Sensory pollutants alter bird phenology and fitness across a continent

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Expansion of anthropogenic noise and night lighting across our planet[1,2] is of increasing conservation concern[3–6]. Despite growing knowledge of physiological and behavioural responses to these stimuli from single-species and local-scale studies, whether these pollutants affect fitness is less clear, as is how and why species vary in their sensitivity to these anthropic stressors. Here we leverage a large citizen science dataset paired with high-resolution noise and light data from across the contiguous United States to assess how these stimuli affect reproductive success in 142 bird species. We find responses to both sensory pollutants linked to the functional traits and habitat affiliations of species. For example, overall nest success was negatively correlated with noise among birds in closed environments. Species-specific changes in reproductive timing and hatching success in response to noise exposure were explained by vocalization frequency, nesting location and diet. Additionally, increased light-gathering ability of species' eyes was associated with stronger advancements in reproductive timing in response to light exposure, potentially creating phenological mismatches[7]. Unexpectedly, better light-gathering ability was linked to reduced clutch failure and increased overall nest success in response to light exposure, raising important questions about how responses to sensory pollutants counteract or exacerbate responses to other aspects of global change, such as climate warming. These findings demonstrate that anthropogenic noise and light can substantially affect breeding bird phenology and fitness, and underscore the need to consider sensory pollutants alongside traditional dimensions of the environment that typically inform biodiversity conservation.

Anthropogenic noise and light pollution are increasing even faster than the human population[1,2]. Laboratory work and small-scale field studies suggest that both pollutants can affect animal behaviour and physiology by altering sensory performance and perceptions of environments[6]. Anthropogenic noise impairs the perception of auditory signals, altering communication, orientation, foraging and vigilance behaviours[4,8,9]. Analogously, anthropic night lighting modifies activities and interactions mediated by vision[10,11] and alters circadian rhythms, which are tightly controlled by photoperiod[5]. Despite growing evidence documenting behavioural responses to these globally pervasive sensory pollutants, fitness consequences of these stimuli are known only from a few species at the local scale[12–15]. Thus, there is a clear need to understand whether fitness consequences of exposure to these stimuli are widespread, whether responses to these stimuli vary across species and, if so, why.

To fill this knowledge gap, we investigated the macroecological consequences of both noise and light pollution across a continent (Fig. 1, Extended Data Figs. 1 and 2) and determined whether species-specific responses to each stimulus can be linked to functional traits or environmental contexts. We used 58,506 nest records from 142 species collected throughout the contiguous United States between 2000 and 2014 by citizen science volunteers through the NestWatch programme of the Cornell Laboratory of Ornithology (Methods, Supplementary Table 1). We combined this dataset with high-resolution geospatial data for anthropogenic noise and night lighting (Supplementary Table 2) to examine how these variables influence first egg-laying date (clutch initiation), clutch size, partial hatching success (in which one or more eggs fail to hatch), clutch failure (nest failure at egg stage) and nest success (fledging of one or more young from nest) using linear and generalized linear mixed-effect models with spatially explicit correlation

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Fig. 1 | Anthropogenic noise and night lighting are widespread and affect a variety of species. a, Colours denote median sound energy (L_{50} = sound levels exceed the value 50% of the measurement period) in A-weighted decibels (dB) from anthropogenic sources. Points denote nest locations that were successful (black) or unsuccessful (red). Sound level data from United States National Park Service Data Store. No claim to original US Government works. **b**, Sample of species for which reproduction is negatively influenced by exposure to noise or light pollution. Top row, noise-affected species: left to right, Northern cardinal, oak titmouse, barn swallow, Eastern bluebird, purple martin. Bottom row, light-affected species: white-breasted nuthatch, Carolina wren, house sparrow, house finch, violet-green swallow. Photograph credits: Carolina wren, public domain; all others, David Keeling.

structure. We accounted for the influence of latitude on responses, because it is a well-known macroecological proxy for environmental drivers of life history variation in avian reproduction[16], and controlled for potential differences between coastal and interior populations. Additionally, we separated the effects of noise and light from other metrics reflective of human activity and urbanization in general by including human population density and proportion of anthropogenic impervious surface in our models (Supplementary Table 2). We scaled all continuous predictors to enable direct comparisons and ensured that our models did not suffer from problems of multicollinearity (Methods). We examined the influence of these variables on nesting metrics of all species and of those that nest in open environments, such as grasslands and wetlands (hereafter, open-habitat species), and in forests (hereafter, closed-habitat species). These two environments contrast strongly in vegetation structure that could provide micro-habitat refugia from anthropogenic stimuli, affording the opportunity to test whether responses to noise and light pollution are stronger in open environments where exposure to these stimuli may be most severe[17,18]. We followed these analyses with species-specific models for 27 species that were represented by at least 100 nests in the dataset (Supplementary Table 3) and used phylogenetically informed models to determine whether individual species' responses (± s.e.) to noise or light are linked to traits hypothesized to predict sensitivities to these stimuli (Table 1, Methods).

All-species models of the five responses revealed weak associations with noise, light and other anthropogenic predictors (Supplementary Table 4). However, open-habitat birds in the brightest conditions were estimated to begin laying eggs, on average, a month earlier than those in the darkest areas (nests = 4,251, β = −4.73, 95% CI −8.21, −1.25), although the confidence interval in brighter conditions was also wide (Fig. 2, Supplementary Table 5). Species in closed habitats exhibited the same apparent trend, advancing laying by approximately 18 d over a smaller range of light exposure; however, the confidence in the effect was lower (nests = 5,076, β = −2.30, 95% CI −5.05, 0.44) (Fig. 2, Supplementary

Table 1 | Hypotheses and predicted relationships between traits and responses to noise and light exposure

Variable	Hypothesis	Stressor | predicted effect
Vocal frequency	Birds with higher-frequency vocalizations should experience less interference from noise	Noise | +
Light-gathering ability	Greater light-gathering ability (that is, better vision in low light) will correlate with sensitivity to light exposure	Light | −
Cavity	Birds that nest in cavities will be less sensitive to noise and light than open-cup-nesting species because cavities may reduce exposure to these stimuli	Noise | + Light | +
Diet	Birds with animal-based diets will be more sensitive to noise than those with plant-based diets; all birds, regardless of diet, will benefit from light through extended foraging time	Noise | − Light | +

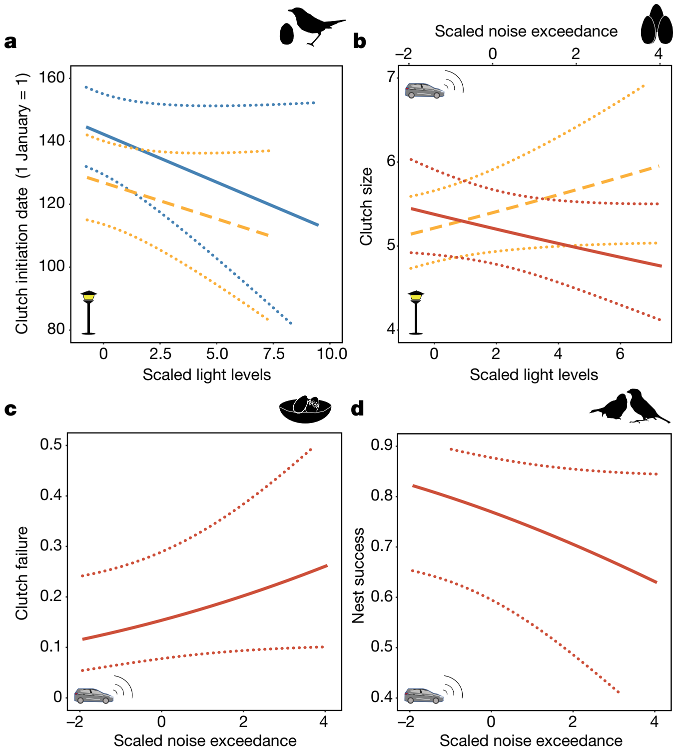

Fig. 2 | Responses to light and noise by birds in open and closed habitats. **a**, Light exposure resulted in advancements in clutch initiation for birds in both open (blue solid line; $n = 4{,}251$, $\beta = -4.73$, 95% CI −8.21, −1.25) and closed (orange dashed line, $n = 5{,}076$, $\beta = -2.30$, 95% CI −5.05, 0.44) environments. **b**, Birds in closed environments also experienced increased and decreased clutch sizes with light (orange dashed line, bottom-axis, $\beta = 0.06$, 95% CI 0.00, 0.13) and noise exposure (red solid line, top axis, $\beta = -0.06$, 95% CI −0.14, 0.01), respectively ($n = 5{,}076$). **c**, **d**, Closed-habitat birds also experienced increased clutch failure ($n = 5{,}076$, $\beta = 0.17$, 95% CI −0.02, 0.37) (**c**) and lower nest success (**d**) ($n = 4{,}980$, $\beta = -0.19$, 95% CI −0.37, −0.003) with noise exposure. Analyses based on spatially explicit linear mixed-effect models (**a**) and generalized linear mixed-effect models (**b**–**d**). Marginal effects and 95% CIs (denoted by dotted lines) are shown.

Table 6). In terms of clutch size, closed-habitat birds produced clutches that were approximately 16% larger in well-lit compared to dark areas (nests = 5,076, $\beta = 0.06$, 95% CI 0.00, 0.13) (Fig. 2, Supplementary Table 6), but there was no apparent influence of light on clutch size among open-habitat birds. There is no simple explanation for these habitat-associated contrasts. Dense vegetation should substantially suppress light from skyglow for birds in closed environments. However, relative to open-habitat birds, those in closed environments tend to have eye geometries that improve low-light vision ($\beta = 0.04$, 95% CI 0.00, 0.09, $\lambda = 0$) (Supplementary Table 8). Thus, closed-habitat birds may take advantage of even low light levels to extend foraging time to support larger clutches and broods.

Closed-habitat, but not open-habitat, birds also tended to experience a decline in clutch size with noise exposure (nests = 5,076, $\beta = -0.06$, 95% CI −0.14, 0.01) (Fig. 2, Supplementary Table 6) such that those in the loudest areas laid clutches that were on average 0.64 eggs (12%) smaller than those in the quietest conditions. Birds that inhabit areas with dense vegetation vocalize at lower frequencies than those in more open areas[19]. Because lower-frequency vocalizations are more susceptible to energetic masking from anthropogenic noise[20], and masking can negatively influence female sexual receptivity and maternal investment in clutch size[21], the decline in clutch size may be an outcome of masking. Elevated noise also tended to increase the probability of clutch failure for closed-habitat birds (nests = 5,076, $\beta = 0.17$, 95% CI −0.02, 0.37) (Fig. 2, Supplementary Table 6). Most importantly, nest success among closed-habitat, but not open-habitat, birds declined with noise exposure (nests = 4,980, $\beta = -0.19$, 95% CI −0.37, −0.003) (Fig. 2, Supplementary Table 6). These results provide multi-species evidence on a continental scale that supports the negative influence of noise exposure on reproductive success previously documented for only a few species[12–14].

Models of responses by individual species revealed widespread but heterogeneous effects of noise and light (Extended Data Figs. 3–8). Half of the species experienced changes in nesting phenology or reproduction due to both stimuli, and 19 of 27 species experienced strong responses to noise or light (Extended Data Fig. 3, Supplementary Table 7). In general, average noise and light pollution exposures for each species exhibited positive covariance ($n = 27$, rho = 0.830, $P < 0.001$), although most species nested across a wide range of values (Extended Data Fig. 3).

Vocal frequency, light-gathering ability of the eye, nesting in cavities or in the open, and diet were all traits related to at least one response to noise or light (Extended Data Fig. 9). Complementing previous work linking vocal frequency and diet to changes in bird distributions in response to noise[20,22], we found that vocal frequency is negatively related to the effect of noise exposure on clutch initiation ($n = 27$, $\beta = -2.66$, 95% CI −4.36, −0.96, $\lambda = 1.00$) and the effect of noise on partial hatch is lower for birds with plant-based diets compared to those with animal-based diets ($n = 27$, $\beta = -0.34$, 95% CI −0.63, −0.06, $\lambda = 0$) (Fig. 3, Supplementary Table 8). Noise may delay clutch initiation for species with lower-frequency vocalizations by interfering with male mate attraction songs[4], which can interfere with stimulation of females by males and delay female sexual receptivity[21]. Alternatively, delayed clutch initiation in noisy areas may reflect later settlement by birds who unsuccessfully compete for quieter breeding territories, although evidence for this explanation is mixed[14,23].

Light-gathering ability of the eye was most consistently related to individual species' responses to light (Extended Data Fig. 9). Increases in the ability to see under low light levels was associated with larger advances in clutch initiation in response to light exposure ($n = 27$, $\beta = -111.11$, 95% CI −173.88, −48.34, $\lambda = 0.66$) (Fig. 3; Supplementary Table 8). Additionally, there was a tendency for birds that nest in cavities to advance clutch initiation in response to light more strongly than those that nest in open cups ($n = 27$, $\beta = -5.91$, 95% CI −12.89, 1.06, $\lambda = 0.47$) (Supplementary Table 8). Our findings of advancements in egg-laying due to light provides robust multi-species evidence to support local-scale studies[15,24] but also provide key context identifying light-gathering ability as an important functional trait that influences phenological responses to light pollution.

Because photoperiod is a primary cue for timing reproduction[25], species that advance breeding as a result of light exposure may be expected to suffer a similar, although reversed, phenological mismatch between peak food availability and food need, as has been documented for climate change[7,25]. Thus, we expected species with better light-gathering abilities that advance clutch initiation more strongly with light exposure might suffer greater reproductive costs. Surprisingly, our data suggest the opposite: better light-gathering ability is associated with an increasingly positive influence of light exposure on nest success ($n = 26$, $\beta = 5.51$, 95% CI 0.39, 10.62, $\lambda = 0$) (Fig. 3, Supplementary Table 8). Better low-light vision was also associated with a decrease in the probability of partial hatch with light exposure ($n = 27$, $\beta = -10.94$, 95% CI −21.23, −0.65, $\lambda = 0$) (Supplementary Table 8), although only mixed evidence suggests that light exposure has the same influence on clutch failure for birds with better low-light vision (Supplementary Table 8). A hypothesis that emerges from these patterns is that strong light-induced advancements in breeding phenology among species that can see well under low-light conditions may allow populations in lit areas to successfully track resource availability peaks that are advancing from warming climates, whereas populations in darker areas will continue to experience

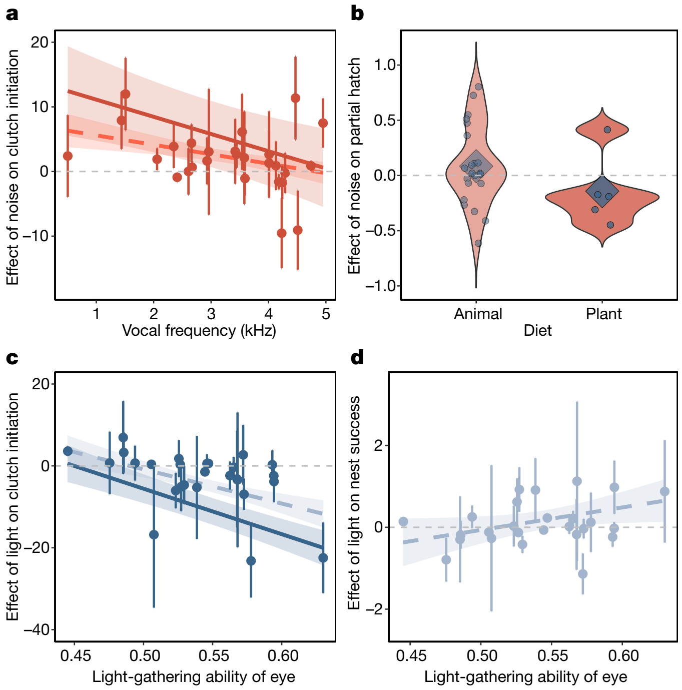

Fig. 3 | Relationships between species-specific responses to noise or light (model estimate ± s.e.) and functional traits. a, Phylogenetic generalized least-squares (PGLS) models suggest that greater peak vocal frequency correlates with less severe delay in clutch initiation in response to noise exposure ($\beta = -2.66$, 95% CI −4.36, −0.96, $\lambda = 1.00$). **b**, The average effect of noise on partial hatching success was neutral for birds with animal-based diets, but increased light tended to decrease incidence of partial hatch among birds with plant-based diets ($\beta = -0.34$, 95% CI −0.63, −0.06, $\lambda = 0$). **c**, Greater light-gathering ability of the eye, measured as the ratio of corneal diameter to transverse width, was linked to a stronger advancement in clutch initiation in responses to light ($\beta = -111.11$, 95% CI −173.88, −48.34, $\lambda = 0.66$). **d**, Effect of light exposure on nest success: species with poor low-light vision showed declines in nest success with light exposure, and those with good low-light vision had increased nest success with light exposure ($\beta = 5.51$, 95% CI 0.40, 10.62, $\lambda = 0$). In **a**–**c**, $n = 27$; in **d**, $n = 26$ owing to removal of house sparrows from models of nest success (Methods). In **b**, violin outlines illustrate kernel probability density; diamonds denote mean effect of noise on nest success per diet. In **a**, **c**, dark solid lines reflect trends where phylogenetic structure (λ) was >0; lighter dashed lines throughout reflect relationships with no phylogenetic structure.

an increased phenological mismatch between food availability and brood rearing as temperatures rise.

Given our finding that sensory pollutants can influence phenology and fitness outcomes for multiple species, understanding how altered sensory environments influence our interpretation of biological responses to climate change is a critical frontier. For example, there is widespread consensus that climate change is advancing reproductive phenology in temperate birds[26], especially as insectivores track changes in their arthropod prey[27]. However, if responses to climate change are collected within light-polluted areas, documented shifts in clutch initiation that are attributed to temperature are confounded with the effects of light exposure and thus likely overestimated. Similarly, delays in the onset of breeding due to noise exposure could offset responses to climate change and result in underestimation. Much of our existing knowledge of phenological responses to climate change comes from studies in North America and Europe[27–29]. Yet because noise and light are pervasive in both regions (especially near cities)[1,2], re-evaluation of documented phenological responses to climate change with explicit consideration of influential environmental sensory gradients could paint a much more nuanced picture of how organisms are coping with all aspects of global change.

Our continental-scale analyses document complex effects of sensory pollution on avian reproduction even while controlling for other potentially influential natural and anthropogenic macroecological variables. We found that closed-habitat birds show more responses to these stimuli than birds affiliated with open environments, and our species-level analyses revealed many important links between responses to noise and light and functionally relevant traits. Specifically, variation in acoustic spectra used by birds to communicate and variation in light-gathering ability of the avian eye were important predictors of responses to noise and to light exposure, respectively. The advancement in reproductive phenology due to light exposure among birds with better light-gathering ability was expected. However, improvements in overall nest success with light exposure for species with better low-light vision were unforeseen, prompting new questions about how responses to sensory stimuli interact with or counteract responses to other forms of global change, such as the warming climate. Because we detected underlying variation in exposure to noise and light among species (Extended Data Fig. 3), determining whether the reported multi-species responses can be attributed to species sorting, general responses across species[30] or both will be important. Future work should also prioritize evaluating how these and other functional traits and contexts are related to sensitivities to these stimuli across more animal species. Such an approach could be both useful and practical for forecasting responses among poorly studied species. Finally, because these sensory pollutants are pervasive[1,2], and our results point to widespread responses to these stimuli, mitigating sensory pollution may be a powerful tool for habitat restoration and improved ecological resilience.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-020-2903-7.

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Methods

Nest watch data from citizen scientists

Through the NestWatch project, the Cornell Laboratory of Ornithology coordinates volunteers who monitor wild bird nests. Volunteers report information on key events in the breeding process, such as the first day an egg is laid (that is, first lay date or clutch-initiation date), the number of eggs (that is, clutch size), the number of eggs that successfully hatch and whether the nest is successful at fledging at least one young (that is, nest success). We originally obtained 186,705 nest records spanning 2000–2014. Following a procedure that maximized the precision and plausibility of nest records (Supplementary Text), our final dataset included 58,506 samples of 142 species (Supplementary Table 1).

Habitat and species-specific samples

From our final dataset, we extracted 27 species with at least 100 nests for the species-specific analyses (Supplementary Table 3). We used habitat descriptions in *The Birds of North America*[31] to categorize species as inhabiting closed, open or mixed habitats. 'Open' denotes the absence of tall vegetation: wetlands, grasslands, shrublands and farmland. 'Closed' habitats include deciduous, evergreen and mixed forests. Species inhabiting both habitat types or open woodlands received a 'mixed' label. As a result, 4,251 nests of 51 species were classified as open-habitat species, 5,076 nests of 22 species were classified as closed-habitat species and 49,179 nests of 69 species were classified as mixed-habitat species (Supplementary Tables 1 and 3).

Environmental and trait data

Summary statistics of untransformed environmental variables available in Supplementary Table 2.

Anthropic night lighting. Anthropic night lighting is scattered by the atmosphere back towards the ground, resulting in an increase in night sky luminance. Data describing the magnitude of zenith skyglow were obtained from the second world atlas of artificial night sky brightness and converted to 270-m resolution[32]. These data reflect the zenith anthropic sky brightness as a ratio to the natural background sky brightness. The atlas is based on a light pollution propagation model with upward emission function calibrated by ground measurements. High-resolution measurements of upward radiance were acquired from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB) sensor on the Suomi National Polar-orbiting Partnership satellite. Six months of satellite data from 2014 were used, and the projected anthropic sky brightness ratio matches the time of satellite overpass, around 1 a.m.

The atlas was computed using several constant assumptions, including the transparency of the atmosphere, the upward emission function of cities, the spectrum of anthropic lights and the hour of the night of the observation. The more that actual conditions differ from these assumptions, the greater the deviation in actual zenith skyglow will be compared to the atlas prediction. For example, when the sky is overcast, a severalfold increase in skyglow is to be expected near cities. The atlas may underestimate the ecological consequences of anthropic night lighting. Zenith brightness gives direct information for only one point in the sky, which is usually the darkest. The DNB is sensitive to light in the range 0.5–0.9 mm; this includes the near-infrared region, beyond the range of the human eye, and leaves out the blue and violet parts of the visible spectrum. Because the VIIRs DNB lacks sensitivity at wavelengths shorter than 500 nm, the blue-light emission peak of white LEDs is not detected and light pollution from this growing source of light in cities is underestimated.

Anthropogenic noise

The anthropogenic noise data were obtained from a georeferenced map of expected environmental sound pressure levels. Geospatial sound models have been developed to interpret and project acoustic conditions across the contiguous United States[33]. These models use machine learning to formulate relationships between sparsely distributed measurements of the ambient sound level and non-acoustic geospatial features such as topography, climate, hydrology and anthropogenic activity. The acoustical data included 1.5 million hours of long-term measurements from 492 sites located in urban and rural areas during 2000–2014. The resulting geospatial sound model was used to project expected sound levels under existing conditions at 270-m resolution. By changing model inputs from their current values to minimize anthropogenic factors, the geospatial sound model was adjusted so that it estimated a natural sound level that includes contributions from biotic and physiographic sources only. The anthropogenic noise exceedance level was calculated by the logarithmic subtraction of the natural from the existing sound projections.

Environmental sound levels vary from one moment to the next and are summarized using a variety of statistics across multiple time scales and frequency ranges. We examined the anthropogenic daytime A-weighted L_{50} sound pressure level (dB re 20 μPa) as our measure of noise exposure. L_{50} is a robust statistic (50th percentile over time) that is less sensitive to infrequent, loud events. A-weighting is the most widely used composite measure of sound in human and wildlife noise studies, whereby sound energy is summed across the spectrum, emphasizing frequencies in which many terrestrial vertebrates have their most sensitive thresholds of hearing[34]. To account for temporal and seasonal variation in the acoustic environment, time of day and day of year were included as model covariates and projections were made for a mid-summer day (defined as 7 a.m. to 7 p.m.).

Urbanization variables: population density and impervious surface area

Increases in human population density and transformation of natural land cover features to those reflective of high-intensity human use (that is, roadways, parking lots and buildings) are quintessential features of urbanization[35,36]. Therefore, we used the 30-m-spatial-resolution grid of per cent developed imperviousness from 2011 National Land Cover Database[37] as a measure of the intensity of human use within the landscape. To quantify human population density, we used the 2010 US Census[38] block data downscaled to 270-m grids. We then used a buffer radius of 500 m (that is, 0.785 km^2) to quantify the mean proportion of impervious surface per 30-m grid and the mean human population density per 270-m grid surrounding each nest.

Traits

We collected additional trait information for the 27 species used for the species-specific analyses. Because species-specific peak vocal frequency, which is the frequency with the highest amplitude, has been shown to be related to changes in abundance among birds[20], we gathered species-specific peak frequency measurements; those for 23 species were obtained from Francis[20] and those for the other four species were calculated from high-quality recordings available at http://www.xeno-canto.org following the same methodology of averaging several recordings per species as described in Francis[20]. We obtained dominant diet (that is, animal-based or plant-based diets) and nesting strategy (that is, cavity or open) information from *Birds of North America Online*[31]. To obtain a variable indicative of an animal's visual light sensitivity, we used the ratio of the corneal diameter to the transverse diameter, which scales values to the size of the visual system and animal. Corneal diameter is approximately equal to the aperture diameter and thus reflects the amount of light entering the eye, whereas transverse diameter is the theoretical upper bound of corneal diameter. The ratio of the two provides a measure of light sensitivity[39–41]. We obtained direct measurements of the corneal diameter and transverse diameter for 16 of the 27 species from several sources[42–46]. To obtain values for the remaining 11 species, we imputed missing values using the phylopars function in the R package Rphylopars[47]. The phylopars function reconstructs ancestral states and imputes missing data using a linear-time algorithm[48,49]. We performed imputations of several eye-measurement variables simultaneously where covariances among traits and evolutionary relationships inform imputation of missing data. The approach used a pruned consensus tree from a recent class-wide phylogeny[50] as the phylogenetic hypothesis and assumed a Brownian motion model of evolution because we found the corneal-transverse ratio to approximate a Brownian motion model of evolution among species with measurements (fitContinuous function in geiger, $n = 62$, $\lambda = 0.981$). To do so, in our data matrix we included 50 additional North American species from which eye measurements were available to improve the imputation of eye traits for the 11 species in our database without eye measurements. For this matrix we included complete information on several morphological traits reflective of size and ecology for all species. We categorized habitat affiliations from *Birds of North America Online*[31], which we converted to an index spanning 1–4 reflecting vegetation density. To represent size we included body mass from the EltonTraits 1.0 database[51], wing chord length from Lislevand et al.[52] and body length[31,53]. To capture aspects of foraging ecology, we used bill length from Lislevand et al.[52] and the proportion of the species diet that consists of invertebrates, fruit, nectar, seeds and other plant material from the EltonTraits 1.0 database[51]. Finally, we also included several eye morphological measurements: eye corneal diameter (87% complete), eye transverse diameter (81% complete), eye axial diameter (83% complete), corneal diameter to eye axial ratio (83% complete) and ratio of corneal diameter to transverse diameter (81% complete). We manually checked imputed values for potentially unrealistic values and compared imputed data for several species to congeners, which tended to be quite similar as expected from a Brownian motion model.

Statistical analyses

We used linear and generalized linear mixed-effect models (LMMs and GLMMs) with a spatially explicit exponential correlation structure using the fitme function in the R package spaMM[54] to examine the effects of the following explanatory predictors: (1) anthropogenic noise, (2) anthropic light (that is, zenith skyglow), (3) latitude, (4) human population density within 500 m from each nest, (5) proportion of impervious surface area within 500 m from each nest and, when applicable, (6) whether or not the nest was located in a coastal area, defined as <50 km from marine and Great Lake coastlines. All continuous predictor variables were centred and scaled using z-transformations before analyses to facilitate direct comparisons of effects.

For each of the 27 species with at least 100 nests, all species and open-habitat and closed-habitat birds, we analysed the following five response variables: (1) clutch initiation date (that is, date of first laid egg), (2) clutch size, (3) clutch failure, (4) partial hatch and (5) nesting success. All models included the same predictors as the all-species and habitat-specific models above with the exception of three species that did not have coastal populations, so that the coastal predictor was excluded for models describing responses by these species (Supplementary Table 3). Ideal analyses of the influence of anthropogenic stressors on the first egg-laying date would only include first nesting attempts by a pair in a single breeding season. Although our procedure to maximize data quality excluded nests with the same geographical coordinates within the same season and probably excluded many second or subsequent nesting attempts (Supplementary Text), the nature of a study at this scale could not restrict analyses to only first attempts with absolute certainty. Nevertheless, our above-described removal of many second attempts and the fact that the majority of our 27 focal species typically have only 1 or 2 broods (Supplementary Table 3) maximizes our ability to reveal changes in nesting phenology due to the predictor variables. For the clutch size, clutch failure, partial hatch and nesting success models, we added the first egg-laying date as an additional explanatory predictor to control for its well-known relationship with reproductive performance[55]. For analyses of clutch initiation date, we used ordinal date (in which January 1 = 1) as the response variable. For these, we used LMMs with Gaussian error. For the clutch size analyses, we used GLMMs with Conway–Maxwell–Poisson error and log link functions because the clutch size data were under-dispersed. For the partial hatching success analyses, we excluded nests that failed during the incubation period (that is, we removed nests with all unhatched eggs). We denoted nests with at least one unhatched egg as '1' and those with all hatched eggs as '0' and used GLMMs with Binomial error and logit link functions to examine partial hatching success. Clutch failure, defined as the complete failure of the nesting attempt during the incubation stage, was analysed with GLMMs with Binomial error and a logit link function. For nesting success analyses, we excluded data for which the ultimate fate of the nesting attempts was not recorded. We also used GLMMs with Binomial error and logit link functions to examine nest success but excluded data from house sparrows because of the presence of management action on this species during the chick-rearing period. We defined nests with at least one fledgling as 'success' and those with no fledglings as 'failure'.

To account for variable responses among species and years to our predictors, for all-species models, plus those restricted to open or closed-habitat species, we included species, year and species within year as random intercepts, as well as uncorrelated random intercepts and random slopes within species for anthropogenic noise and light, latitude, human population density and proportion of impervious surface. Each model also included an exponential spatial correlation structure using the Matérn correlation function. Initial spatially explicit mixed-effect models failed to run on a variety of platforms using our original latitude and longitude resolution (that is, three decimal places) due to the size of the correlation matrix and the complexity of the random effects. Therefore, we rounded the latitude and longitude variables used in the correlation structure to one decimal place, providing a resolution of approximately 11.1 km, but maintaining a resolution that should capture macroecological gradients that could influence patterns of reproductive success. Additionally, initial runs of the spatially explicit model of clutch size for all species using Conway–Maxwell–Poisson error failed to finish in >120 days. Therefore, we used 10 randomly drawn pseudo-replicates of 5,000 nests for models and used the average parameter estimates for interpretation[20] (Supplementary Table 4).

To test for relationships between responses to noise or light and traits, we used phylogenetic generalized least squares (PGLS) with the gls function in the R package nlme[56]. We simultaneously estimated the phylogenetic signal (λ) of the model following Revell[57], but also incorporated recommendations from Ives et al.[58] that accounts for error in the response variable. To do so, we used a weighting function with fixed variance of one over the square root of the s.e. of the response estimate[59]. To reveal any phylogenetic relationships between each trait and responses to noise or light, we considered traits one at a time in our models. All traits were tested with all responses, with the exception that light-gathering ability was used as a predictor only for models involving responses to light and vocal frequency was used as a predictor only for models involving responses to noise. If initial λ estimates fell outside of the range 0–1, we fixed λ at the boundary (that is, at 0 or 1). Following suggestions of Jones and Purvis[60], we examined the potential influence of outliers by checking and removing observations with Studentized residuals ≥3.0. Outliers were detected in several models, but their removal did not alter interpretations (Supplementary Table 8). Finally, we repeated all analyses involving the ratio of corneal diameter to transverse diameter ratio (that is, light-gathering ability) as a predictor variable using non-imputed data. With the exception of the analysis of clutch failure responses to light, analyses on the restricted dataset did not differ from those based on the full dataset that included imputed values of this ratio (Supplementary Table 8).

For mixed-effect models evaluating responses to noise or light and PGLS models evaluating how responses (and s.e.) are related to traits, we embraced a more nuanced approach to reporting relationships between parameter estimates than the dichotomous approach of significance testing[61–63]. Specifically, we report and discuss apparent trends and provide 95% confidence intervals (CIs) to reflect the relative precision of estimates. In the Supplementary material, we also report 85% CIs to identify effects that also warrant consideration for inference and for developing future testable hypotheses[23,64]. Because CI estimates require re-running mixed-effect models iteratively for each parameter estimate in spaMM's fitme function, and the computational demands of individual models required runtimes that ranged from days to several months, we calculated CIs as the s.e. of the parameter estimate multiplied by 1.440 (85%) and 1.960 (95%) for all-species, open-habitat birds and closed-habitat bird models. CI ranges for PGLS parameter estimates were derived using the confint function from the stats package[65]. The same function was used to calculate 95% CIs for all species-specific responses (Supplementary Table 7), but we also used the s.e. of the parameter estimate multiplied by 1.44 to generate 85% CIs for the computational reasons outlined above.

Potential collinearity and redundancy

Anthropogenic noise and light levels are often correlated with one another and other environmental variables associated with human activities, necessitating careful inspection of models for issues of multicollinearity. Tools for assessing multicollinearity are not readily available for models in the spaMM package. Thus, we reran our models using the lmer and glmer functions from the lme4 package and the glmmTMB function with Conway–Maxwell–Poisson error from the glmmTMB package[66] to check for potential collinearity and redundancy among the explanatory predictors by calculating the variance inflation factor (VIF) using the check_collinearity function in the performance package[67]. We used the recommendation of Dormann et al.[68] that VIF >10 could reflect problematic issues of multicollinearity. VIF values of all explanatory predictors in all-species models, and for closed and open-habitat species models, were <5 (Supplementary Table 9). For the 13 individual species models (9.6% of models) that had VIF >10 (Supplementary Table 10), we explored whether removal of parameters contributing to high VIF values altered model interpretations. Only in three cases did this prove to be the case (Supplementary Table 11). For these three models, we re-ran spatial versions in fitme within the spaMM package as above and used the parameters from the reduced models for subsequent trait analyses and interpretation (Supplementary Table 7).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The datasets analysed during this study are available at https://doi.org/10.5061/dryad.dbrv15dzc; Additional publicly available data used in this study include: Anthropogenic noise levels from the National Park Service Data Store (https://irma.nps.gov/DataStore/Reference/Profile/2217356); New World Atlas of Artificial Night Sky Brightness (https://dataservices.gfz-potsdam.de/contact/showshort.php?id=escidoc:1541893&contactform); the 2011 US National Land Cover Database (https://www.mrlc.gov/data/nlcd-2011-land-cover-conus-0); US Human population density data (https://data.census.gov/cedsci/); EltonTraits 1.0 database (http://www.esapubs.org/archive/ecol/E095/178/), *Birds of North America Online* (recently changed to *Birds of the World*, https://birdsoftheworld.org/bow/home) and vocal frequency (https://doi.org/10.5061/dryad.75nn1932) and body morphology data (https://doi.org/10.6084/m9.figshare.3527864.v1). Source data are provided with this paper.

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Author contributions C.D.F., J.R.B. and C.J.W.M. conceived the project. C.B.C. and J.V. contributed geospatial NestWatch data and data validation, D.J.M and K.M.F. provided key data on noise and night lighting and L.P.T. provided key trait data. M.S., A.A.W., J.N.P. and C.D.F. performed analyses with advice from M.A.D. and N.H.C. All authors contributed to the writing of the manuscript.

Competing interests The authors declare no competing interests.

Additional information

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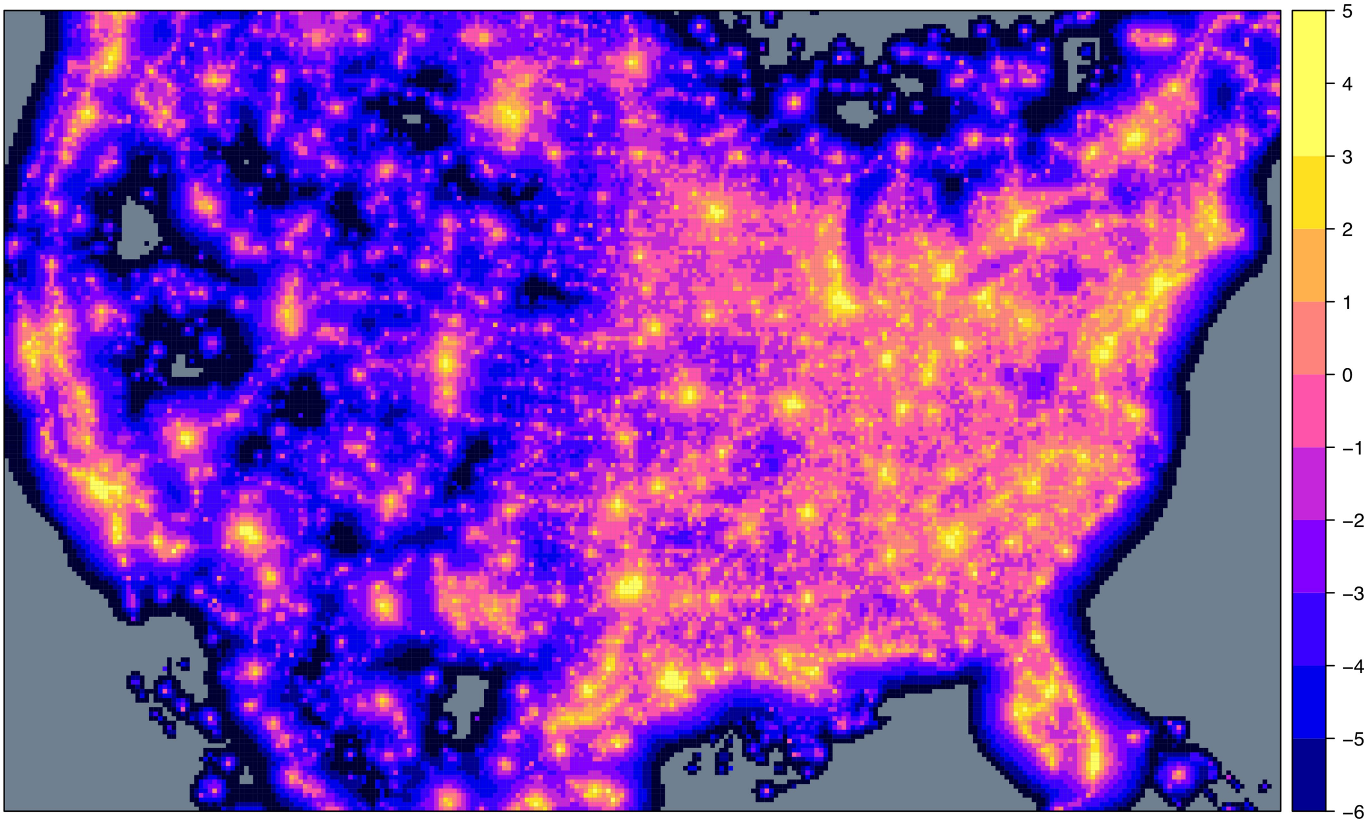
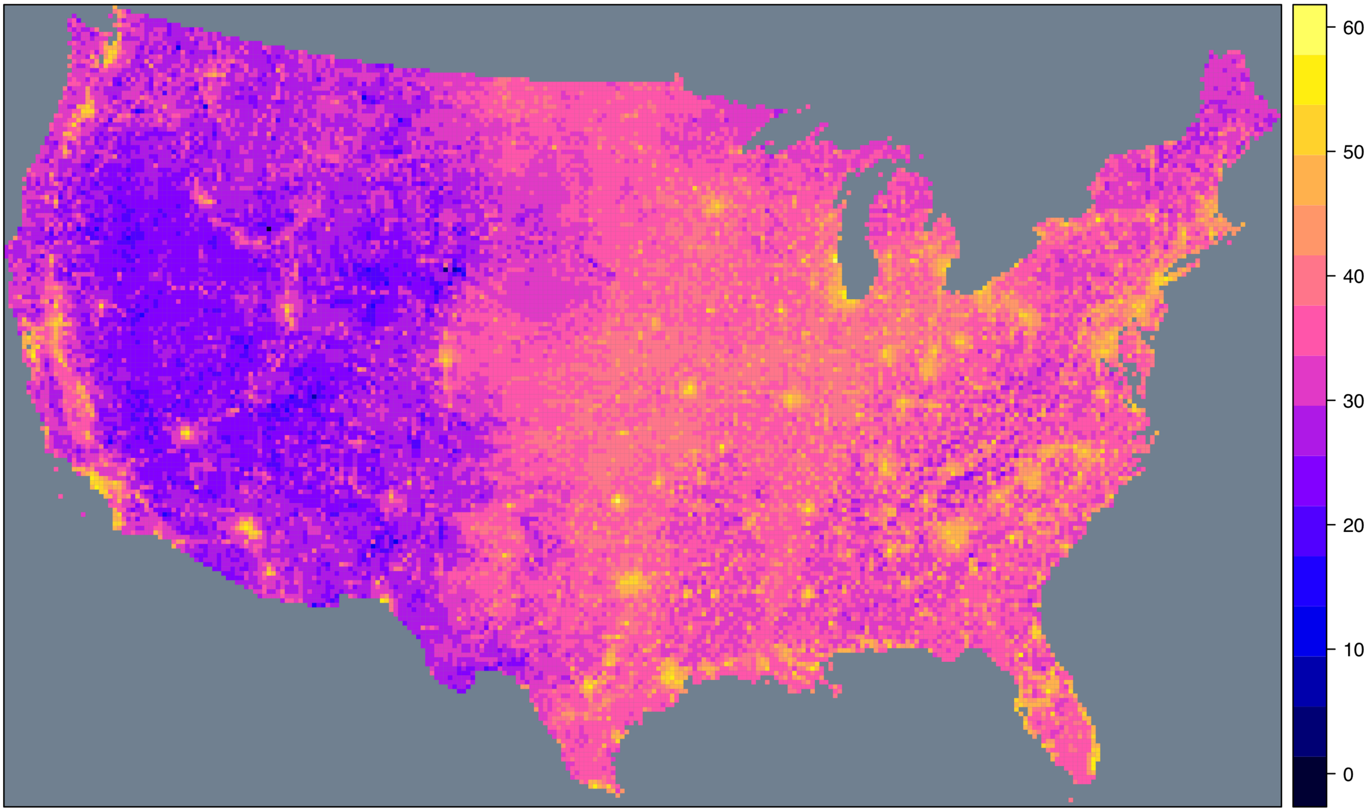
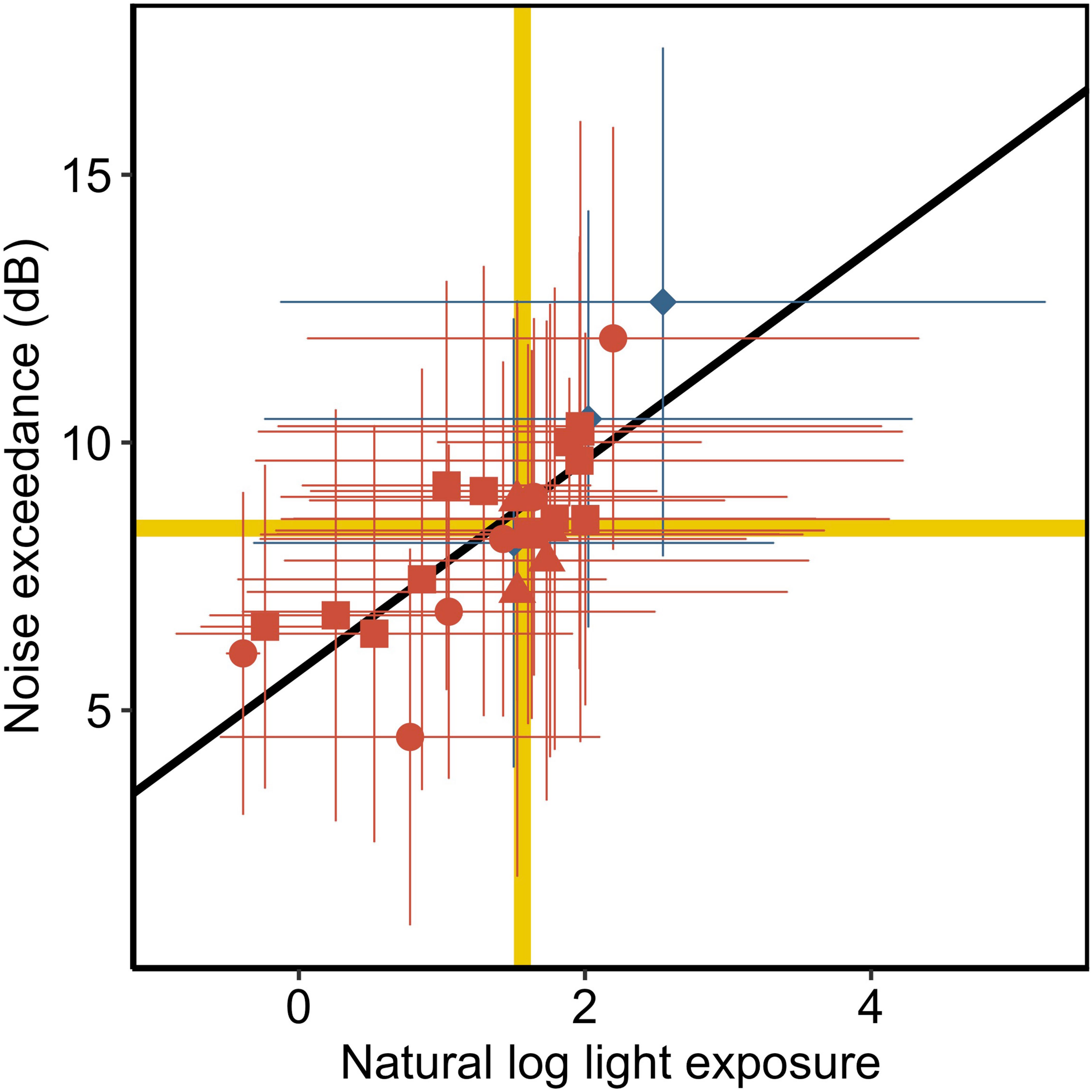


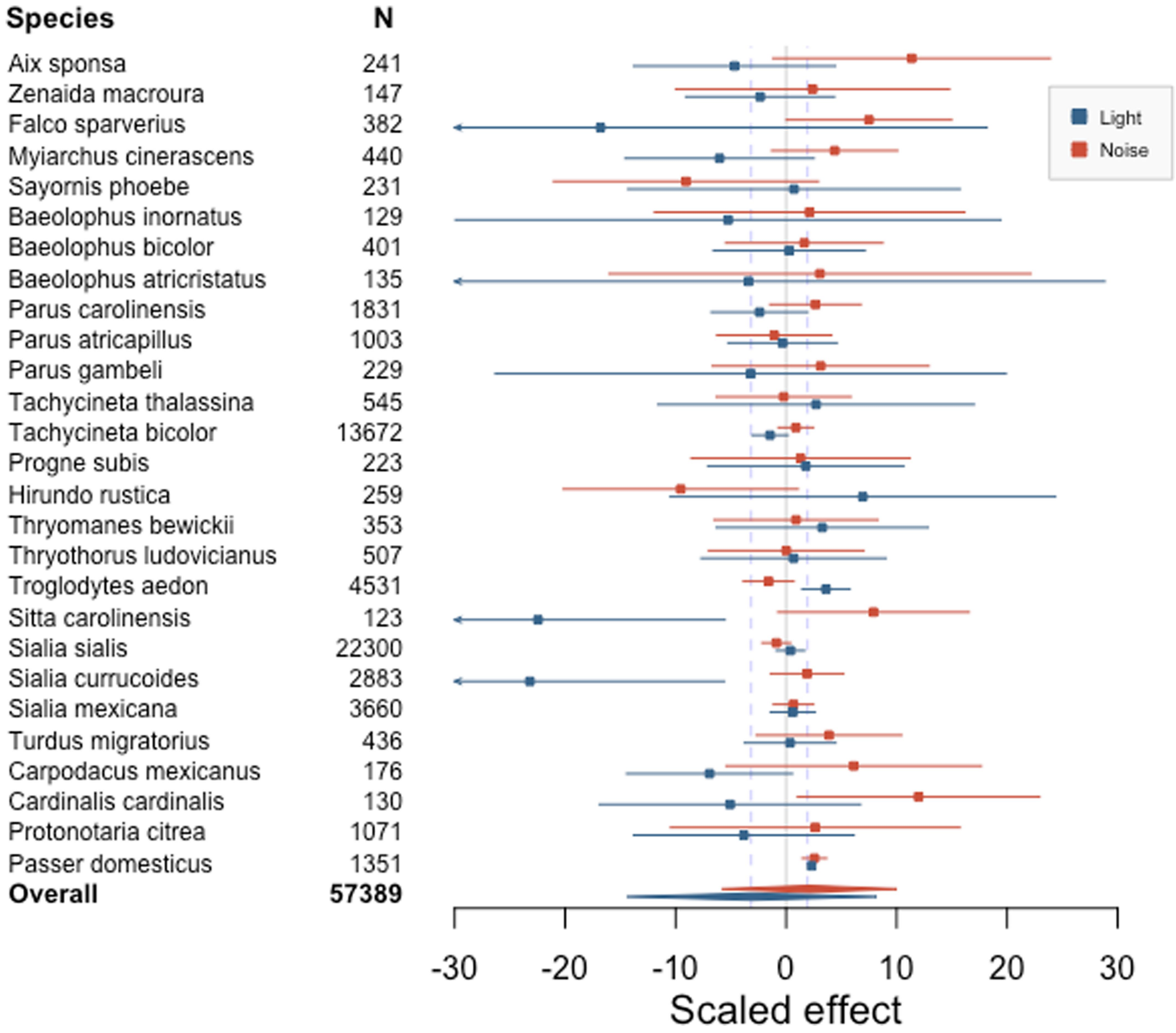
Extended Data Fig. 1 | Natural log of zenith artificial sky brightness as a ratio to the natural background sky brightness. Brighter colours indicate higher light levels.



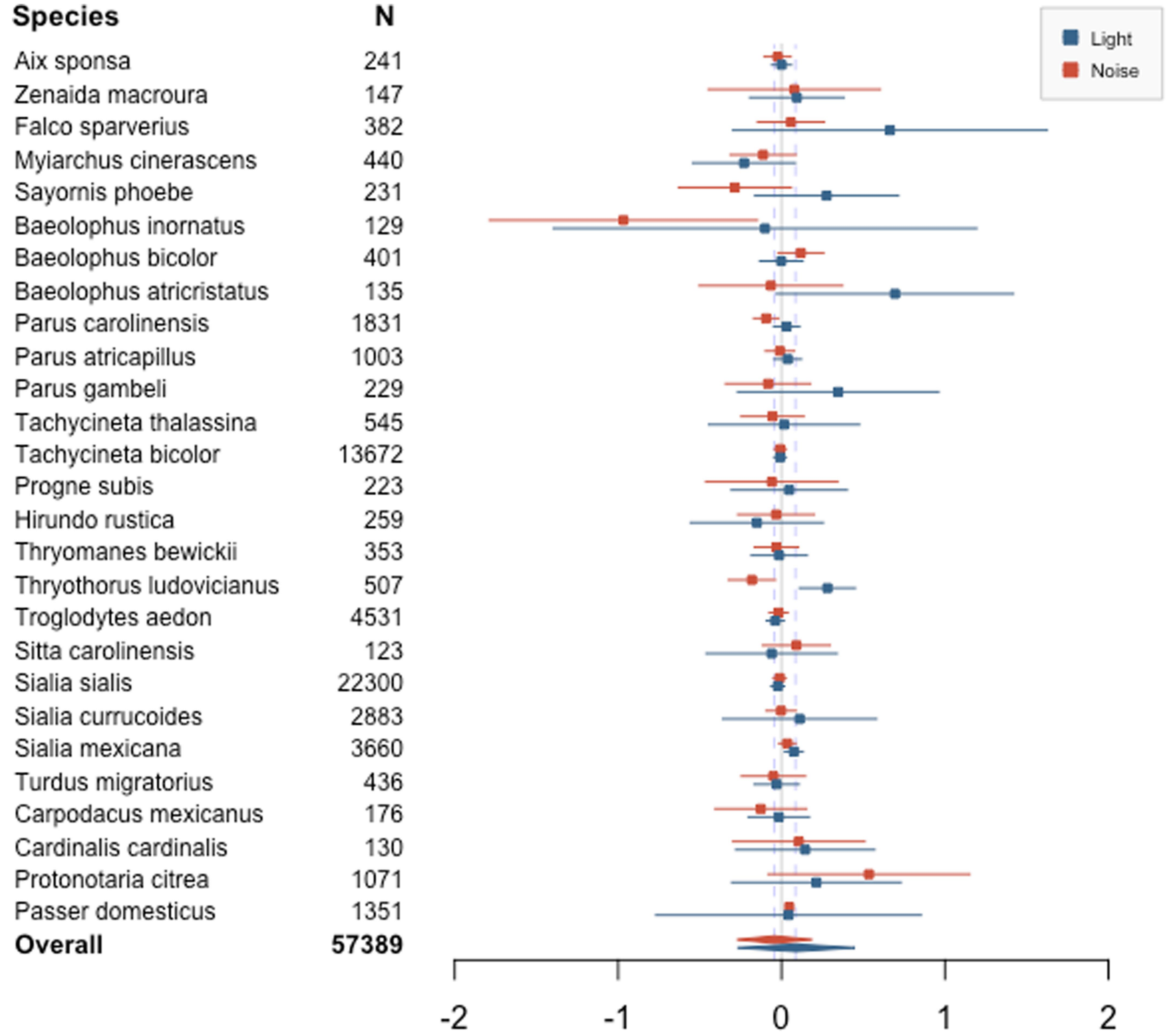
Extended Data Fig. 2 | Anthropogenic component of sound levels (L_{50}, A-weighted dB) across the contiguous United States. Brighter colours indicate higher sound levels. Sound levels used in analyses were exceedance values, calculated by the logarithmic subtraction of the natural from the existing sound projections.



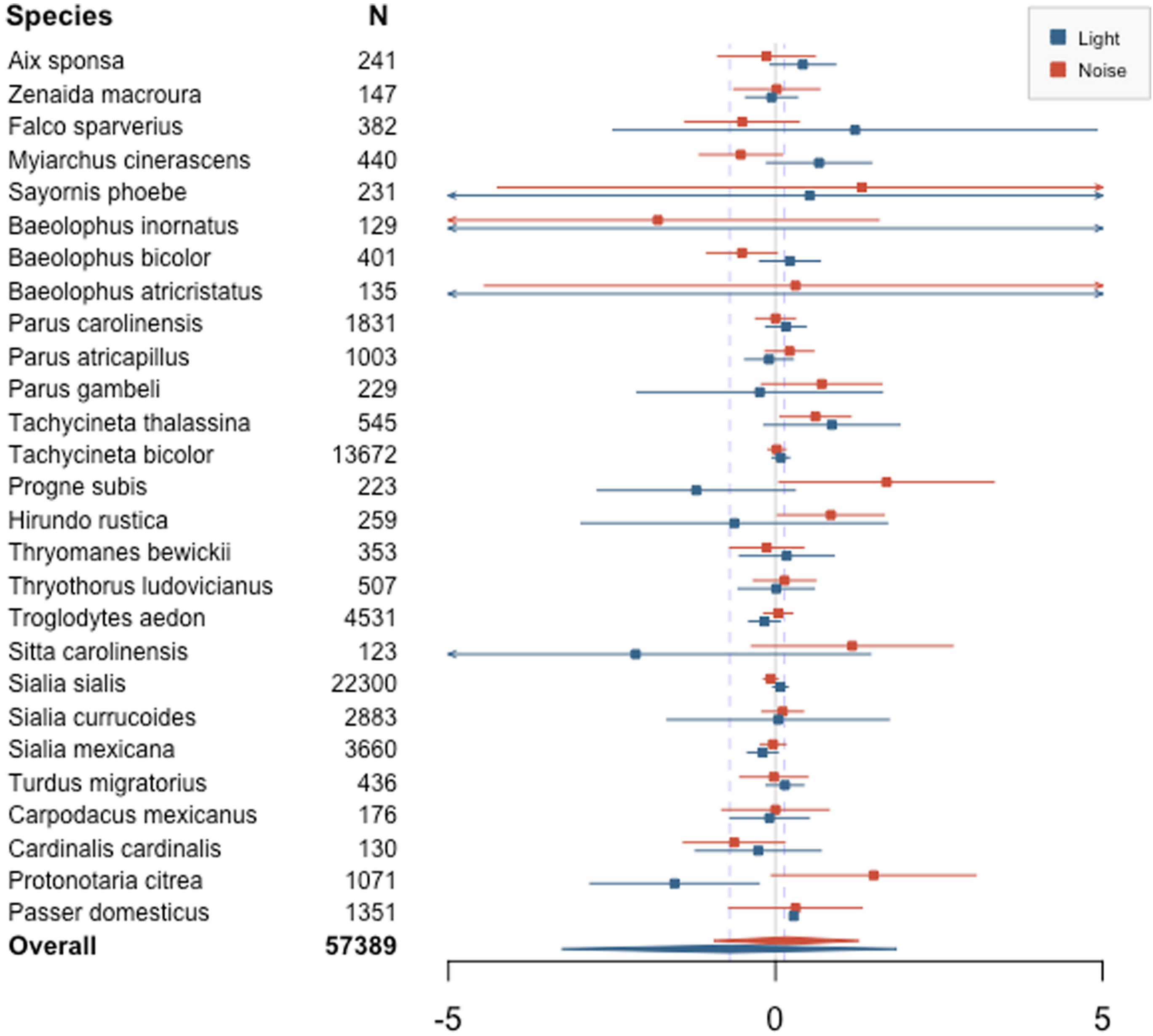
Extended Data Fig. 3 | Exposure to noise and light. Reproduction or breeding phenology was influenced by noise or light for most species, and mean exposure to noise and to light per species were positively correlated (solid black line, Spearman's correlation test; *n* = 27, rho = 0.830, *P* < 0.001). Points and error bars denote mean ± s.d. Twenty-four of the 27 species had apparent responses warranting consideration with 85% CIs that did not overlap zero. Red squares denote species affected by both noise and light, red triangles and circles indicate those affected by either noise or light, respectively, and blue diamonds denote species that appear uninfluenced by either stimulus. Thick horizontal and vertical yellow lines represent mean exposure levels to light and noise, respectively, across all nests in the dataset.



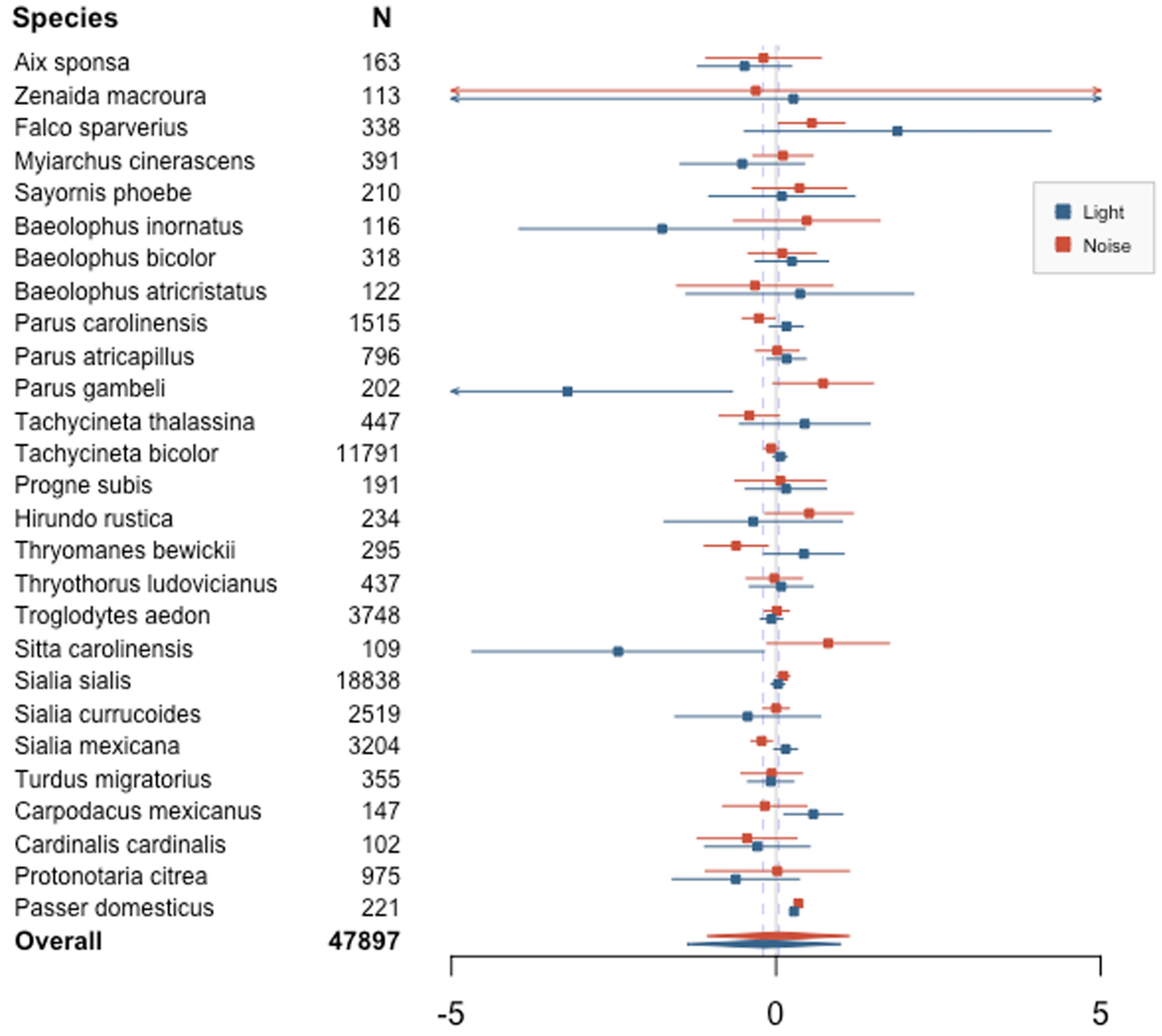
Extended Data Fig. 4 | Forest plot illustrating estimated effect sizes and 95% CI of noise (red) and light (blue) on clutch initiation date. Spatially explicit linear mixed-effect model parameter estimates are centred and scaled for direct comparison. Diamonds for 'Overall' reflect means for listed species, where the diamond centre denotes the mean effect (vertical dashed lines) and the width of the diamond reflects the 95% CI. See Supplementary Table 7 for more model results for each species.



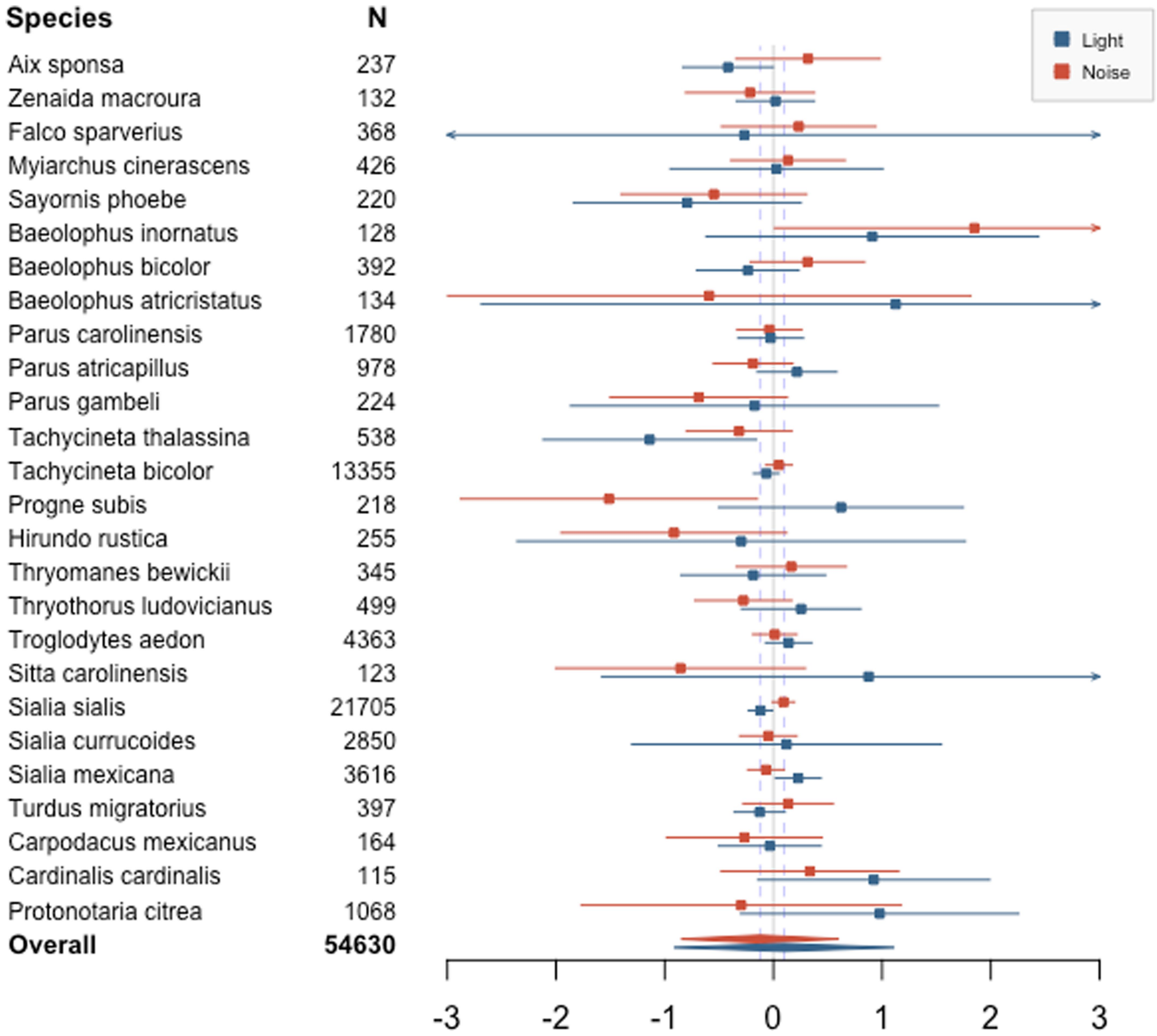
Extended Data Fig. 5 | Forest plot illustrating estimated effect sizes and 95% CI of noise (red) and light (blue) on clutch size. Spatially explicit generalized linear mixed-effect model parameter estimates are centred and scaled for direct comparison. Diamonds for 'Overall' reflect means for listed species, where the diamond centre denotes the mean effect (vertical dashed lines) and the width of the diamond reflects the 95% CI. See Supplementary Table 7 for more model results for each species.



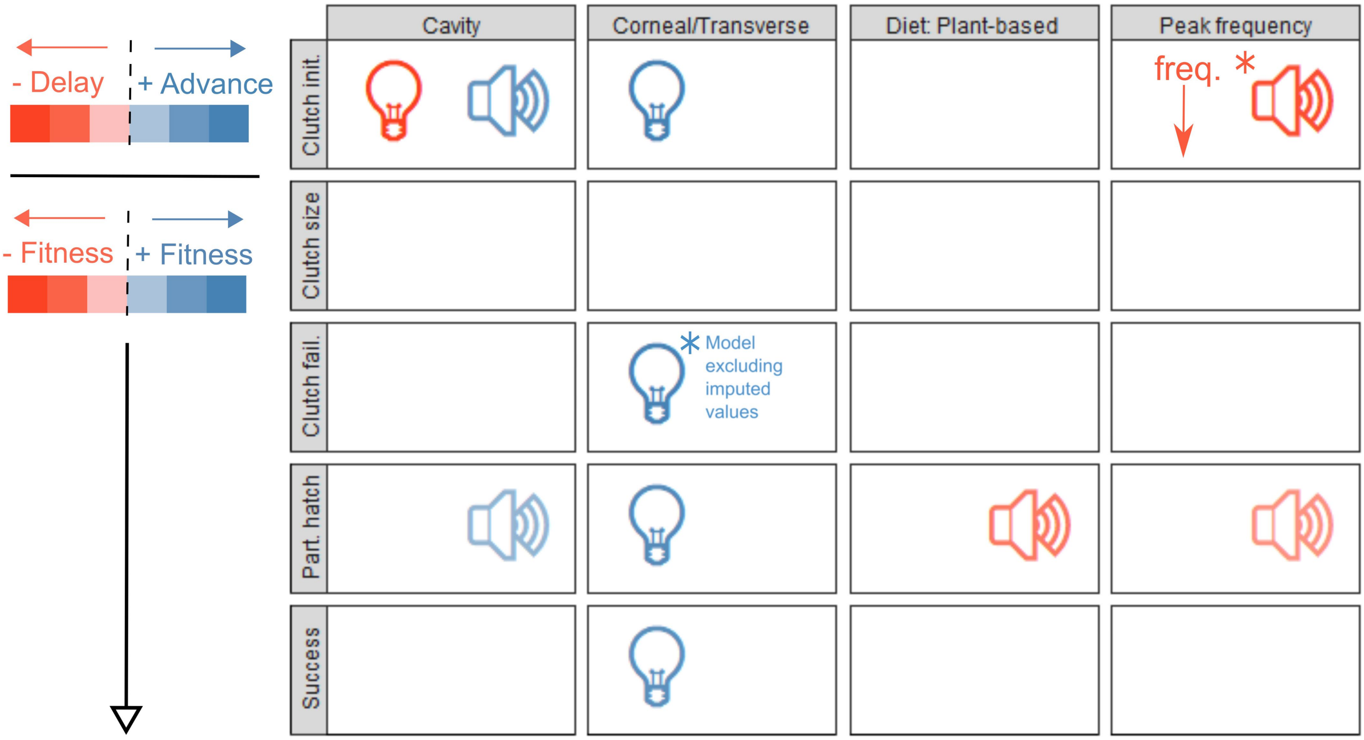
Extended Data Fig. 6 | Forest plot illustrating estimated effect sizes and 95% CI of noise (red) and light (blue) on clutch failure. Spatially explicit generalized linear mixed-effect model parameter estimates are centred and scaled for direct comparison. Diamonds for 'Overall' reflect means for listed species, where the diamond centre denotes the mean effect (vertical dashed lines) and the width of the diamond reflects the 95% CI. See Supplementary Table 7 for more model results for each species.



Extended Data Fig. 7 | Forest plot illustrating estimated effect sizes and 95% CI of noise (red) and light (blue) on incidence of partial hatch. Spatially explicit generalized linear mixed-effect model parameter estimates are centred and scaled for direct comparison. Diamonds for 'Overall' reflect means for listed species, where the diamond centre denotes the mean effect (vertical dashed lines) and the width of the diamond reflects the 95% CI. See Supplementary Table 7 for more model results for each species.



Extended Data Fig. 8 | Forest plot illustrating estimated effect sizes and 95% CI of noise (red) and light (blue) on overall nest success. Spatially explicit generalized linear mixed-effect model parameter estimates are centred and scaled for direct comparison. Diamonds for 'Overall' reflect means for above-listed species. where the diamond centre denotes the mean effect (vertical dashed lines) and the width of the diamond reflects the 95% CI. House sparrow (*Passer domesticus*) not included here because of management actions on nests of this species during the nestling period. See Supplementary Table 7 for more model results for each species.



Extended Data Fig. 9 | Multiple traits linked to responses to noise and light exposure. Light bulbs reflect responses to light, and speakers reflect responses to noise. Red symbols reflect a decline in fitness, or delay in timing for clutch initiation, and blue symbols reflect an improvement in fitness, or advancement in timing for clutch initiation. Symbol shading reflects the strength of the observed effect. See Supplementary Table 8 for individual model results. Light bulb and speaker symbols are from the R package emojifont[69].

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	The only software used for data collection was the imputation of corneal diameter transverse ratios for a subset of species using R 3.6.1 with package Rphylopars 0.2.11.
Data analysis	All analyses were performed in R 3.6.1 in packages spaMM 3.0.0, nlme 3.1-140, geiger 2.0.6.2, lme4 1.1-21, glmmTMB 0.2.3, stats 3.6.1, performance 0.4.6, Rphylopars 0.2.11.

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- A list of figures that have associated raw data
- A description of any restrictions on data availability

The datasets analyzed during this study are available at https://doi.org/10.5061/dryad.dbrv15dzc; Additional publicly-available data used in this study include: Anthropogenic noise levels from the National Park Service Data Store (https://irma.nps.gov/DataStore/Reference/Profile/2217356); New World Atlas of Artificial Night Sky Brightness (https://dataservices.gfz-potsdam.de/contact/showshort.php?id=escidoc:1541893&contactform), the 2011 U.S. National Land Cover Database (https://www.mrlc.gov/data/nlcd-2011-land-cover-conus-0); U.S. Human population density (https://data.census.gov/cedsci/); EltonTraits 1.0 database (http://www.esapubs.org/archive/ecol/E095/178/), Birds of North America Online (recently changed to Birds of the World, https://birdsoftheworld.org/bow/home), vocal frequency (https://doi.org/10.5061/dryad.75nn1932), body morphologies (https://doi.org/10.6084/m9.figshare.3527864.v1).

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used a large nesting database (NestWatch; nestwatch.org) to explore the influence of human activities on several aspects of avian reproduction and to determine how traits relate to species-specific responses to noise and light pollution.
Research sample	NestWatch is a participatory nationwide monitoring program where citizens monitor nests so that the reproductive biology of birds can be studied at a larger scale and over a longer period of time. We used 58,506 existing nest records from the NestWatch Program that met our criteria of precision and plausibility, as outlined in the supplement. This spanned 142 species (Table S1). Additionally, focused analyses were conducted on 27 species (Table S3).
Sampling strategy	We used all nests in our global models and analyzed species-specific responses to anthropogenic stimuli for all nests with >= 100 nests.
Data collection	Nesting data were collected by thousands of citizen scientists volunteers via Cornell Lab of Ornithology's NestWatch Program. Additional data were collected from existing sources: Anthropogenic noise levels from the National Park Service Data Store (https://irma.nps.gov/DataStore/Reference/Profile/2217356); New World Atlas of Artificial Night Sky Brightness (https://dataservices.gfz-potsdam.de/contact/showshort.php?id=escidoc:1541893&contactform), the 2011 U.S. National Land Cover Database (https://www.mrlc.gov/data/nlcd-2011-land-cover-conus-0); U.S. Human population density (https://data.census.gov/cedsci/); EltonTraits 1.0 database (http://www.esapubs.org/archive/ecol/E095/178/),, Birds of North America Online (recently changed to Birds of the World, https://birdsoftheworld.org/bow/home), vocal frequency (https://doi.org/10.5061/dryad.75nn1932), body morphologies (https://doi.org/10.6084/m9.figshare.3527864.v1).
Timing and spatial scale	We included nests that were monitored between 3 March, 2000 and 24 September, 2014 and for which reliable reproductive metrics were taken. This date range was used because it most closely matched available geospatial data used in our analyses. To generate insights that were as generalizable as possible and included as many species as possible and different environmental features, the spatial scale of the study was set to the contiguous United States.
Data exclusions	There were 186,705 nests in the database initially. Using pre-established criteria to maximize nest data precision and plausibility, this was reduced to 58,506 unique nests. See supplemental text.
Reproducibility	We conducted extensive sensitivity analyses to explore model robustness consider how spatial autocorrelation, and multicollinearity could influence interpretation. Moreover, our data package provides sample code for repeating all analyses.
Randomization	We took advantage of already available nesting data and geospatial data, thus did not randomize as one would in a predetermined design.
Blinding	Data included in this study were retrieved from many independent sources and had been generated for different purposes. Blinding to group allocation was not relevant in this study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology
☒	☐	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging