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Abstract

The extent of artificial night light and anthropogenic noise (i.e., "light" and "noise") impacts is global and has the capacity to threaten species across diverse ecosystems. Existing research involving impacts of light or noise has primarily focused on noise or light alone and single species; however, these stimuli often co-occur and little is known about how co-exposure influences wildlife and if and why species may vary in their responses. Here, we had three aims: (1) to investigate species-specific responses to light, noise, and the interaction between the two using a spatially explicit approach to model changes in abundance of 140 prevalent bird species across North America, (2) to investigate responses to the interaction between light exposure and night length, and (3) to identify functional traits and habitat affiliations that explain variation in species-specific responses to these sensory stimuli with phylogenetically informed models. We found species that responded to noise exposure generally decreased in abundance, and the additional presence of light interacted synergistically with noise to exacerbate its negative effects. Moreover, the interaction revealed negative emergent responses for several species that only reacted when light and noise co-occurred. Additionally, an interaction between light and night length revealed 47 species increased in abundance with light exposure during longer nights. In addition to modifying behavior with optimal temperature and potential foraging opportunities, birds might be attracted to light, yet suffer inadvertent physiological consequences. The trait that most strongly related to avian response to light and noise was habitat affiliation. Specifically, species that occupy closed habitat were less tolerant of both sensory stressors compared to those that occupy open habitat. Further quantifying the contexts and intrinsic traits that explain how species respond to noise and light will be fundamental to understanding the ecological consequences of a world that is ever louder and brighter.

Ashley A. Wilson and Clinton D. Francis contributed equally.

See also Commentary on this article by Alaasam and Ouyang, 27, 3953–3955.

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1 | INTRODUCTION

Pervasive growth in industrialization and transportation networks now exposes much of the world to anthropogenic night light and anthropogenic noise (henceforth "light" and "noise," respectively). These sensory stimuli pose a global environmental challenge in terrestrial environments (Swaddle et al., 2015). An estimated one-tenth of the planet's land area experiences artificial light at night (Gaston et al., 2014)—a value that rises to 23% if skyglow (atmospheric light pollution) is included (Falchi et al., 2016). Light pollution has the potential to threaten the 30% of vertebrates and 60% of invertebrates that are nocturnal and sensitive to light (Hölker et al., 2010). Responses by sensitive species could cause ecological cascades through processes such as disrupted plant–pollinator interactions (Knop et al., 2017) and altered food webs (Manfrin et al., 2017). Moreover, anthropogenic noise is associated with urban development and transportation networks, as the ecological impact of roads alone is estimated to affect one-fifth of the total land cover of the United States (reviewed in Blickley & Patricelli, 2010) and is increasing in space and intensity (Barber et al., 2010). Studies that have isolated anthropogenic noise to understand its effects have reported decreases in species diversity (Perillo et al., 2017; Proppe et al., 2013) and changes in community structure (Francis et al., 2009). Despite increasing efforts to assess the conversation relevance of impacts of light and noise alone on various taxa, few studies have investigated how aggregate multisensory exposure (henceforth "multimodal") influences wildlife (Swaddle et al., 2015), although these sensory stimuli often co-occur in human-dominated landscapes (Dominoni, Halfwerk, et al., 2020).

Sensory stimulation from light and noise varies from synchronous exposure to asynchronous exposure, both of which can vary within a single day or across seasons (Dominoni, Halfwerk, et al., 2020). For example, species near urban areas or traffic corridors are exposed to excessive noise during periods of high traffic density. These periods overlap with dawn chorus timing and can interfere with conspecific communication, territory status, and reproductive output (Francis & Barber, 2013), especially during the pre-breeding season (Warren et al., 2006). Additionally, light exposure occurs primarily at night, which has the potential to disrupt circadian clocks, photoperiodism, melatonin production, and partitioning of activity between day and night for certain species (Gaston et al., 2013). As such, peak intensities of either stimuli may occur at disparate times, but an organism can be exposed to both sensory stimuli daily and with simultaneous exposure during part of the day in some seasons.

Furthermore, environmental features can affect the propagation and intensity of light and noise exposure. For instance, a study that mapped sound propagation from playbacks in three terrestrial habitats found forests had broader sound pressure level gradients than prairie or urban habitats due to more sound reflection and reverberation (Job et al., 2016). Seasonally changing environmental conditions could also alter an organism's response to sensory stimuli. For example, high thermoregulatory costs and periods of nutritional stress during winter are assumed to increase energy demands (King & Murphy, 1985), yet increased illumination from artificial night light could provide adequate visual information for species to extend diurnal or crepuscular behaviors into the night (Longcore & Rich, 2004). The prolonged perceived photoperiod, especially at higher latitudes with longer nights, could provide the opportunity for extended foraging and increased food consumption (Gaston & Bennie, 2014). As such, the combination of the spatial properties and the relative timing of stimuli exposure provide important contexts for understanding the total physiological stress that an organism experiences at any one time, as well as how it responds to subsequent exposure to additional stressors and their interactions (Gunderson et al., 2016).

Conventional approaches to understanding interactive effects of two or more stressors typically adopt *additive* effects as the null expectation (Crain et al., 2008; Folt et al., 1999). That is, if noise and light both cause a response, the expected magnitude and direction of the combined response are equal to the sum of the effect evoked by noise and the effect evoked by light. However, exposure to one stimulus could potentially enhance or mitigate the effect of the other, or evoke a new emergent response only when both stimuli co-occur (Halfwerk & Slabbekoorn, 2015). These deviations from the expected additive model are known as *cumulative interactions* (Table 1; Dominoni, Smit, et al., 2020; Partan & Marler, 1999; Piggot et al., 2015). While a few studies have investigated the combined influence of light and noise, they primarily focused on a specific behavioral or physiological measurement for a single species (Casasole et al., 2017; Dominoni, Smit, et al., 2020; Dorado-Correa et al., 2016; Raap et al., 2017) or a paired interspecific relationship (McMahon et al., 2017). Of these examples, only Raap et al. (2017) and Dominoni, Smit, et al. (2020) considered additive and one type of cumulative interaction (synergism), but did not incorporate the precision of the effect of the interaction when drawing conclusions. Quantifying uncertainty in the interaction effect size is necessary for assessing relative confidence in the effect, which is especially important for informing management decisions (Piggot et al., 2015) and can help predict responses for when stressors are added or removed from a system (Côté et al., 2016). Therefore, using a systematic approach of determining the magnitude, direction, and precision of interactions can provide novel insight on how the multimodal influence of light and noise influences a wide array of species-specific responses.

Several meta-analyses have quantified taxon-specific responses to understand how species respond to either light or noise pollution individually (Bennie et al., 2016; Kunc & Schmidt, 2019; Owens & Lewis, 2018; Rich & Longcore, 2013; Slabbekoorn et al., 2018), yet this approach may

TABLE 1 Definitions and examples of cumulative interaction responses between two environmental variables

Interaction response	Definition	Example
Antagonistic	The addition of a second variable ameliorates the influence of the existing variable, indicating a diminished response to a composite stimulus compared with either unimodal component in isolation (Munoz & Blumstein, 2012)	The three-way interaction between nitrate, high temperature, and scarring interacted antagonistically to produce less community distance or distinctness on the microbiome of the coral *Pocillopora meandrina* than scarring or high temperature alone (Maher et al., 2019)
Dominant	The presence of two or more variables elicit a strong response, but one variable accounts for most or all of the biological response (Folt et al., 1999)	Herbicide reduces the growth of populations of the model microalga *Chlamydomonas reinhardtii*, yet the reduced growth remains unaltered when microalga are exposed to additional variables, such as nutrient depletion (Brennan & Collins, 2015)
Emergent	A response emerges only when both variables are presented in combination (Halfwerk & Slabbekoorn, 2015)	Chickens (*Gallus gallus domesticus*) ignored chemical and visual warning cues and did not discriminate between palatable and unpalatable formulas when presented in isolation, but were shown to avoid food items when both cues were presented together (Rowe & Guilford, 1996)
Synergistic	The combined effect of multiple variables that exceeds the sum of individual variable effects. The heightened perception of the environment may help the animal capitalize on the multimodal cues and enhance fitness-related factors, or the animal may become more sensitive to the increased variable intensity (Bartlett et al., 2016)	The interactions between acid rain and low pH soils and between acid rain and habitat fragmentation elicited stronger negative influences on the breeding success of wood thrushes (*Hylocichla mustelina*) than the expected sums between each variable combination (Hames et al., 2002)

overlook why species-specific responses to these sensory stimuli diverge in magnitude and direction. Instead, knowledge of the morphological traits and habitat affiliations (henceforth "functional traits"), as well as ecological contexts (e.g., season, daylength, life-history stage) that are relevant to how species detect and interact with acoustic and visual stimuli could not only help explain this variation but also allow specific predictions of evolutionary responses to these anthropogenic stimuli (Hopkins et al., 2018). If functional traits can predict responses of common species to these environmental perturbations, then comparative studies could be used to forecast responses of low abundance, narrowly distributed, or threatened species (Murray et al., 2002). To date, relatively few studies have sought to use trait-based analysis to understand responses to noise or light. For instance, a handful of efforts have been made to describe how changes in abundance in response to anthropogenic noise can be explained by vocal frequencies (Francis, 2015; Goodwin & Shriver, 2011; Proppe et al., 2013). To our knowledge, only one study has used trait-based analyses to understand responses to light (Senzaki et al., 2020). Thus, adopting trait-based analyses represent a promising avenue for understanding the consequences of these sensory stimuli for conservation planning and management.

Here, we had three aims: (1) to investigate multi-species responses when exposed to artificial night light, anthropogenic noise, and the interaction between the two, (2) to investigate responses to the interaction between light exposure and night length, and (3) to identify functional traits that explain variation in species-specific responses to these sensory stimuli with phylogenetically informed models. For the first and second aims, we used avian count data from across the contiguous United States collected through the community science program Project FeederWatch. We used a spatially explicit approach to model changes in presence-only abundance among 140 species in response to the multimodal influence of light and noise, the interaction between light and night length, plus other natural and anthropogenic variables that could influence abundance. For our third aim, we used phylogenetic generalized least squares to test for relationships among functional traits or habitat affiliations and species-specific responses to light and noise.

In general, most studies have reported negative effects of sensory stimuli in relation to an aspect of individual behavior (Rich & Longcore, 2013; Slabbekoorn et al., 2018), and thus we expected most species would decline in abundance with exposure to light and noise. Furthermore, we predicted that the interaction between noise and light would elicit an overall decline in abundance across all 140 species, and the majority of these responses would deviate from the expected additive response as cumulative interactions (Harvey et al., 2013). Despite the many examples of negative consequences of light reviewed above that led to our prediction of an overall decline in abundance, an alternative possibility is that light extends the perceived photoperiod and birds take advantage of usable light. As such, we predicted birds would increase in abundance with artificial light exposure during longer nights. Finally, we expected the functional traits of eye morphology, diet, propensity to form flocks, plus habitat affiliations to influence responses (Table 2).

TABLE 2 Predictions of functional trait relationships with overwintering avian abundance when exposed to light and noise

Functional trait	Explanation	Hypotheses	Stimuli|Predicted effect on abundance
Light gathering ability	The ratio between the corneal and transverse diameters within the eye, which provides a measure of light sensitivity	Birds with better low-light vision are more sensitive to changes in lighting conditions and will respond more strongly to artificial night light (Hall & Ross, 2007)	Light|−
Diet preference	(1) Herbivore (plants, seeds, fruit, and nectar), (2) omnivore (equal proportion of plant and animal diet), (3) insectivore (invertebrates), and (4) carnivore (vertebrates, scavenger)	Anthropogenic noise can conceal biologically relevant cues and interfere with prey detection (Francis, 2015). As such, omnivorous species and those with animal-based diets will be more sensitive to noise. Conversely, the altered perceived photoperiod can extend foraging opportunities for diurnal species (Titulaer et al., 2012), which will propagate an increase in abundance for all diet types	Noise|− Light|+
Flocking behavior	(1) Aggregate in winter flocks, either with conspecifics or mixed species flock, (2) does not flock	Foraging in intra-specific groups can reduce costs associated with noise-induced vigilance (Le et al., 2019). Birds vocalize more frequently when they become disoriented by artificial night light, which attracts additional members of their flocks (Winger et al., 2019)	Noise & Light|+
Habitat preference	(1) Closed (dense tree cover), (2) mixed (partial tree cover), (3) wetlands (ponds, lakes, marsh), (4) open (no tree cover), (5) disturbed (fragmented, developed lands)	Species in open and developed areas are less protected from light and noise, as foliage from canopies shield birds from light (Canham et al., 1990) and acoustic cues degrade with decreasing vegetation cover (Nemeth & Brumm, 2009). Therefore, higher exposures to sensory stimuli will result in decreased abundances	Noise & Light|−
Urban tolerance	(1) Habitat depends on human-made structure, (2) habitat is natural and not human dependent	Urban species that tolerate urbanization will acclimate to anthropogenic stimuli such as light and noise, and will be more equipped to survive in polluted areas (Hu & Cardoso, 2009; McCabe et al., 2018) than non-tolerant species	Noise & Light|+

2 | METHODS

2.1 | Project FeederWatch data

Project FeederWatch is a community science project run by the Cornell Lab of Ornithology (www.feederwatch.org), where thousands of participants report bird observations at feeder locations across the contiguous United States. For a 21-week period from November to April, participants record maximum bird counts per species in two half-day increments. Participants also record the number of observation hours into blocks of 0, 1, 4, and 8 h per sampling event (i.e., effort hours) and geographic coordinates of the feeder. We started with all count data restricted to the contiguous United States from 2007 through 2012. We removed observations that were missing information and limited reported counts to not exceed 30 individuals per species to eliminate potential data entry errors and maintain observations within a more typical range. We then subset the data to only those species with >500 observations across all years to confine analyses to species with a substantial sample size. In total, the dataset consisted of 3,458,576 observations and 140 species (Figure 1; Table S1). However, using a broad-scale community science dataset comes with certain caveats. For example, participants provide abundance data for only species that visit feeders with no information on absences, which could lead to underestimation of responses by species that strongly avoid accessible feeders exposed to light, noise, or other stressors. Nevertheless, these data come with the advantage of providing fine-scale observations across a wide range, and combination, of environmental conditions using a standardized protocol (Table 3).

2.2 | Macroecological variables

2.2.1 | Artificial night light

We estimated mean radiance values (nW) of artificial night light at all locations from 2012 monthly averages based on remotely sensed data acquired by the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB) sensor on the Suomi National Polar-orbiting Partnership satellite. The spatially explicit estimates of point-source light are measured daily and averaged to represent a lunar BRDF-corrected (bidirectional reflectance distribution function) mean monthly value of light that excludes the influences of clouds, terrain, seasons, atmospheric effects, snow, and stray light (Román et al., 2018). We first calculated the mean and then log-transformed the nighttime light estimates across all months to create an annual value and reduce heteroscedasticity in the predictor, created rasters with a 1 km^2 resolution, and extracted the light value at each feeder location.

2.2.2 | Anthropogenic noise

We obtained anthropogenic noise data from recent country-wide geospatial models that estimate acoustic conditions at a resolution
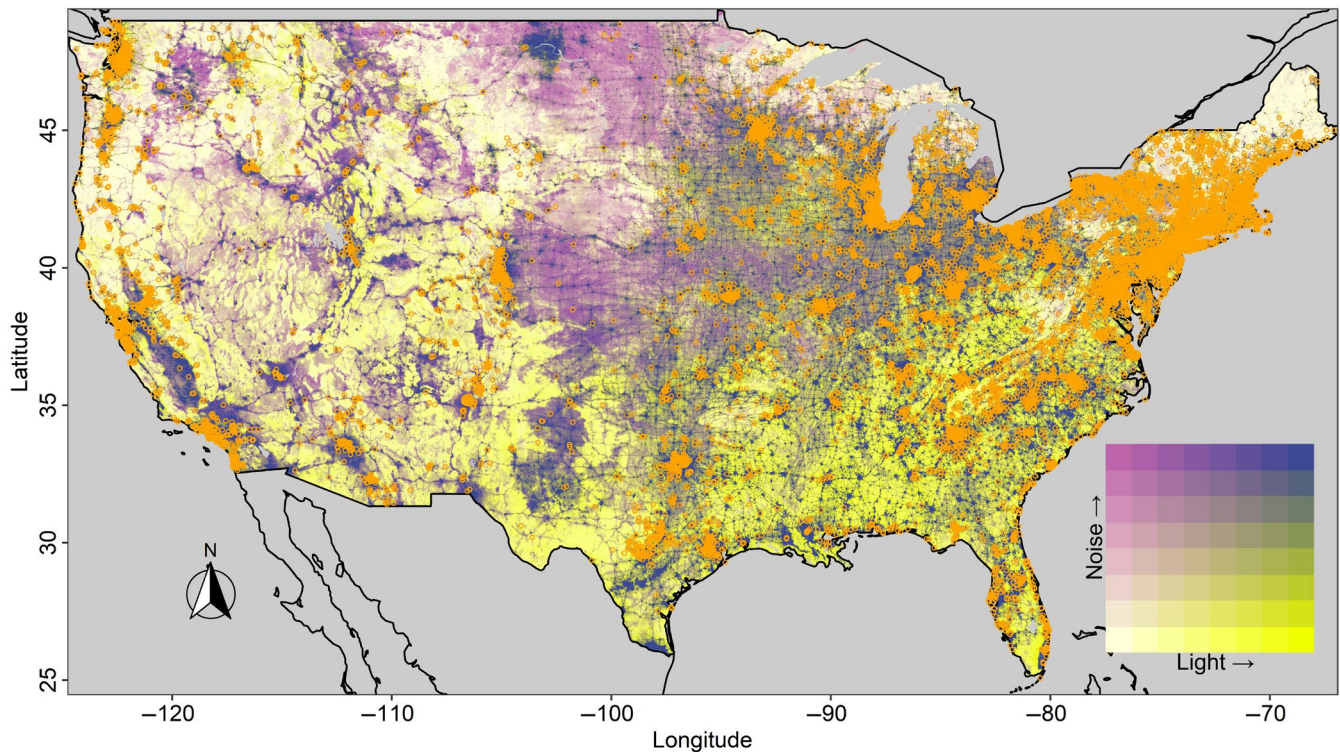
FIGURE 1 Bivariate choropleth map of the United States depicting feeder locations observed by participants in Project FeederWatch (orange points) overlaid on colors depicting the convergence and divergence of artificial night light and anthropogenic noise estimates. Colors depicting sensory pollutants were derived by placing the values of each pollutant's distribution into eight quantiles and then assigning each cell in a raster a value based on the level of overlap of the quantiles for each pollutant at a given location. As such, locations colored pink or yellow represent areas with divergent values where one sensory pollutant is elevated relative to the other (e.g., bright pink = high noise, low light; bright yellow = low noise, high light). In contrast, tan colored areas represent where both pollutants occur at relatively low levels, while the dark purple regions highlight places where the highest estimates of each pollutant converge

TABLE 3 Summary statistics of untransformed predictor variables used in analyses. All variables were centered and scaled in analyses to facilitate model convergence and direct comparison of predictor effects

Predictor	Mean	SD	Minimum	Maximum
Noise (exceedance, dB(A))	10.87	4.19	0.91	32.08
Light (radiance, nW (logarithmic))	0.56	0.71	−1.28	2.28
Human population density (per km²)	656.73	918.70	0.00	41463.00
Percent anthropogenic impervious surface (per 0.27 km²)	16.36	18.05	0.00	100.00
Human footprint (index from 0 to 50)	27.92	11.92	0.00	50.00
Latitude (degrees)	39.83	4.00	25.08	48.95
Night length (hours)	13.60	1.10	10.62	15.77

of 270 m (Mennitt & Fristrup, 2016). Sound models projected the median (i.e., L_{50}) A-weighted sound pressure levels dB re 20 μPa (L_{A50}), which represents the A-weighted sound pressure level that is exceeded half of the time and is less sensitive to infrequent, loud events (Klingbeil et al., 2020). By changing model inputs from their current values to minimize anthropogenic factors, the geospatial sound model estimated a natural sound level that includes contributions from biotic and physiographic sources only. To characterize the anthropogenic component of the acoustic environment, we used "exceedance" sound levels (Buxton et al., 2017). These values were calculated by the logarithmic subtraction of estimated natural median sound levels from existing median sound level estimates (i.e., natural and anthropogenic) and are expressed in A-weighted decibels (dB(A)).

2.2.3 | Urbanization

Because sources of light and noise are related to anthropogenic activity and development, we included metrics of urbanization to control for the influence of other aspects of anthropogenic activity extraneous to the environmental stimuli we sought to study. Anthropogenic impervious surface can reflect the intensity of human use within the landscape by quantifying artificial covers, such as roofs of buildings and roads. For this variable, we obtained 30 m spatial resolution grid of percent developed imperviousness from the 2011 National Land Cover Database (Xian et al., 2011), which we scaled up to a resolution of 270 m to match the resolution of our noise data prior to matching impervious surface values to feeder coordinates. To quantify human population density, we used the 2010 US Census (United States Census Bureau, 2010) block data downscaled to 1 km grids (Nelson et al., 2015). The human footprint index spans 0–50 and reflects eight human pressures at 1 km^2 resolution in the years 1993 and 2009, making it the most complete and highest-resolution globally consistent terrestrial dataset on cumulative human pressures on the environment (Venter et al., 2016). We extracted values from the 2009 dataset because it aligned most closely with the years of PFW observations used in this study.

2.2.4 | Duration of night

To determine whether responses to night light depend on night length (i.e., an interaction between the two), we calculated the duration of night from the latitude and Julian date of each observation using package *geosphere* in the statistical program R (v. 3.6.1; R Core Team, 2019) and subtracted the photoperiod length from the daily 24-h period.

2.3 | Species-specific response models

We used the total number of individuals per species (abundance) as the response variable and used the previously mentioned macroecological variables as fixed effects. We also included latitude as a fixed effect in our models because it correlates strongly with variation in energy, predation risk, climatic gradients, and other aspects of environmental variation (Hillebrand, 2004). Because the estimates for light and noise were on a log-scale, we log-transformed the remaining variables, and then centered and scaled all variables with a z-transformation. Additionally, we incorporated interaction terms between artificial night light and anthropogenic noise and between light and night length. To account for the potential influence of variation among observers, we used participant ID and the number of observation effort hours as random effects. We also included the winter season of observation (e.g., winter of 2007–2008) as a random effect to account for large-scale variation across winters. We log-transformed the count data and, owing to the large sample sizes, in preliminary

analyses found models performed well with Gaussian error, which was used for all models.

For each species, we compared models with and without the Matérn correlation component in the *fitme* function of the R package *spaMM* (Rousset & Ferdy, 2014). The Matérn correlation component is described by two correlation parameters, the scale parameter ρ, and a "smoothness" parameter ν. By fixing $\nu = 0.5$, we evaluated spatial models with the exponential spatial correlation exp($-\rho$*distance). Best fit models were designated by having the lowest AIC value. To decrease the computation time for the spatially explicit models, we rounded latitude and longitude coordinates to 1 decimal place, providing a resolution of 11.1 km, which should still capture spatial variation in major environmental gradients that may influence abundance. Finally, due to computational demands, for species with more than 100,000 observations, we randomly subset the data to 20,000 observation pseudoreplicates and ran the models 10 times with and without the spatial correlation structure. We then averaged all the estimates for spatial and non-spatial models and used averaged AIC values to determine whether the spatial or non-spatial model received more support from the data. We generally favor a more nuanced approach to interpreting the size and precision of effects than dichotomous significance testing (Amrhein et al., 2019; Hulbert et al., 2019; Senzaki et al., 2020). However, this can be difficult when considering many models. As such, we used 85% confidence intervals (CI) that do not overlap zero to identify apparent effects that warrant some consideration for inference (Arnold, 2010; Kleist et al., 2018; Ware et al., 2015). Because CI estimates require re-running linear mixed-effect models (LMMs) iteratively for each parameter estimate with the *fitme* function, and because computational demands of many of the spatial models required runtimes of several days, for practical purposes we calculated CIs as the s.e. of the parameter estimate multiplied by 1.44. We verified this approach provides nearly identical CIs as those calculated with the *fitme* function by comparing CIs from both methods for a subset of species using both spatial and non-spatial models (Table S9). To assess general trends of how species respond to light and noise, we calculated the weighted means and standard errors by summing the product of each species' estimate and sample size and dividing by the total number of observations.

2.4 | Testing for multicollinearity

Anthropogenic noise and artificial night light levels are often correlated with one another and other environmental variables associated with human activities (Halfwerk & Slabbekoorn, 2015; McMahon et al., 2017; Swaddle et al., 2015), necessitating careful inspection of models for issues of multicollinearity. Because functions to check for multicollinearity in fitme models are not readily available, we checked for potential collinearity and redundancy among the explanatory predictors by calculating the Variance Inflation Factor (VIF) among non-spatial models using the *lmer* function in the R package *lme4* (Bates et al., 2014). We obtained the maximum VIF

value for each species-specific model and assessed potential issues of multicollinearity if VIF >10 (Dormann et al., 2013, Table S3). For the five species with VIF >10, we removed non-light and non-noise parameters with the greatest VIF value in a reduced model until the maximum VIF value was <10 (Table S4). If the reduced model did not change the interpretation of the influence of these parameters (e.g., estimates in full and reduced model both had 85% CIs that did not overlap zero), then we kept the original full model. Spatially explicit and non-spatial models were used if they were the best fitting model per species as previously described.

2.5 | Interpreting interaction direction and magnitude

For the interactions, we tested Noise:Light and Light:Night Length. We treated the additive response between interaction terms as the null model (Crain et al., 2008; Folt et al., 1999), where we would expect the interaction response to equal the sum of the effect sizes between variable A and variable B (henceforth denoted as "E" for expected response). If the expected effect size overlapped with the 85% CI of the interaction response (henceforth denoted as "I" for a species-specific model), then it was labeled as an additive response (Galic et al., 2018; Figure 2). Non-overlapping responses deviated from the expected additive model prediction and were labeled as a cumulative response. However, assuming interactions are cumulative based on whether they are more negative or positive than expected may lead to erroneous conclusions about the direction of the effect or the role of local context (Piggott et al., 2015). As such, we incorporated a systematic approach of evaluating and defining cumulative interaction responses with the magnitude and direction of the effect sizes of variables A and B (Piggott et al., 2015; Table 1; Table S5). A positive antagonism is less positive than expected, and a negative antagonism is less negative than expected, but neither exceeds the effect size of either variable A or B. Note that a negative antagonism can result in an overall positive response but the
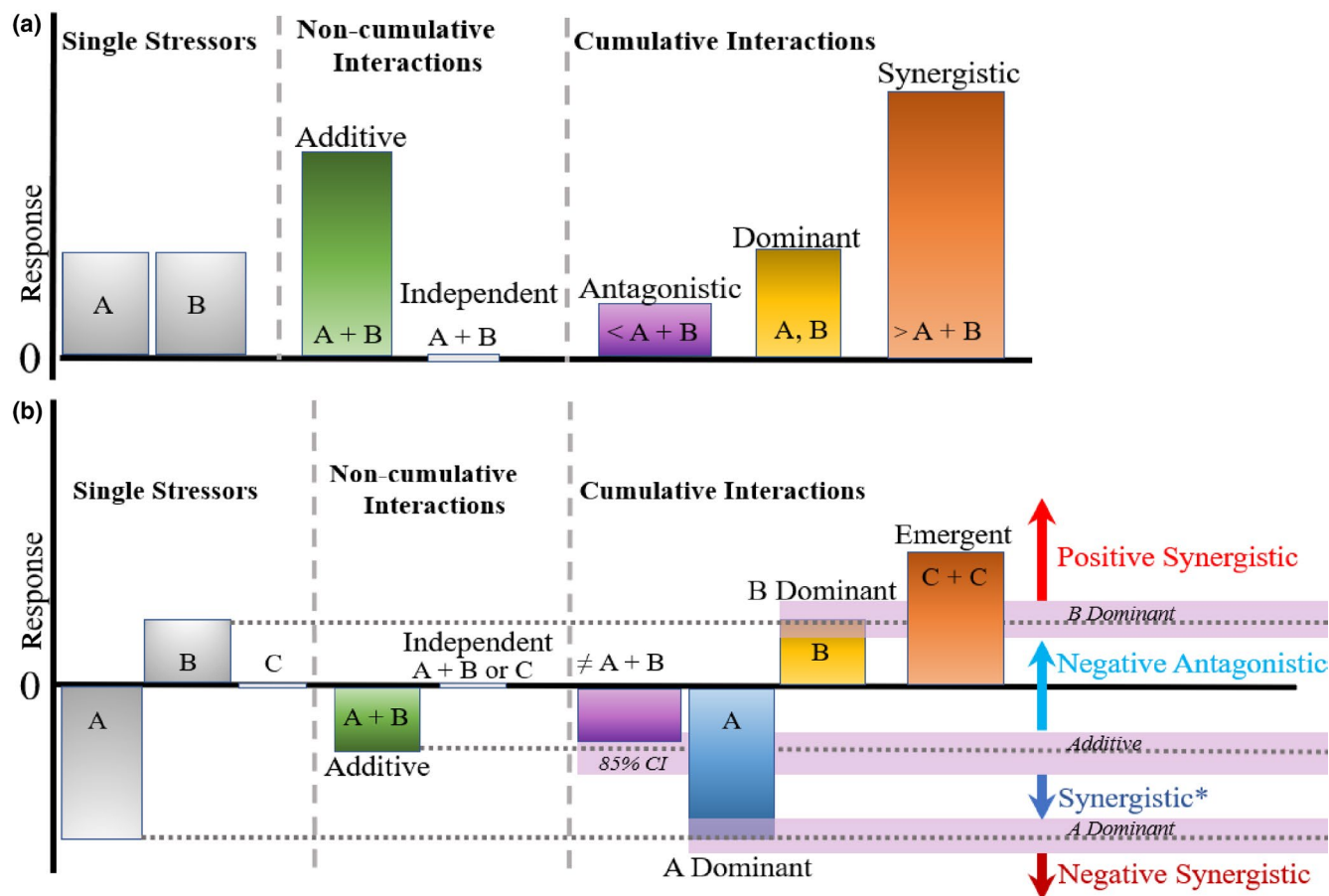

FIGURE 2 Conceptual approach to interpreting interaction types determined from the magnitude and direction of the interaction effect in absolute terms, as adapted from Côté et al. (2016) and Galic et al. (2018). (a) Non-cumulative interactions occur when the effect size is equal to the summation between two variables (A + B) or is independent with no response. Deviations from the expected null model result in cumulative interactions, where the response is less than (antagonistic or dominant) or more than (synergistic) expected. (b) The interaction type and direction from variables with opposing effects is evaluated by whether the effect size of the interaction response overlaps with the 85% confidence interval (85% CI, purple bands) of additive and dominant responses, and whether the magnitude is greater or less than the expected null model. Emergent interaction responses can arise when species only respond to the combined efforts of both variables (C + C; Halfwerk & Slabbekoorn, 2015)

interpretation is the interaction elicits a response that is less negative than expected; for example, if $-A + B = -E < I < B$ (Figure 2). A positive synergistic response is more positive than expected, and a negative synergistic response is more negative than expected, and both are greater in magnitude compared to the effect size of either variable A or B. These responses can also occur if the interaction response has an opposite direction compared to the individual variables; for example, $A + B = -I$ is a negative synergistic response. However, we also included a synergistic* response from Galic et al. (2018) for interaction responses that were more positive or negative than expected but less than the individual variable effect sizes; for example, if $-A + B = -E > -I > -A$ (Figure 2). If a species did not respond to either individual variable (with an effect size equal to "C") but responded when both variables were present ($C + C > E$), then the resulting cumulative influence would be an emergent response, which can also be considered positive or negative synergistic as quantified above. We also labeled cumulative interactions as dominant, where one variable accounted for most or all of the biological response, and was determined if a variable effect size overlaps with the 85% CI of the interaction response ($A + B = A$ or B; see Folt et al., 1999). However, if a species-specific model met both of the criteria for dominant and additive responses, we were not able to discriminate between the two categories and labeled it as indistinguishable. Moreover, if a species responded to at least one variable but not the interaction between them, then the single variable(s) response was independent from the added multimodal influence. Finally, we concluded that a species was uninfluenced by light, noise, or night length if a species did not respond to any stimulus individually or via an interaction.

2.6 | Selection of species traits

To analyze whether predictive traits explained species-specific responses to light and noise, we gathered readily accessible trait data reflective of morphology, behavior, and ecology (Table S7). We obtained diet preferences and average body mass from the EltonTraits 1.0 database (Wilman et al., 2014). To condense the number of factors for diet preference, we categorized species with the "PlantSeed" and "FruiNect" diets as herbivores, "Omnivores" remained as such, any "Invertebrate"-based diet that were specifically arthropods were labeled as insectivores, and "VertFishScav" were labeled as carnivores. To capture seasonal changes in diet for some species, we refined this categorization to reflect winter diets with descriptions from Birds of North America Online (Rodewald, 2015), resulting in 12 species (8.3% of species) altering their diet preference to "Herbivore." We obtained measurements of average wing chord and bill length for 73% of the species from Lislevand et al. (2007), and the other 27% were supplemented from various sources (see Table S7). We obtained body length, habitat association, and non-breeding flocking behavior data (one or zero for either conspecific or mixed species flocks) from Birds of North America Online (Rodewald, 2015). We classified urban tolerance based on habitat affiliation

descriptions from Birds of North America Online and following Hu and Cardoso (2009).

To obtain a variable indicative of a species' visual sensitivity to light, we used the ratio of the corneal diameter to the transverse diameter within the eye (henceforth "light gathering ability"), which scales values to the size of the visual system and animal (Hall & Ross, 2007; Kirk, 2006). We obtained direct measurements of the corneal diameter and transverse diameter for 66 and 62 of the 140 species, respectively, from several sources (Ritland, 1983; Blackwell et al., 2009; Hall et al., 2009; Moore et al., 2013; Tyrrell & Fernández-Juricic, 2017, unpubl. data). For the remaining 78 species, we imputed missing values using the *phylopars* function in package *Rphylopars* (Goolsby et al., 2017), which uses a phylogeny and an incomplete feature matrix that describes the available observations on one or more continuous features (Bruggeman et al., 2009). Estimation of missing parameters is computed by combining the known phylogenetic and phenotypic covariances with the tree topology, which is represented by a "Brownian motion" phylogenetic model. For imputation, we used a recent class-wide avian phylogeny (Jetz et al., 2012) and a feature matrix including body mass (g), body length (mm), and wing chord (mm), bill length (mm), the proportion of a species diet that consists of invertebrates, fruit, nectar, seeds, and other plant material from the EltonTraits 1.0 database, nocturnality (one or zero), plus several measurements of eye geometry: eye corneal diameter (47% complete), eye transverse diameter (44% complete), and eye axial diameter (45% complete). Finally, we divided the complete compilation of corneal diameters by the transverse diameters to obtain the light gathering ability.

2.7 | Trait relevance to species-specific responses

To test for relationships between responses to light and noise with functional traits, we used phylogenetic generalized least squares (PGLS) with the *gls* function in the R package *nlme* (Pinheiro et al., 2015). We simultaneously estimated phylogenetic signal (λ) of the model (Revell, 2010) where phylogenetic strength was evaluated on a scale between 0 and 1. In the event that PGLS estimated lambda outside of this range, we fixed lambda to the respective minimum or maximum bound. Furthermore, we accounted for the precision of estimated responses to light and noise by including a weighting function with fixed variance of one over the square root of the standard error of the response estimate (Garamszegi, 2014). Trait influence on bird responses to noise or light was assessed one at a time to facilitate interpretation of phylogenetic structure in the relationship between single variables and responses to noise or light. Diet preference, habitat preference, urban tolerance, and flocking behavior were used for both noise and light responses. Light gathering ability was only assessed in models explaining variation in response to light. To avoid potential heteroscedasticity from phylogenetic outliers, we removed any species with a studentized residual ≥3.0 and reran the PGLS analyses (Jones & Purvis, 1997; Medina & Francis, 2012). Below we report the relationships between functional traits and avian responses from models where phylogenetic outliers were removed but

also include model results with and without phylogenetic outliers in the supplement (Table S8). We considered the impact of a trait influencing responses to light and noise if the confidence interval did not overlap 0, and we report 95% CIs to reflect higher precision of estimates and 85% CIs for other apparent trends that warrant consideration for inference (Arnold, 2010). Phylogenetic structure in responses (±SE) was analyzed using the *fitcontinuous* function in the *geiger* R package (Harmon et al., 2008).

3 | RESULTS

3.1 | Macroecological variables

Spatial models outperformed non-spatial models for 86 of 140 species, and there was a tendency for spatial models to outperform non-spatial models for species with more than 10,000 observations (Table S1). Parameter estimates from each approach were nearly identical for species with smaller sample sizes, but tended to diverge more for those with larger sample sizes (Table S2). Of the 140 species modeled, 69 species (49% overall) had a unimodal response to either artificial night light or noise. In general, species experienced a negative response when exposed to anthropogenic noise, but because of the mixed responses the overall effect across all species was not strong (overall weighted-mean β = −0.014, 85% CI: −0.045, 0.018; Figure 3). Importantly, variation in species-specific responses to anthropogenic noise displayed moderately strong phylogenetic structure (λ = 0.65, Figure S2). Among the 56 species (40% overall) that responded to anthropogenic noise, the mean apparent trend was avoidance (weighted-mean β = −0.034, 85% CI: −0.066, −0.001). Species experienced a weak positive response when exposed to artificial night light (overall weighted-mean β = 0.003, 85% CI: −0.033, 0.039; Figure 3), yet due to varying species responses, the overall effect across all species was negligible. In

contrast to responses to noise, we found no evidence that variation in response exhibited phylogenetic signal (λ = 0, Figure S3). Only 28 species (20% overall) responded to light exposure and the mean apparent trend for these species was weak avoidance (weighted-mean β = −0.008, 85% CI: −0.044, 0.028). Both light and noise elicited avian responses similarly to other broad-scale urbanization factors (Figure S1). Considerable heterogeneity in responses to other variables reflective of urbanization revealed similar, weak weighted-mean effects, such as impervious surface (42% response, overall weighted-mean β = −0.006, 85% CI: −0.022, 0.010) and human footprint (16% response, overall weighted-mean β = 0.001, 85% CI: −0.005, 0.006). Human population density revealed a weak negative apparent trend similar to that of noise, but the proportion of species that responded was smaller (37% response, overall weighted-mean β = −0.033, 85% CI: −0.063, −0.003).

3.2 | Interaction between artificial night light and anthropogenic noise

We found evidence for an interaction between light and noise for 50 species. When exposed to both sensory stimuli, 35 species (70% of interaction responses) experienced a negative response to the multimodal influence, yet again because of the mixed responses the effect was weak (weighted-mean β = −0.014, 85% CI: −0.028, 0.001; Figure 4). Of all interaction responses, 11 species had a non-cumulative response, where four species had an additive response where the expected response overlapped with the 85% CI of the actual response (Figure 4, Table 1, Table S6). For example, red-breasted sapsuckers (*Sphyrapicus ruber*) had an expected response of 0.014, which overlapped with the 85% CI of the actual response ($\beta_{\text{Interaction}}$ = 0.022, 85% CI: 0.007, 0.034; Figure 5; Table S1). In all, 39 species experienced a cumulative response that deviated from the expected additive model (Figure 4, Table S6). Five species experienced an
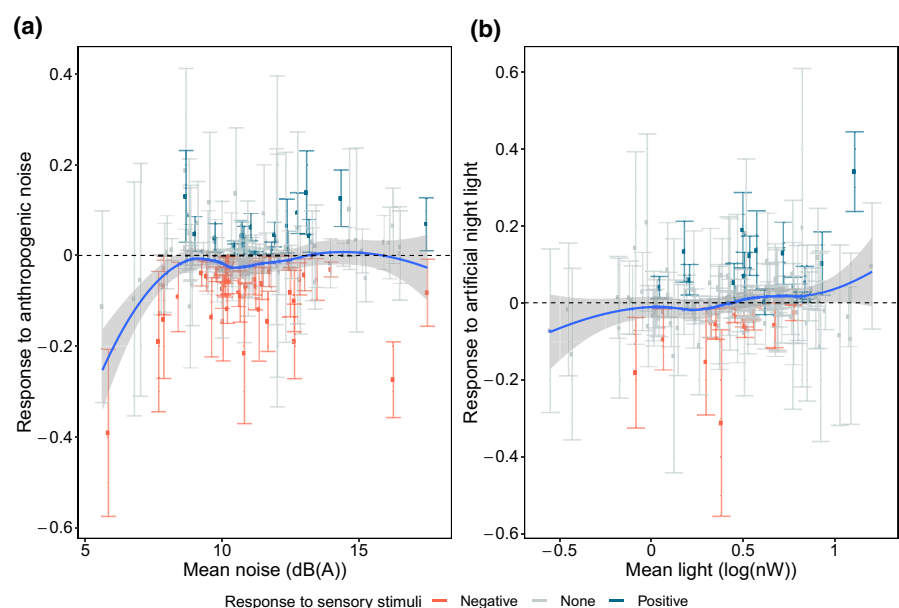

FIGURE 3 Avian responses to (a) anthropogenic noise and (b) artificial night light when exposed to increasing stimuli intensity. The locally weighted smoothing line represents general avian responses to either noise or light across all 140 species. Effect sizes of species-specific responses are plotted against mean values of noise and light exposure, with error bars representing 85% confidence intervals. Colors represent directions of response effect sizes (negative, positive, or no response)
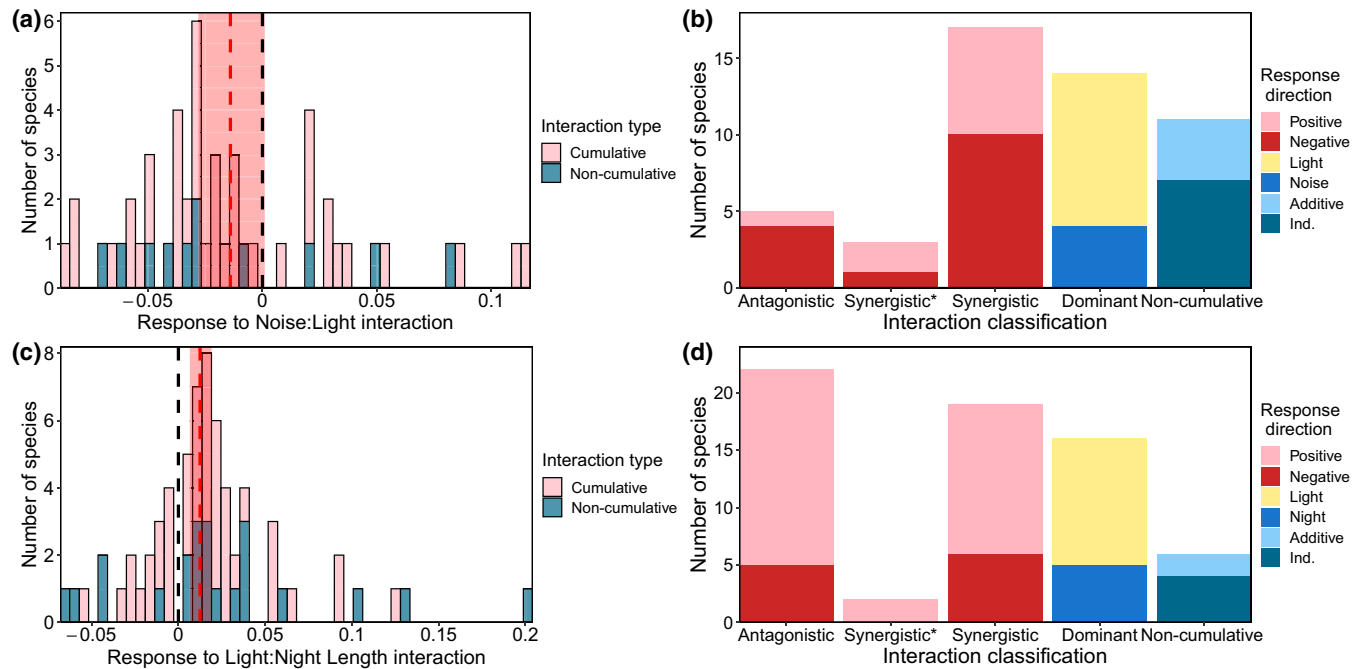
FIGURE 4 Species responses to the interaction between noise and light (a, b) and between light and night length (c, d). Histograms show the distribution of the number of species that responded to the Noise:Light interaction (a) and the Light:Night Length interaction (c) for cumulative and non-cumulative interactions. The weighted-mean of all species responses is indicated by the dotted red line with an 85% confidence interval band. Stacked bar plots show the number of interaction classifications and associated directions for species responses to the Noise:Light interaction (b) and the Light:Night Length interaction (d). Responses were either cumulative (antagonistic, synergistic*, synergistic, or dominant) or non-cumulative (additive or indistinguishable (ind.))

antagonistic effect, where the interaction ameliorated how species responded to light and noise. For example, the actual response for rufous hummingbirds (*Selasphorus rufus*) was less negative than expected, but the effect was lower than the positive response to light alone ($\beta_{Interaction}$ = 0.021, 85% CI: 0.001, 0.040; Figure 5; Table S1), resulting in a negative antagonistic response. Conversely, 20 species (40% of interaction responses) experienced a synergistic response, where the actual response was greater than what was expected. This was true for the black-chinned hummingbird (*Archilochus alexandri*), which experienced an interaction response that was more positive than expected ($\beta_{Interaction}$ = 0.086, 85% CI: 0.054, 0.120). In all, 14 cumulative responses were dominant, where 10 species had the interaction response driven by light.

Not all species that experienced a unimodal response to light or noise also responded to an interaction between the two. In this dataset, 37 species (26% overall) did not respond to the interaction, indicating that the addition of the second stimulus did not influence how species respond to their sensory environment. However, and perhaps more importantly, the combined presence of light and noise can elicit emergent responses for species that did not react to either light or noise. In all, 19 species from this dataset experienced an emergent response, with 11 synergistic, 3 noise-dominant responses, and 5 indistinguishable non-cumulative responses. Eight of the 11 emergent synergistic responses (73%) were negative, indicating that these species are less tolerant to the multimodal influence than the responses to light alone, noise alone, and the expected additive effect between the two.

3.3 | Interaction between artificial night light and night length

We found evidence for 65 responses to artificial night light when it interacted with night length (Figure 4, Table S6). Of the species that responded to the interaction, 47 species (72%) increased in abundance with artificial night light and longer nights (weighted-mean β = 0.012, 85% CI: 0.007, 0.019). Moreover, the models revealed changes in abundance for 49 additional species when the influence of night length was included. Of all interaction responses, six responses were non-cumulative, and only two responses were additive as expected. In all, 59 species experienced a cumulative response that deviated from the expected additive model (Figure 4, Table S6), and these responses were roughly split between antagonistic (22 species), synergistic (21 species), and dominant responses (16 species). For antagonistic responses, most species (~80%) experienced a positive antagonism, where the actual response was less positive than expected. However, a few negative antagonistic responses resulted in a positive interaction effect size. For instance, the pygmy nuthatch (*Sitta pygmaea*) experienced a negative response to light alone (β_{Light} = −0.182, 85% CI: −0.326, −0.038), yet increased in abundance when light interacted with night length ($\beta_{Interaction}$ = 0.020, 85% CI: 0.002, 0.038; Figure 5; Table S1). Similarly, most of the synergistic responses (~70%) resulted in a positive response. Roughly 25% of these responses were emergent, where the species only responded when light and night length interacted. For example,
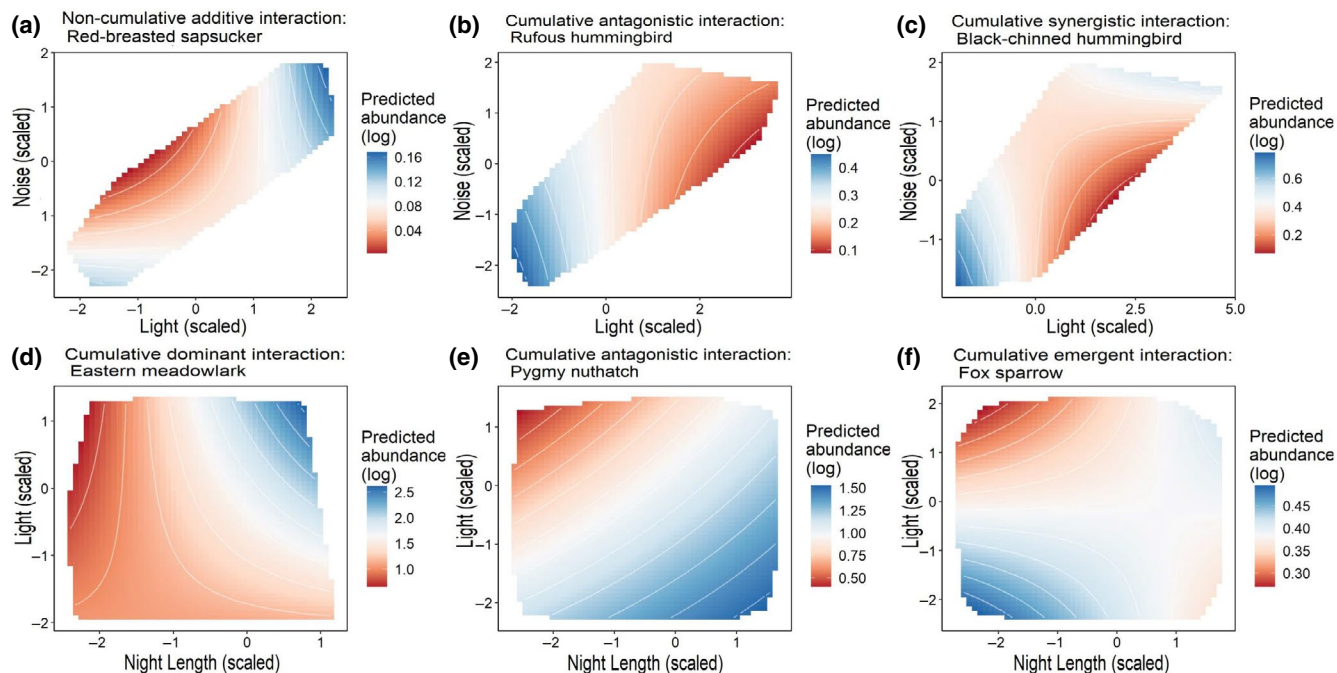
FIGURE 5 Examples of different interaction response types using partial dependency plots for non-cumulative and cumulative interactions between noise and light (a–c) and light and night length (d–f) for six representative species. The color scale represents the intensity of how the interaction variables influence the predicted response, with the region of values representing the species-specific area the predictor space model was trained on. Non-cumulative interactions arise when the interaction effect size does not deviate from the expected additive response (a). Cumulative interactions arise when the interaction response deviates from the expected response. Both (b) and (e) show the antagonistic interaction response that is less negative than what was expected but with a magnitude smaller than the response to light. Dominant responses occur when the effect size of a variable drives the biological response, such as the effect size of light in the interaction with night length for eastern meadowlarks (d). Synergistic responses result in an interaction effect size that is greater than expected. For example, black-chinned hummingbirds (c) have an interaction that is more positive than expected, but is smaller than the response to light, resulting in a diminished positive region when both noise and light intensity increase. However, fox sparrows (f) experience an emergent synergistic response and only respond to light and night length when those factors interact

fox sparrows (*Passerella iliaca*) did not respond to light or night length alone, but did experience a positive response to the interaction ($\beta_{\text{Interaction}}$ = 0.017, 85% CI: 0.012, 0.023). The majority of dominant responses (~70%) were driven by the response to light. For instance, the effect size of the response to light for the eastern meadowlark (*Sturnella magna*) overlapped with the 85% CI of the interaction response (β_{Light} = 0.143, 85% CI: −0.108, 0.393; $\beta_{\text{Interaction}}$ = 0.200, 85% CI: 0.115, 0.286; Table S1), thus driving the response away from the expected additive response and mitigating the influence from night length (Figure 5).

3.4 | Functional traits predicting avian response to light and noise

Habitat affiliations and diet were the only contexts and traits associated with responses to noise or light (Table S8). In contrast to our predictions, species that occupy closed habitats were less tolerant of both noise and light exposure than species that occupy mixed (Noise Ref: Mixed, β_{Closed} = −0.031, 95% CI: −0.061, 0.000, λ = 0.27; Light Ref: Mixed, β_{Closed} = −0.037, 95% CI: −0.067, −0.007, λ = 0) and open environments (Noise Ref: Open, β_{Closed} = −0.031, 85% CI: −0.060,

−0.002; Light Ref: Open, β_{Closed} = −0.052, 95% CI: −0.090, −0.015). Yet, closed habitat species were also less tolerant to light compared to species in wetland (Light Ref: Wetland, β_{Closed} = −0.074, 95% CI: −0.132, −0.016) and especially disturbed environments (Light Ref: Disturbed, β_{Closed} = −0.093, 95% CI: −0.137, −0.049; Figure 6; Table S8). The high tolerance to light by species in disturbed habitats was further emphasized by the strong differences between species that occupy mixed (Light Ref: Mixed, $\beta_{\text{Disturbed}}$ = 0.056, 95% CI: 0.014, 0.099) and open habitats (Light Ref: Open, $\beta_{\text{Disturbed}}$ = 0.041, 85% CI: 0.006, 0.076). Additionally, species that occupy wetland habitat were less tolerant of noise compared to mixed (Noise Ref: Mixed, β_{Wetland} = −0.049, 85% CI: −0.094, −0.004) and open environments (Noise Ref: Open, β_{Wetland} = −0.050, 85% CI: −0.096, −0.003). A post hoc analysis of light gathering ability across habitat affiliations provides some support for a functional link for the most extreme differences in responses to light among habitats. Specifically, closed habitat species had greater light gathering ability than disturbed habitat species (Ref: Disturbed, β_{Closed} = 0.029, 85% CI: 0.003, 0.056, λ = 0.19). PGLS trait models also revealed insectivores were more tolerant of noise exposure compared to herbivores (Ref: Herbivores, $\beta_{\text{Insectivore}}$ = 0.041, 95% CI: 0.006, 0.075, λ = 0.42) and omnivores (Ref: Omnivores, $\beta_{\text{Insectivore}}$ = 0.028, 85% CI: 0.000, 0.056).
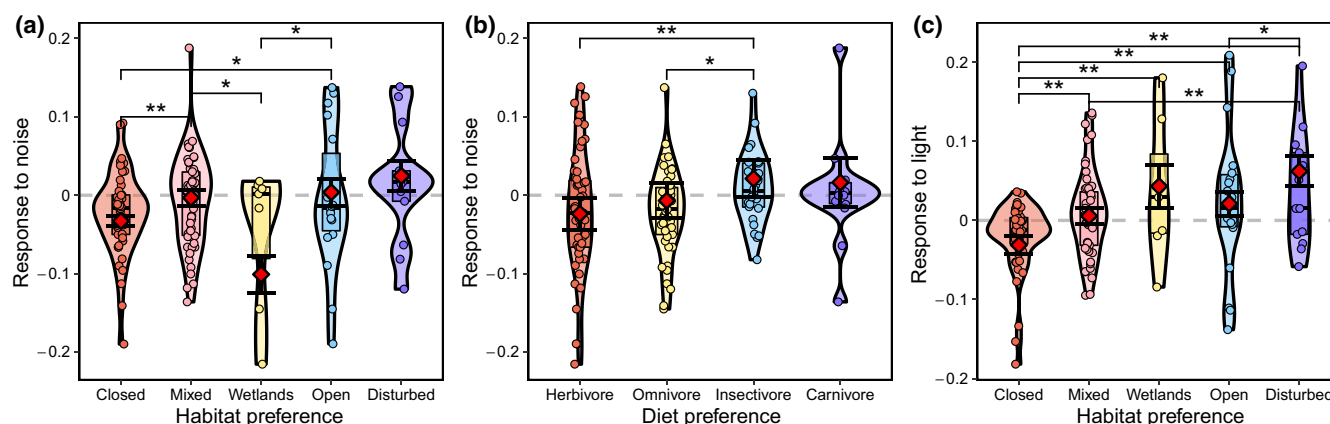
FIGURE 6 Violin plots representing functional trait relationships with avian response to anthropogenic noise (a, b) and artificial night light (c) with the predicted mean, symbolized by the red diamond, and standard error bars. The influence of a trait on the response was determined if the confidence interval did not overlap zero, where a single asterisk denotes an 85% CI and a double asterisk denotes an 95% CI

4 | DISCUSSION

Despite calls to study the multimodal influence of anthropogenic noise and artificial night light on natural populations (Halfwerk & Slabbekoorn, 2015; Swaddle et al., 2015), there is still a dearth of research investigating the potential of cumulative responses to these sensory stimuli for a wide array of taxa. Moreover, the few multimodal studies that exist are all small scale (e.g., Ferraro et al., 2020; McMahon et al., 2017) and do not consider the gradients of exposure to these anthropogenic stimuli that occur at the landscape, regional, and global scales. Our continental-wide study is the first, to our knowledge, to systematically evaluate the impact of the interaction between these stimuli in terms of non-cumulative and cumulative responses on changes in abundance, and we did so for 140 prevalent bird species in North America. Not only did several species strongly respond when exposed to both stimuli, but these responses were primarily cumulative, where the actual response deviated from the expected additive response. Moreover, the interaction revealed negative emergent responses of species that only reacted to the multimodal influence of light and noise. Additionally, the interaction between light and night length revealed an increase in abundance with light exposure during longer nights for many species, emphasizing that environmental context is equally important when assessing the impacts of these stressors. Below we discuss potential mechanisms, as well as functional traits, for explaining avian responses to these sensory stimuli.

4.1 | Species response to artificial night light and anthropogenic noise

We found 40% of species in this dataset responded to noise exposure, and the majority of those species (70%) generally decreased in abundance. Birds may avoid anthropogenic noise due to masking, under which they are unable to detect biologically relevant cues such as conspecific communication or sounds made by predators

(Barber et al., 2010; Zhou et al., 2019). Individuals that can still detect cues but fail to appropriately process and respond may be experiencing distraction mechanisms, which can disrupt cognitive processes, or misleading mechanisms, which may lead to misdirected, inappropriate, and even maladaptive responses (Dominoni, Halfwerk, et al., 2020; Grade & Sieving, 2016). The noise-induced impaired ability to detect or discriminate predation cues may elicit a continual state of perceived unpredictability and reduced security (Kleist et al., 2018), which could cause individuals to avoid noisy areas. Alternatively, species might compensate for increases in perceived risk by aggregating in flocks with the tradeoffs of increased competition, disease transmission, and increased conspicuousness to predators (Rubenstein, 1978). These and other anti-predator strategies might be related to the lack of responses to noise (62 species) or even increased abundance (17 species) for some species. However, increases in abundance or no change in abundance may not reflect the ultimate fitness consequences of noise. For example, migrating birds exposed to noise from a "phantom road" had lower body condition than those that were in adjacent quiet locations, which would likely impact survival (Ware et al., 2015). Additionally, accumulated stress from exposure to sensory stimuli could establish long-term adverse effects by dysregulating development, metabolism, immune responses (Langgartner et al., 2015), and impeding reproductive success during the breeding season (Ouyang et al., 2011).

Artificial night light did not elicit strong species-specific responses to the same extent as noise, as only 28% of species responded to this stimulus. However, context seems to matter, as nearly half of the species in this study responded to the interaction between light and night length (see below). Still, that fewer species responded to light than noise could be due to other local-scale variables that we could not include here, such as habitat composition and fragmentation (Ciach & Fröhlich, 2017) and the spectral composition of light (Ulgezen et al., 2019). Additionally, when we accounted for the multimodal influence of the interaction between noise and light, models revealed most

species (70% of responses) decreased in abundance, which matched our predictions. An organism's tolerance of one stressor tends to be lower when other stressors are in operation (Myers, 1996), and in this case the inclusion of light often exacerbated the negative influence of noise. When organisms are exposed to constant lighting, the alteration of the circadian timing results in the disruption of the rhythmicity of hormones such as glucocorticoids and melatonin, which can induce a cascade of effects such as disrupted sleep patterns, inefficient metabolic processes, and immunological modulation (Navara & Nelson, 2007). While these changes may not elicit changes in abundance, they could alter an organism's physiological state and decrease tolerance to heterotypic pervasive stressors (Gunderson et al., 2016), such as anthropogenic noise. Importantly, our results should be considered relatively conservative because feeder observations did not include species absences and thus limits our inference about whether species completely avoid some sensory environments. As such, future local-scale research with true absence data could extend the insights from our study.

The extent of the number of species that respond to light and noise can be further demonstrated by the discovery of emergent interactions, as several species-specific responses were identified by the multimodal influence of both stimuli. Emergent properties present more information than isolated parameters in an ecological system (Nielson & Müller, 2000), and therefore provide additional context of how species are responding to light and noise when they overlap spatially and/or temporally. Specifically, the majority of emergent responses (73%) resulted in species avoiding polluted areas, which increases the necessity and urgency of effective management strategies mitigating the influence of anthropogenic stimuli.

4.2 | Species response to artificial night light and longer nights

In general, for the interaction between light and night length, the majority of species that responded (72% of interaction responses) increased in abundance when exposed to artificial night light and longer nights. The presence of artificial night light has the potential to expand the temporal niche and elongate the perceived photoperiod. Yet, there have been relatively few studies that have formally examined the effect of artificial light on altering behavior or restructuring temporal niche partitioning (Gaston et al., 2013). Northern mockingbirds (*Mimus polyglottos*) and common blackbirds (*Turdus merula*) expand foraging times when artificial light is present (Russ et al., 2015; Stracey et al., 2014). However, these studies recorded behavior during the breeding season when birds have a different foraging pattern. Research regarding the influence of light at night for wintering bird activity near urban feeders pre- and post-twilight have reported conflicting results. For example, a winter-long observational study of 24 common feeder species in a residential area in Norway found only three species were regularly active at night (Byrkjedal et al., 2012). Other studies suggest that there is weak evidence to support birds are altering the timing of foraging with the

presence of light pollution (Da Silva et al., 2017), and birds tend to arrive later in the morning to feeders rather than earlier when artificial light is present (Clewley et al., 2016).

Temperature could also be a contributing factor in determining whether a species utilizes light to extend foraging time. For example, the three species that increased activity at night described by Byrkjedal et al. (2012) advanced foraging when temperatures were colder than normal, most likely because they suffered higher mass loss on colder nights. Depending on a species' thermal tolerance, increased light levels from anthropogenic sources might not be beneficial enough to justify prolonged foraging activity, or they could interact with temperature to allow adaptive responses to exploit the extended photoperiod. Alternatively, birds might be innately attracted to sources of artificial light. For example, a study that compared roosting preferences of male great tits (*Parus major*) in a laboratory setting under lit and dark conditions found males preferred to roost under lit conditions (Ulgezen et al., 2019). While selecting these sites might provide birds an advantage by increasing food availability, as well as extra-pair paternity gains during the breeding season, the additional exposure to light could have negative consequences on individual physiology and fitness (reviewed in Dominoni, Halfwerk, et al., 2020). Further research is needed to assess whether the benefits of light-polluted areas outweigh the costs of exposure to light at night in the context of night length and ambient temperature, perhaps by taking advantage of a latitudinal gradient.

4.3 | Functional traits predicting avian response to light and noise

Avian response to light and noise differed strongly among habitats. Specifically, species that occupy closed habitats were less tolerant of both stimuli compared to those that occupy open habitat. Avian responses to these stimuli can be explained by the physical properties of the stimuli and how they operate in different environments. Communication among birds is often adjusted to local acoustic conditions such that birds in forested environments have low-frequency signals (Boncoraglio & Saino, 2007; Tobias et al., 2010). However, low-frequency calls of forest-dwelling birds are prone to masking by anthropogenic noise (Nemeth & Brumm, 2009) and previous research suggests that breeding birds with low-frequency vocalizations are more sensitive to noise exposure than those with higher-frequency signals (Goodwin & Shriver, 2011; Francis, 2015). Although we did not explicitly evaluate call frequency here given the high number of functionally different calls within and among species (Marler, 2004), it is possible that lower-frequency signals among forest birds could explain their decline in abundance with noise exposure relative to birds affiliated with other habitats. Light intensity, spectral composition, and timing vary drastically between closed and open habitats such that forests are darker. Moreover, birds that occupy disturbed habitat are exposed to light even when they avoid light-polluted areas such as streets and business districts, which could contribute

to acclimation and increased tolerance (Dominoni et al., 2014). The differences in light sensitivity among habitat affiliations were supported by closed-habitat species possessing greater light gathering ability, which is a pattern confirmed by a similar trait-based study among breeding birds (Senzaki et al., 2020). In addition to differences in habitat preference and sensory sensitivity, phylogenetically controlled models also revealed insectivores were more tolerant of noise than herbivores and omnivores. This finding contrasts with comparable research on diet preferences explaining avian sensitivity to noise (Francis, 2015; Senzaki et al., 2020). However, in the context of our study, even primarily insectivorous species were visiting feeders and thus foraging in a manner quite different from foraging modes used for insect capture. Thus, the context of foraging may matter for these species.

In addition to finding functional traits that predicted avian response to light and noise, we measured the phylogenetic strength of general avian response to these stimuli. Specifically, we found changes in abundance in response to noise are moderately conserved among residential overwintering birds. To further investigate how birds perceive and respond to noise, future research should test the relationship between intrinsic traits that represent anatomical and physiological sensitivities to sound. For example, in a survey that ranked the degree of traits impacting the survival, persistence and performance of a species, experts identified the ability to discriminate in noisy environments, auditory spectral resolution, and auditory bandwidth as the most plausible traits to predict vertebrate sensitivity to noise (Ditmer et al., 2021).

Conversely, we found no evidence that variation in response to light showed phylogenetic structure, suggesting avian responses to light could be more indicative of environmental contexts than evolutionarily conserved intrinsic characteristics. This is counter to our expectations, as the natural day/night cycle is a fundamental organizing force in biology that regulates the timing of many behaviors and physiological processes across all forms of life (Gaston et al., 2013). On its own, the light gathering ability trait exhibited a strong phylogenetic signal, reinforcing this expectation. Even though comparable research found the light gathering ability explains nesting responses during the breeding season (Senzaki et al., 2020), in our study this trait was unrelated to changes in abundance of predominantly non-breeding birds with respect to artificial night light. As such, rather than using anatomical traits, non-breeding bird responses could be predicted by traits representing ecological sensitivities, such as activity patterns, trophic level, vagility, and habitat specializations (Ditmer et al., 2021).

5 | CONCLUSION

In our continental-wide analysis, we revealed considerable heterogeneity in avian responses to light and noise alone, as well as the interaction between them. Based on overall responses to the interaction between light and noise, we suggest management efforts should focus on ameliorating excessive noise for predominately non-breeding birds during the winter, which should decrease the impact from synergistic responses, as well as the negative impact from noise alone. There is still much to learn about responses to these stimuli and smaller-scale studies should take our cumulative-effects approach of assessing responses to light and noise. Local-scale studies will allow for adequately replicated field manipulations to investigate potentially nonlinear responses to overlapping stressors for well-described communities (Brown et al., 2013). Moreover, detailed follow-up analyses could identify why certain species respond to light and noise with an antagonistic, synergistic, emergent, or dominant interaction, and if interaction response types are linked to a functional trait or environmental context. Careful temporal sampling of stimuli intensities will also allow management to clearly define "sensory danger zones" as specific temporal windows or spatial areas in which light and noise overlap and impact potentially vulnerable species (Dominoni, Halfwerk, et al., 2020). Pairing these sensory danger zones with functional traits and contexts that predict responses of targeted species to these co-occurring stimuli can encourage management efforts to enact regulation that prevents the spread and limits their intensity in protected areas (Buxton et al., 2017). Knowing when (seasonal and diurnal patterns), where (locations of anthropogenic disturbance), how (sensory mechanisms), and why (functional traits) sensory stimuli influence species will help management efforts effectively mitigate impacts from these globally pervasive anthropogenic pollutants.

AUTHORS' CONTRIBUTIONS

JRB, NHC, CDF, and AAW conceived of the project. ETM contributed the Project FeederWatch data and data validation and LPT contributed the key trait data. AAW conducted the most data analysis with contributions from MAD and CDF. AAW and CDF led writing of the manuscript and all other authors contributed to the writing and approved of the final version.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare.com at http://doi.org/10.6084/m9.figshare.14472561.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.