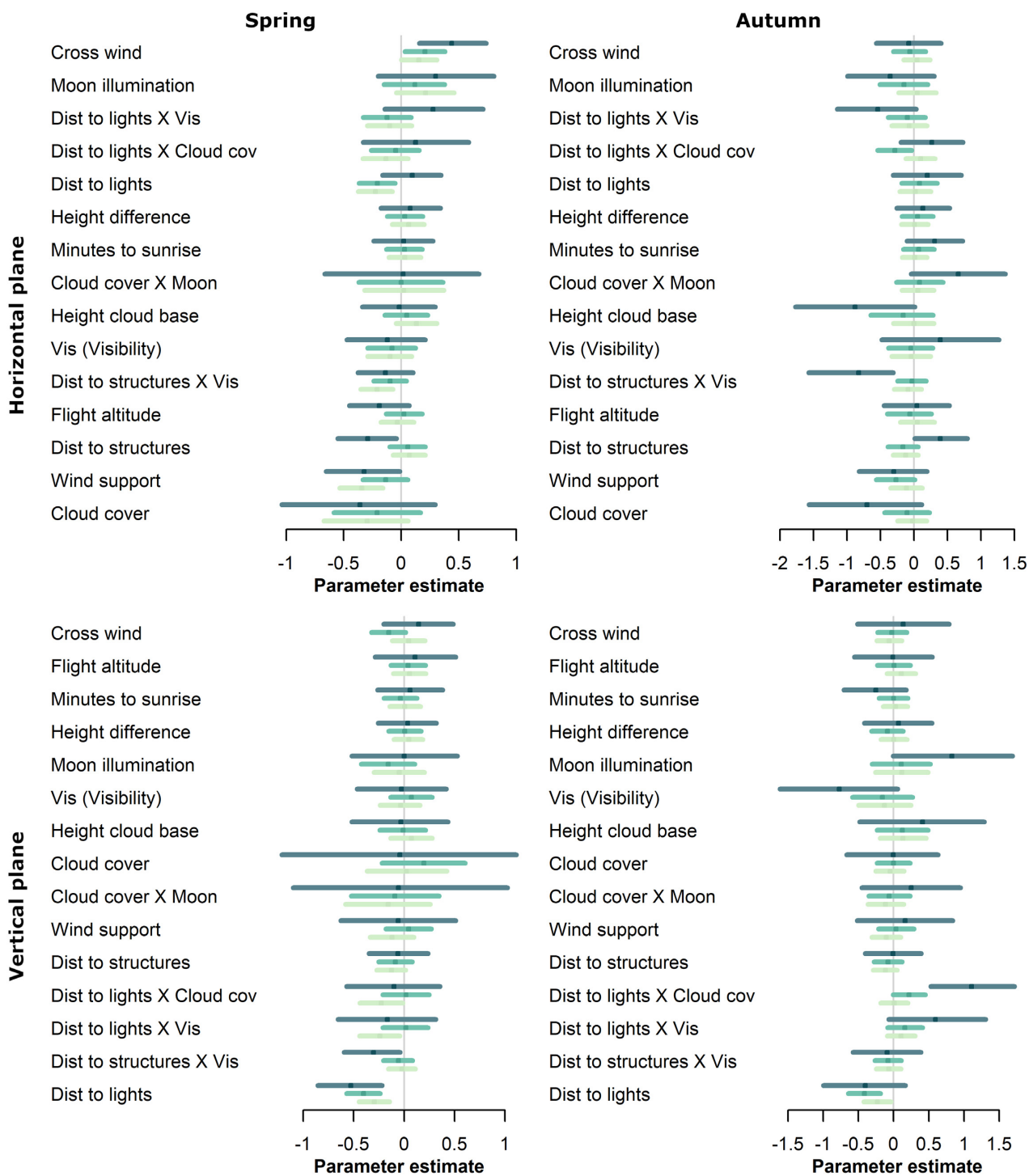


Fig. 5 Credible intervals (80%) of standardized parameter estimates derived from Bayesian generalized linear models of predictor variables that explain change points in flight paths of nocturnally migrating birds on the horizontal plane (top panel) and vertical plane (bottom panel) in spring (left) and autumn (right). Each line represents the credible intervals of each quantile regression, with shades of colors within each variable indicating level of quantile (i.e., light green = 90%, cyan = 95%, darker = 99%; color version available online).

Vertical plane, spring

Change points of the top three magnitudes were ~65–75% likely to occur close to our lights compared to ~10–20% far from them, and the probability of change points of the 90% magnitude was related both to the interac-

tion of distance to lights with visibility and to the interaction of distance to lights with cloud cover. In both cases, the probability of occurrence under a high cloud cover (Fig. 5) and good visibility (Supplementary Fig. 17) closest to lights was ~75% but ~10% or lower at

the farthest distance. Conversely, the probability of occurrence closest and farthest to lights under a low cloud cover fluctuated around 50% (Fig. 5), while under poor visibility, it decreased from ~60 to ~30% (Supplementary Fig. 17). Interestingly, the probability of change points of the highest magnitude was also related to the interaction between distance to structures and visibility, such that under poor visibility they have ~40% chance of occurring closest to structures compared to ~70% at the farthest distances to structures. Under good visibility and closest to structures, the probability is of ~70%, while farthest away, it is ~30%. In contrast to the horizontal plane, the probability of change points in the vertical plane was not related to crosswinds nor to distance to structures, although it was nearly significant for change points of the second and third levels of magnitude, respectively.

Vertical plane, autumn

Change points of the first and second levels of magnitude were more likely to occur near our lights. The interaction between distance to lights and cloud cover was related to the probability of change points of the highest magnitude, such that under the lowest cloud cover they had ~90% chance of occurring closest to lights and nearly 0% at the farthest distance. Conversely, under the highest cloud cover, the probability of occurrence was ~20% at the closest distance, and ~80% at the farthest distance.

Mist-netting

On average, mist-netting stations operated for 51 days each season, and mist-net hours ranged between 2612 and 3246 (Supplementary Table 21). The total number of captured birds was >1500 every season at our experimental plot but <1000 at each control site. For all sites and seasons, >98% of captured birds were Passeriformes. On average, we operated FBBO for 43.7, 50.6, and 51.2 mist-net hours per day in autumn 2016, and spring and autumn 2017, respectively. We operated North Bay for an average of 72.0 and 64.9 mist-net hours per day in spring and autumn 2017, and Harford Glen for 66.6 mist-net hours per day in autumn 2016.

In autumn 2016 and spring 2017, we attempted eight trials at our experimental plot, but only five could be completed due to missed sampling days within the treatment windows. In autumn 2017, we attempted and completed seven trials. We did not find differences in capture rates at our experimental plot by light treatment during any season (Supplementary Table 22). We found no differences in capture rates by age group between light treatments at our experimental plot in autumn (Supplementary Table 23). We mist-netted simul-

taneously at our experimental plot and at least one control site during spring and autumn 2017. We found no differences in capture rates with light treatment between sites during any season (Supplementary Table 24); mean respective differences in capture rates in spring 2017 at the experimental and control sites were 0.009 and 0.013, while in autumn 2017, they were -0.087 and -0.034 (i.e., all close to zero).

Discussion

To our knowledge, this is the first study to document that low-rise downward-pointed lights, perhaps the most widespread kind of artificial lighting, affect the movement of nocturnally migrating birds via experimentation. Previous studies have documented the stark effects of upward pointed lights, or that lights placed at high altitudes along flight paths can have on migrating birds (e.g., Larkin and Frase 1988; Jones and Francis 2003; Gauthreaux and Belser 2006; Evans et al. 2007; Longcore et al. 2012; Van Doren et al. 2017; Rebke et al. 2019; Lao et al. 2020; Zhao et al. 2020). In contrast, our analysis of flight paths (averaging ~1.5 min long) revealed only subtle and temporary deviations from linearity. Circular flight paths occur around lights on top of communication towers and bright beams of light (Larkin and Frase 1988; Van Doren et al. 2017), or birds are attracted and collide against both tall and low structures that are brightly illuminated (Longcore et al. 2012; Winger et al. 2019). Studies encompassing large geographic scales and the effect of night-sky brightness derived from radiance emitted by an indeterminate number of sources of light have found attraction to bright areas, mostly urban clusters, during stopover (McLaren et al. 2018; Cabrera-Cruz et al. 2020). Considering the settings of our lighting installation (downcast lights), as well as the limited spatial scale of our experiment (three sources of light illuminating two edges of a 15 m × 15 m plot surrounded by trees), it may be unsurprising that we observed very subtle reactions on nocturnal migrants in flight, and no attraction of birds on the ground. One interpretation is that light settings similar to ours have a weak effect on attracting nocturnal migrants, which may at least sometimes largely ignore small and isolated sources of light after thousands of years of encountering natural- and human-caused fires, long before the invention of the light bulb. Another mutually exclusive interpretation is that even low-rise downcast lights elicit a behavioral reaction on migrating birds.

Low-rise downcast lights seldom occur isolated. For example, in the United States, parking lot lights alone account for >30% of all luminaries installed in the country for outdoor illumination, while streetlights and roadway lights combined account for >18% (Buccitelli

et al. 2017). These lighting settings are present throughout urban and rural areas alike. Thus, although the settings of our experiment aimed at creating an isolated patch of light in a dark landscape, our study site was in fact part of a sparsely lit agricultural landscape. Analysis of variance showed that the distance of change points to the location of our experimental lights was no different when the lights were on or off, and the frequencies of various turn directions relative to lights (toward, away, up, or down) did not differ by light treatment. Taken together, these results suggest that turns and height changes did not relate to our experimental lights *per se*. However, we discovered *post hoc* that, for all seasons, distance of change points to our experimental lights is positively correlated with distance to the autumn 2016 radar site ($r = 0.75\text{--}0.91$; Supplementary Table 25), where they used bright outdoor security lights to illuminate the premises. Furthermore, the facility at this site (a silo) often emitted a loud engine-like noise from their usual operations. Sounds from the ground are audible at altitudes within those of the flight paths we sampled (Griffin and Hopkins 1974), and nocturnal migrants in flight react to some unexpected sounds (Larkin 1978).

Not all flight paths we sampled were near our experimental plot. We documented potential behavioral reactions as close as 25 m to our lights but also as far as 2000 m, under both lights-on and -off conditions. A 2 km radius around our experimental plot encompasses scattered residences and other farm facilities (Fig. 1). Thus, other lights and, potentially, noise may have compounded or confounded the effect of our “distance to lights” predictor depending on whether they were turned in synchrony or asynchrony to our experimental lights. Hence, we cannot conclusively determine that our experimental downcast lights were solely responsible for the observed responses. However, paths with and without horizontal and vertical behavioral reactions were generally closer to our experimental plot when the lights were on in spring than in autumn, suggesting that there actually was an effect.

Furthermore, our models support the notion that the subtle in-flight behavioral reactions we observed relate to low-rise lights in both planes of movement. In spring, distance to lights was a significant predictor of behavioral reactions in both planes of movement. Reactions in the horizontal and vertical planes were >30 and $>60\%$, respectively, more likely to occur at ~ 35 m from the lights than at >1.5 km (except for reactions of the strongest magnitude in spring). In autumn, the probability of behavioral reactions in the horizontal plane was not related to distance to lights, but some reactions in the vertical plane were approximately

40% more likely to occur <50 m from the lights than at >2200 m.

Light emissions from small aggregations of buildings in isolated towns and villages are detectable from high-resolution satellite images of the earth at night (Li et al. 2019), and the sky glow produced by lighting fixtures with even the minimal possible upward light emission can be detected up to 200 km away by an observer located at a higher altitude (Luginbuhl et al. 2009). Thus, even isolated or scattered low-rise lights are likely to be also visible to night-migrating birds. Our models suggest that change points of the highest magnitude that we measured in the horizontal plane of movement are more likely to occur in close proximity to human structures in spring, but far from them in autumn. The direction of the relationship observed in spring is according to our prediction. For autumn, however, it is opposite to what we expected. The interactions between distance to lights and structures with visibility and cloud cover also have apparently counterintuitive relationships.

The interaction between ALAN and some meteorological variables enhances the positive phototaxis of night-migrating birds. Clouds during overcast nights enhance the scattering of light in rural areas by a factor of 0.8–2.8 (Kyba et al. 2011; Bará 2016), and fog enhances the effect that ALAN in buildings has on birds (Baxter 1971). Nocturnal migrants are attracted to lights and to illuminated structures under foggy conditions (Evans et al. 2007), and circular flight paths around lights on communication towers occur in relation to low cloud heights (Larkin and Frase 1988). Our models show that in spring and under a high cloud cover, vertical reactions of the 90% quantile were $>70\%$ more likely to occur at ~ 40 m from lights than at ~ 2 km, but also were $>60\%$ more likely to occur closest to lights under good visibility. In autumn and under a high cloud cover, vertical reactions of the strongest magnitude were $\sim 75\%$ more likely to occur at nearly 3 km from the lights than at ~ 150 m, while they were $\sim 90\%$ more likely to occur closest to lights under clear skies. Furthermore, in spring, some reactions in both planes of movement were 30–50% more likely to occur farthest from structures under poor visibility but 15–40% more likely to occur closest to them under good visibility. Contrastingly, the strongest horizontal reactions in autumn were 100% more likely to occur farthest away from lights under poor visibility. Thus, reactions under poor visibility conditions occurred closest to lights in spring but farthest away in autumn.

Autumn is the season when hatch-year birds make their first migration. Total captures of birds on the ground match well with migration traffic rates of nocturnal migrants measured with other radar systems during nights previous to the captures, especially during

mornings following nights with no rain (Nilsson et al. 2018; but see Alerstam 1972). At FBBO, we captured two times more juvenile than adult birds during autumn 2016 (Supplementary Table 21). If the age ratios of birds captured on the ground are an indication of the composition of the bird community migrating at night and considering that we operated the radar during nights without precipitation, then we might have sampled a larger proportion of flight paths from juvenile than from adult birds. Juvenile birds are more susceptible to disorientation by light pollution than adults (Gauthreaux 1982). Thus, if structures located within the radius where we identified change points were illuminated at night, as we know some were, then migrating birds in autumn reacting to them from a farther distance may indicate a higher sensitivity to a novel sensory stimulus. The composition of the community of nocturnal migrants in autumn with a larger proportion of juveniles may also explain our finding that change points in both planes of movement are more likely to occur in autumn than in spring, as young birds in general seem to have higher attraction to light than adults (Åkesson et al. 2021). We consider that the observed relationship of change points with distance to lights, distance to structures, and their interactions with visibility and cloud cover supports the idea that low-rise lights affect the flight behavior of migrating birds at night.

Multiple meteorological variables affect the movement of aerial migrants (Becciu et al. 2019), and the response of migrating birds to the same environmental predictor may vary by season. We did not find evidence that cloud cover or visibility elicits either horizontal or vertical reactions alone, but they do interact with lights, as discussed above. Similarly, Rebke et al. (2019), reported attraction of night-migrating birds in response to continuous lights, especially under high-cloud-cover conditions, but also under clear skies. In the vertical gradient, Cabrera-Cruz et al. (2019) documented that nocturnal migrants fly at relatively higher altitudes over bright (light-polluted) urban areas under good visibility conditions in autumn but not in spring; while these results are not directly comparable to ours in terms of flight altitudes, they are similar in that the interaction between ALAN and visibility affects the movement of nocturnal migrants along the vertical gradient.

Wind is an important predictor of nocturnal bird migration intensity (Richardson 1978, 1990; Van Doren and Horton 2018), and it affects multiple aspects of flight at different scales (Liechti 2006; Shamoun-Baranes et al. 2017). Our models suggest that horizontal reactions were 20–50% more likely to occur under strong crosswinds and ~50% more likely under headwinds in spring. In autumn, however, the effect of wind was less influential as horizontal reactions were ~40%

more likely to occur under headwinds, but this effect was only nearly significant. Gusty wind or turbulence is correlated with sudden reactions of individual migrating birds (Larkin 1978), perhaps representing adjustments in the path when the wind blows beyond the gust rejection capabilities of the bird (Cheney et al. 2020), potentially explaining the observed relationships. Vertical reactions were unaffected by either crosswind or wind support.

Movement requires energy. Turning increases the energetic cost of transport for both terrestrial and aerial animals (Wilson et al. 2013), and sinuosity in flight increases the energetic cost of bird movement (Amélineau et al. 2014). The subtle reactions that we observed, particularly those where targets regained their original flight direction, imply an active compensation to their main vector of movement, which likely requires energy. While descending flights or drifting may occur with little energy expenditure, regaining altitude may not (Bowlin et al. 2015). The flight paths that we sampled represent a minuscule fraction of the distances traveled by many nocturnal migrants in the Nearctic–Neotropical migration system, but nocturnal migrants regularly navigate ALAN-peppered landscapes (Cabrera-Cruz et al. 2018). Consequently, the number of reactions that we observed may also represent a minuscule sample of those experienced during their migrations. Although the fine-scale reactions reported here may represent a small contribution to energy expenditure, it does not preclude broader-scale responses and cumulative energy costs.

Despite the potential confounding of our experiment with nearby permanent lights, our results indicate that behavioral reactions do relate to downcast lights, suggesting that the effects of ALAN on migrating land birds are not limited to bright lights pointing upward, lights on top of tall structures, and tall illuminated structures in urban areas. Certainly, further evaluations are needed to corroborate this. The high correlation between distance of change points and the radar location in autumn 2016 suggests that radar detects behavioral reactions better at a close range (i.e., finer spatial resolution closer to radar). Thus, future work evaluating the effect of low-rise lights on birds aloft might consider collecting high-resolution flight paths with a tool other than tracking radar, to avoid correlations of this nature and to be able to sample paths from lower-flying birds. Most important, however, would be choosing a study area with fewer or no sources of artificial light and noise around, or experimenting with more lights spread spatially throughout the study area. Analysis of high-resolution movement tracks using an approach that integrates the three dimensionality of our data or similar data may yield a better perspective of behavioral

reactions. The integration of change point analysis (Gurarie et al. 2009) with potential path volumes (Demšar and Long 2019) might be a promising avenue of research.

Mist-netting did not show support for any of our predictions regarding stopover incidence. Our experimental design maintaining lights on and off for three and five consecutive nights, coupled with our strict requirement of only analyzing data from treatments with at least two days of mist-netting, may have influenced this to some extent. Bird migration occurs in pulses (Gauthreaux et al. 2003). It is possible that our cycle of lighting consistently coincided with days of high or low migration, or that the data we dismissed from analyses to allow for a one-day separation between treatments may have contained information relevant to testing our hypothesis, thus confounding our results. This could be an issue especially for mist-netting at our control sites where sampling effort was more limited than at the experimental plot. We did not measure anthropogenic noise, but this factor reduces the occupancy of otherwise a suitable habitat by species sensitive to loud sounds (reviewed in Ortega, 2012; Shannon et al., 2016), potentially affecting total bird captures and capture rates. Thus, results from our among-site comparisons should be interpreted with caution.

Work analyzing whether low-rise lights ground nocturnal migrants may benefit from larger-scale and longer-term efforts. Random assignment of lights-on and -off treatment blocks could prevent potential conflicts with the pulsed nature of bird migration, and multiple-site comparisons should ideally dedicate equal sampling efforts across sites. Moreover, mist-netting at night might be better suited for identifying attraction and grounding of night-migrating birds to low-rise lights (Zhao et al. 2014, 2020). Alternatively, for daytime mist-netting, focusing on captures from early hours of the morning might help detect a signal of the effect of low-rise lights. Future efforts could test for potential species- or age-specific effects (Gauthreaux 1982; Winger et al. 2019, Elmore et al. 2021), or whether body condition affects ALAN-mediated grounding. Beyond the total number of captures or capture rates, future work could also analyze whether low-rise lights change the community structure of nocturnal migrants (e.g., species composition and abundance), as it does during the breeding period in The Netherlands (Spoelstra et al. 2015).

Concurrent monitoring of nocturnal bird migration with different methods may yield more conclusive and nuanced results. Measurements of nightly migration intensity from weather radars or of local traffic rates estimated with a different method, as well as species identification from acoustic monitoring of night flight

calls, would allow accounting for density and confusion effects. Future analyses could consider and measure the effect of surface albedo at experimental areas, as ground cover and vegetation affect the upward reflection of lights among and possibly within seasons, especially in the northeastern United States (Levin 2017; Wallner and Kocifaj 2019), and this, in turn, may influence the response of migrating birds. Similarly, anthropogenic noise levels could be measured on-site concurrently with bird migration, with attempts to disentangle its effect from that of ALAN (e.g., Senzaki et al. 2020). Furthermore, it is still unknown whether and to what extent anthropogenic-related alterations of the nocturnal landscape, whether physical or sensorial, affect the energetic cost of movement for nocturnal migrants.

It is not necessary for ALAN to be on tall buildings nor even outdoors to have an impact on nocturnal migrants. Collisions of night-migrating birds against low-rise buildings in rural areas are common, and attraction to their lights is a suspected culprit (Hager et al. 2017). Lighted windows are positively associated with bird-window collisions (Parkins et al. 2015), and can be responsible for a large proportion of the night-sky brightness (Bará et al. 2019). The contribution of street and other outdoor lighting to night-sky brightness varies greatly among and within cities (Bará et al. 2019; Kyba et al. 2020). However, relatively simple best practices of lighting such as reducing the brightness of luminaries (Kyba et al. 2020) and fully shielding outdoor lights (Duriscoe et al. 2014) can reduce the city sky glow by 5% and up to 42–88%, respectively. Cox et al. (2020) estimate that the per-capita contribution to light pollution is higher in rural than in urban areas. Hence, best practices may also reduce the contribution from low-rise lights in rural areas, and it can likely reduce the perception of ALAN by night-active aerial animals such as migrating birds moving over nonurban areas. Protection of nocturnal migrants with lights-out programs during migration seasons may have a greater impact if implemented beyond urban areas and were to include management of low-rise lights and reducing light from windows.

Author contributions

J.J.B. and S.A.C.-C. conceived and designed the study and analyses. S.A.C.-C. acquired tracking radar data and coordinated mist-netting efforts across sites. R.P.L. provided training and assistance on tracking radar deployment and operation. M.E.G. and J.G.G. acquired bird-banding data and coordinated work at Foreman's Branch Bird Observatory, including the operation of experimental lights. T.J.Z. assisted with various aspects of the North Bay bird-banding operation. S.A.C.-C.

analyzed all data and wrote a first draft of the manuscript. J.J.B. provided guidance for data analysis and feedback at all stages of manuscript preparation. All authors contributed to and approved the final version of the manuscript.

Ethical statement

University of Delaware Institutional Animal Care and Use Committee (IACUC) authorization number: 1298–2016–0, approved on March 22, 2016, issued to J.J.B. The University of Southern Mississippi provided IACUC approval for North Bay (spring 2017): protocol number: 17081101. Lead bird banders: *Foreman's Branch Bird Observatory*: James Gruber and Maren Gimpel; banding permit held by James Gruber. *North Bay*: Pierre-Alexandre Dumas and Timothy Kita (2016), Julia Shieldcastle (2017); permit for 2016 held by Melanie Dance under Susan Heselton; permit for 2017 held by T.J. Zenzal. *Harford Glen*: Pierre-Alexandre Dumas, Timothy Kita, and Amanda Koss (2016), and Emily Stone (2017); permit held by Amanda Koss under Susan Heselton.

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Supplementary data

Supplementary data available at *ICB* online.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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