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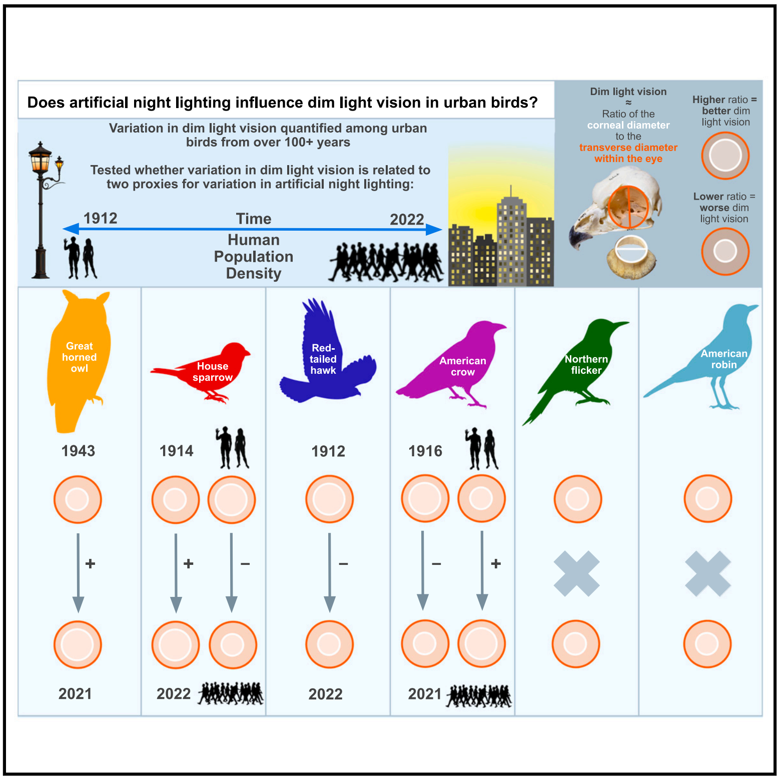
Eye catching light: Anthropogenic light at night and its evolutionary influence on the avian eye

Graphical abstract



Highlights

- Evolutionary responses to artificial light at night are largely unexplored
- Substantial variation in dim light vision exists within each of the 6 focal species
- Artificial light at night proxies were related to dim light vision for 4 of 6 species
- Artificial light at night may serve as a force of natural selection on urban birds

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In brief

Zoology; Ornithology; Evolutionary biology

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Eye catching light: Anthropogenic light at night and its evolutionary influence on the avian eye

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SUMMARY

Variation among avian species in their responses to artificial night lighting was recently linked to differences in dim light vision, but whether dim light vision is under selection from human-caused night lighting is unexplored. Here, we approximated dim light vision using eye geometries from museum specimens of six species collected across 100+ years and sought to determine whether proxies for artificial night lighting were related to within-species variation in dim light vision. We found variation in dim light vision was strongly linked to artificial night lighting proxies for three species and weakly linked for a forth, but the relationship varied by species. This variation is likely related to differences in ecological traits and may also reflect whether artificial night lighting facilitates increased temporal activity or results in physiological costs for each species. These results suggest that altered sensory environments are likely a source of selection shaping the sensory abilities of animals in the anthropocene.

INTRODUCTION

There is more artificial light at night (ALAN) today than ever before,[1] a trend that will continue with the ongoing spread of urbanization, exposing a wide range of organisms to evolutionarily novel nocturnal illumination conditions and cycles.[2–4] Birds in particular exhibit well-documented behavioral[5,6] and physiological[7] responses to artificial night lighting. For example, Japanese quail (*Coturnix japonica*), house sparrows (*Passer domesticus*), and California scrub-jays (*Aphelocoma californica*) exposed to nighttime light in laboratory conditions can experience altered melatonin production, a key hormone for regulating circadian rhythm.[8–10] This response to artificial night lighting can have negative physiological consequences; examples include increased stress hormones in captive zebra finches (*Taeniopygia guttata*), malaria infection in wild great tits (*Parus major*), and mortality from West Nile virus exposure in captive house sparrows.[9,11,12] Alternatively, other species exposed to artificial night lighting experience higher reproductive output and success through advancement of lay date, improved provisioning rates, and increased foraging efficiency.[13–16]

One promising avenue for explaining species-specific variability in response to artificial night lighting is by leveraging variation in the dominant avian sensory system: vision.[17] More specifically, how well birds can see in dim light.[15,18,19] For instance, birds with better dim light vision have been found to nest earlier and have improved nest success when they are exposed to nighttime light.[15] Dim light sensitivity also relates to the degree of retinal stimulation when light enters the eye, one mechanism for entrainment of melatonin cycles that influence various physiological states and rhythms.[8,9] Because artificial night lighting disrupts melatonin cycles and expression[9] and melatonin is linked to immune function,[20] declines in immune function and survival with exposure to night lighting are often interpreted as consequences of melatonin disruption.[9,21] Both the positive and negative physiological and reproductive consequences that some species experience in response to artificial night lighting suggest that within-species variation in dim light vision could represent a target of natural selection.

Quality of dim light vision can be approximated by the ratio of eye geometries, such as the ratio of the corneal diameter to the transverse diameter[22–24] or the cornea diameter to the axial length of the eye (Figure 1).[18,19] A larger cornea diameter relative to either the transverse diameter or axial length corresponds to increased visual sensitivity in dim light conditions by allowing larger pupil dilation and more light photons to enter the eye. The ratio of the cornea diameter to the axial length or transverse diameter estimates an organism's ability to see detail in dim conditions while removing the effect of body size.[15,24] For most organisms, obtaining this ratio requires measurement of soft tissues of the eye or using the orbit diameter within the skull to approximate transverse diameter or axial length. However, birds, like many of their reptilian relatives, have bony structures in their eyes called sclerotic rings that approximate the size of the cornea[18] and are present in many museum skeletal collections. This unique resource provides an exceptional opportunity to study contemporary evolutionary change in the avian eye since the development of reliable electricity and electric lighting

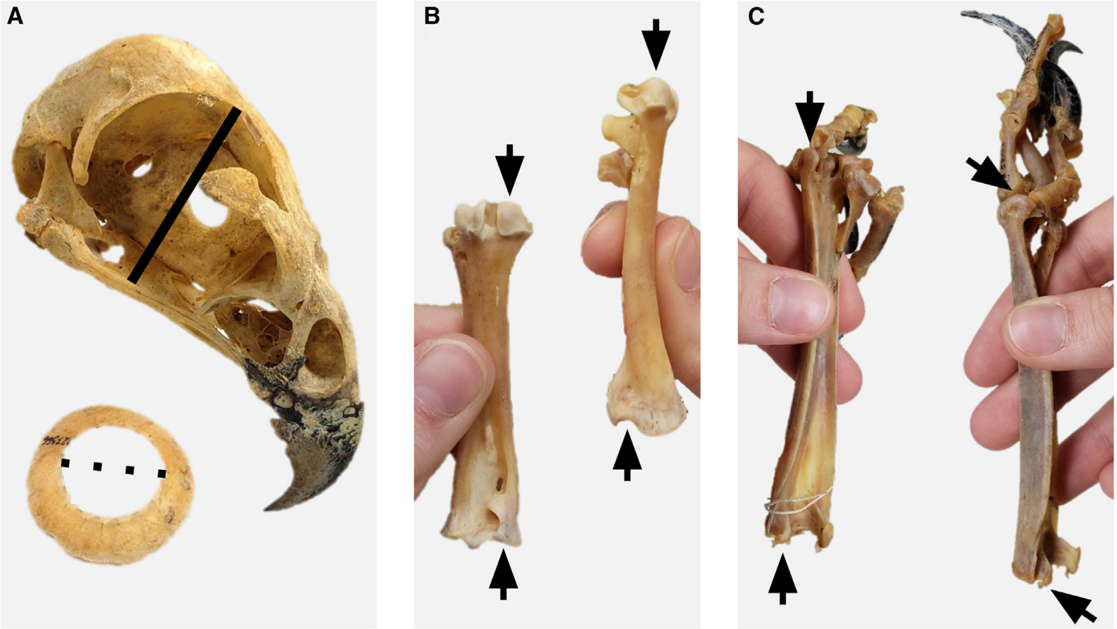

Figure 1. Measurement points for orbit diamter, sclerotic ring diameter, and tarsus length

Diagram showing measurements for (A) orbit diameter within the skull (solid line) and inner sclerotic ring diameter (dotted line) for a red-tailed hawk, (B) tarsus measure points for a great horned owl, and (C) tarsus measure points for a red-tailed hawk.

more than one century ago. Since that time electric lighting has proliferated rapidly and increased in intensity, exposing urban birds, and other organisms, to higher levels of artificial night lighting with each passing year.[1,3] Thus time can serve as a reasonable proxy for artificial night lighting exposure within cities and provides the opportunity to determine how dim light vision in urban birds varies with increasing levels of nighttime light. Additionally, because not all cities are the same size or have grown at the same rates or times, historical estimates of population density can also be used as a reasonable proxy for artificial night lighting given the strong link between population size and nocturnal illumination.[25,26]

Here, we use museum collections of six quintessential urban bird species sampled from across the contiguous USA (Figure 2) to test two opposing hypotheses of how artificial night lighting may serve as a source of directional selection on the avian eye geometries that determine dim light vision; the protection and temporal niche shift hypotheses. Because urban birds exposed to artificial night lighting have documented increased nighttime activity[11,12,27,28] and increased nighttime foraging,[14,29] and species with better dim light vision appear to have improved reproductive success when exposed to artificial night lighting,[15] under the temporal niche shift hypothesis we predict dim light vision to increase over time among urban birds. Furthermore, because artificial night lighting is more intense in more densely populated cities,[30] we expect dim light vision to positively covary with higher human population densities. Alternatively, because retinal stimulation by artificial night lighting can alter melatonin production[8,10] and melatonin dysregulation from artificial night lighting can increase stress, impair immune function, and increase mortality risk from disease,[9] under the protection hypothesis we predict dim light vision among urban birds has decreased over time and that the decrease should be most pronounced in cities with higher human population densities. To better understand the skeletal changes responsible for alterations in dim light vision, we also individually examined the underlying morphological components of the dim light vision ratio, orbit and cornea size.

RESULTS

Dim light vision

There was a range in dim light vision, transformed to scale between 0 and 100, based on species identity (Figure 3, see Neate-Clegg et al.[31] and Ritland[24] for additional data in Figure 3). The lowest dim light vision of a specimen was 38.29, from a Northern flicker, and the highest was 66.89, from a great horned owl. House sparrows had the lowest average dim light vision at 44.06 and great horned owls had the highest at 63.03 (Figure 3). American crows and American robins had the most similar dim light vision, with averages of 48.76 and 48.04 respectively. Additionally, considerable variation in dim light vision existed within each species upon which selection could act (Figure 3).

Model selection for dim light vision

Proxies reflective of the intensity of artificial night lighting occurred in supported models for all six species (Table 1). The top-ranked model for American crow contained the interaction between human population density and year, plus tarsus length; however, the variance inflation factor (VIF) for that model indicated extremely high levels of multicollinearity (VIF >10,000) and so the additive model with year, density, and tarsus length was considered the single supported model. The model with

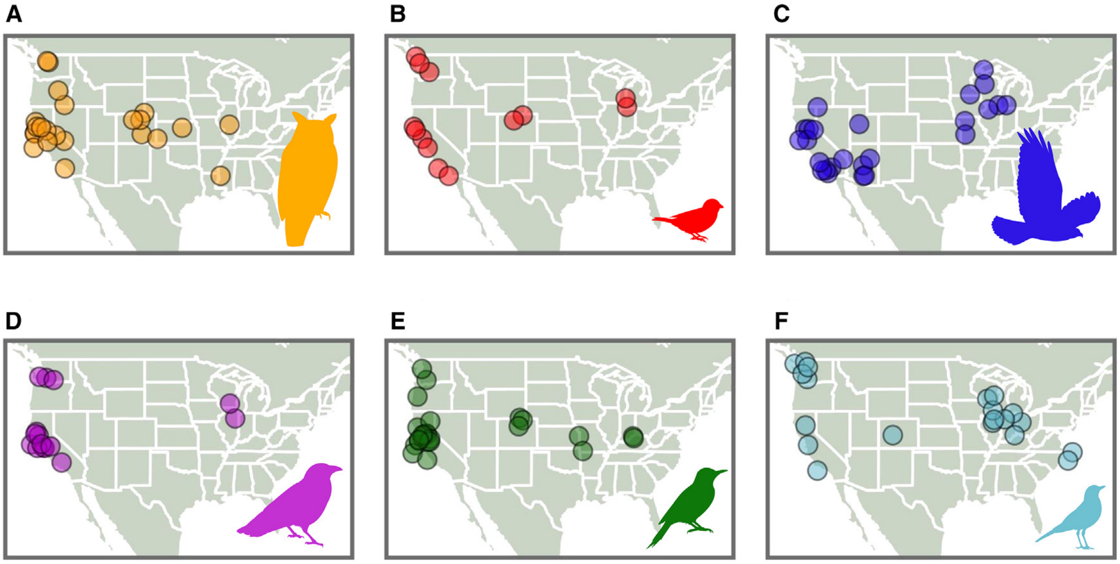

Figure 2. Collection locations of target species specimens
Maps showing specimen collection locations for (A) great horned owls, (B) house sparrows, (C) red-tailed hawks, (D) American crows, (E) Northern flickers, and (F) American robins. Points are slightly jittered to decrease overplotting.

year, density, and tarsus length was also the top-ranked model for house sparrows, but the model with year and tarsus length had nearly equal support, closely followed by one with only tarsus length. The top-ranked model for both great horned owls and red-tailed hawks contained year and tarsus length and a second model with only tarsus length was competitive for great horned owls. The model with density and tarsus length was the top ranked model for both Northern flickers and American robins and a second model with only tarsus was also competitive for Northern flickers (Table 1).

Species specific patterns of dim light vision

Variation in dim light vision was related to collection year for four species and human population density for two species. House sparrow and great horned owl dim light vision has increased over the last 75–100 years (house sparrow $\beta = 0.038 \pm 0.013$ SE, 95% confidence interval [CI] 0.010, 0.065; great horned owl $\beta = 0.029 \pm 0.017$ SE, 95% CI -0.006, 0.064 respectively; Figure 4). However, the estimated effect for great horned owls was less precise and the model with only tarsus length was also supported by the data. For house sparrows, there was a trend, but with low precision, for dim light vision to negatively covary with log-adjusted human population density ($\beta = -0.836 \pm 0.443$ SE, 95% CI -1.775, 0.103). As a sensitivity analysis, we confirmed the increase in dim light vision with year among house sparrows by taking advantage of an additional 16 specimens that lacked tarsus length measurements ($\beta = 0.037 \pm 0.010$ SE, 95% CI 0.017, 0.057).

In contrast to the temporal changes in dim light vision among house sparrows and great horned owls, red-tailed hawk and American crow dim light vision declined over the last 100+ years (red-tailed hawk $\beta = -0.020 \pm 0.009$ SE, 95% CI -0.038, -0.001; American crow $\beta = -0.027 \pm 0.007$ SE, 95% CI -0.043, -0.012 respectively; Figure 4). In addition to collection year, the American crow model included log-adjusted human population density, which had a positive relationship with dim light vision ($\beta = 0.573 \pm 0.136$ SE, 95% CI 0.289, 0.857; Figures 4 and S2). Tarsus length failed to explain variation in dim light vision for all species and, although tarsus length appeared in the highest-ranked models for both Northern flickers and American robins, no variables were related to dim light vision in these species.

Underlying morphological drivers of dim light vision change

We found that sclerotic ring and orbit diameter had different levels of importance in driving patterns in dim light vision depending on the species. For house sparrows and red-tailed hawks, orbit diameter was the main driver in determining change in dim light vision over time (house sparrow $\beta = -0.006 \pm 0.002$ SE, 95% CI -0.010, -0.002, red-tail hawk $\beta = 0.014 \pm 0.006$ SE, 95% CI 0.001, 0.027 respectively; Figure 5). Changes in orbit size among house sparrows also was responsible for the negative relationship between dim light vision and higher human population densities ($\beta = 0.307 \pm 0.064$ SE, 95% CI 0.171, 0.444; Figure 5). For these species, there were no discernible relationships between sclerotic ring diameter and time or human population density. However, models for American crows exhibited the opposite pattern; variation in sclerotic ring diameter was the main driver for declines in dim light vision over time ($\beta = -0.006 \pm 0.002$ SE, 95% CI -0.011, -0.002), although there were no discernable patterns in either their orbit or sclerotic ring diameters at different human population densities. In American crows, tarsus length was also strongly linked to orbit diameter ($\beta = 0.196 \pm 0.050$ SE, 95% CI 0.091, 0.301) and sclerotic ring diameter ($\beta = 0.118 \pm 0.023$ SE, 95% CI 0.071, 0.166,

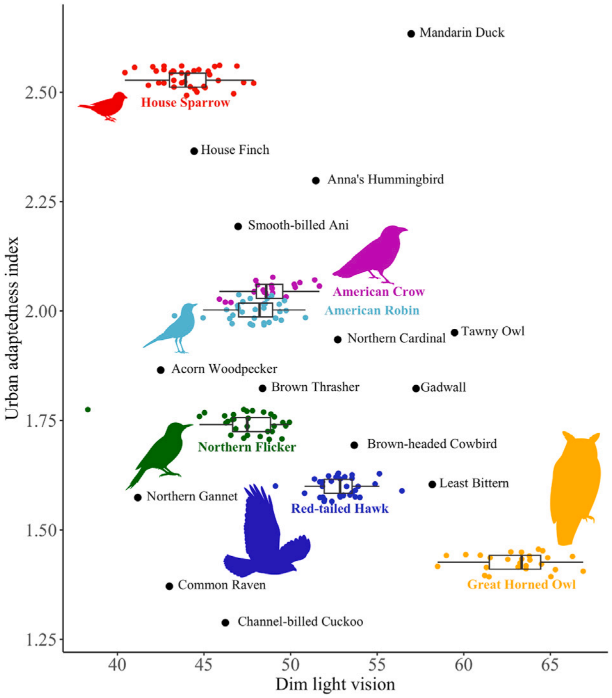

Figure 3. Urban adaptedness indices by dim light vision of target species

Dim light vision for all specimens within target species plotted in reference to their urban adaptedness scores from Neate-Clegg (scores for USA specimens averaged for individual species and jittered for visualization). Select dim light vision data and urban adaptedness scores from other species are plotted for reference to demonstrate breadth of dim light vision values and urban adaptedness among the species included in our study, plus the substantial intra-specific variation in dim light vision documented for each of our six target species. We transformed the dim light vision ratio to scale between 0 and 100 to facilitate interpretation of effects and figures. Higher values of dim light vision indicate an increased ability to detect light in dim conditions.

Figure 5). Finally, although dim light vision tended to increase over time for great horned owls, both variation in the sclerotic ring and orbit diameter were unrelated to year but instead linked to variation in tarsus length (sclerotic ring $\beta = 0.094 \pm 0.051$ SE, 95% CI -0.012, 0.200; orbit $\beta = 0.287 \pm 0.085$ SE, 95% CI 0.109, 0.464); however, the precision of the effect of tarsus length on sclerotic ring diameter was low.

DISCUSSION

Artificial night lighting is pervasive and spreading, with its extent and brightness increasing by approximately 2% every year[3] and mounting research suggests it has far-reaching physiological and ecological consequences for wildlife.[32] Recent evidence also suggests night lighting may be a source of selection. For instance, urban moth populations exhibit a reduced flight-to-light response compared to rural populations.[33] Here, we provide evidence that artificial night lighting may also be an agent of natural selection influencing the morphology and vision of urban birds. First, we document substantial variation in dim light vision within species and this within-species variation appears to rival across-species variation (Figure 3), which has previously been shown to explain variation in habitat affiliations and foraging traits.[34,35] We evaluated two opposing hypotheses to explain within-species variation in dim light vision: the temporal niche shift hypothesis and the protection hypothesis. Under the first, we predicted that dim light vision among urban-adapted species would positively covary with indices of artificial night lighting, potentially in response to fitness benefits from light-pollution-induced shifts in their temporal niches. Under the second, we predicted that dim light vision should decrease with indices of light exposure among urban-adapted species to mitigate the negative physiological and fitness consequences of retinally received light exposure. Given the phylogenetic and functional diversity among our six target species, it may not be surprising that we found support for both hypotheses. Moreover, support for both hypotheses in American crows suggests selection on dim light vision may be nuanced with trade-offs between ecological opportunities and physiological costs that warrant future attention by researchers.

The positive trend detected between dim light vision and collection year for house sparrows and, in a less precise way, great horned owls, plus dim light vision and human population density for American crows is consistent with the temporal niche shift hypothesis. Various avian species have expanded their hours of activity into the night in response to nocturnal light exposure,[5,27–29] utilizing times that are now dim instead of

Table 1. Model ranking by AICc scores for each species-specific model, with dim light vision as the dependent variable

Species	Year x Density + Tarsus	Year + Density + Tarsus	Year + Tarsus	Density + Tarsus	Tarsus	Null
Great horned owl	110.32	107.53	104.53*	107.22	104.74*	115.14
Red-tailed hawk	75.78	71.92	69.73*	75.10	71.86	118.28
Northern flicker	145.96	143.01	144.02	140.15*	141.39*	143.21
American crow	75.89[a]	79.27*	91.18	88.36	92.76	90.10
American robin	104.55	102.41	106.17	99.30*	103.36	127.88
House sparrow	93.17	89.52*	89.92*	94.36	91.34	144.16

Supported models (i.e., ΔAICc ≤ 2) are followed by an asterisk. Year reflects collection year, and density represents log-adjusted human population density per km^2 for the county in which the specimen was collected and tarsus reflects tarsus length. Due to high multicollinearity in the American crow model with an interaction between year and density, the model with additive effects of year and density was selected for American crows as the only supported model

[a] Issues of multicollinearity, thus next-best model considered best-supported in model selection.

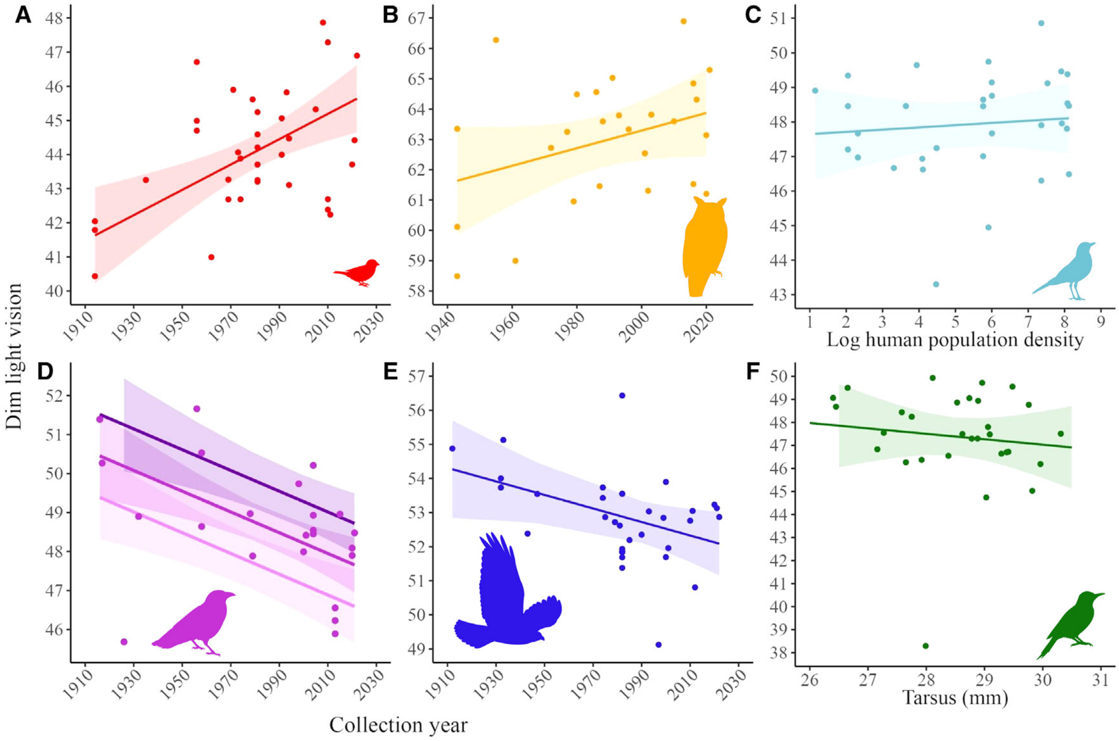

Figure 4. Relationship between dim light vision and influential variables from top-ranked models from Table 1

Change in dim light vision over time for (A) house sparrows, (B) great horned owls, (D) American crows, and (E) red-tailed hawks. The natural log of human population density and tarsus length were in top-ranked models explaining dim light vision for (C) American robins and (F) Northern flickers, respectively, but the precision of effects of either variable was low. Trend line represents marginal effects and shading represents 95% confidence interval (95% CI) of the estimated effect. (A) Trends displayed for house sparrow reflect sensitivity analysis with larger sample size (see text). (D) Different colors for trend lines and 95% CIs reflect estimates at three human population densities (light, medium, and dark reflect 22, 136, and 854 people per km^2, respectively). Dim light vision ratios were transformed to scale between 0 and 100 to facilitate interpretation of effects and visualization of results.

dark.[2] Although not explicitly documented for house sparrows and American crows, these species could be experiencing a similar temporal niche shift. Outwardly, the trend for dim light vision in great horned owls over time is puzzling given that this species is colloquially considered nocturnal. Although this trend was relatively imprecise and should be interpreted with caution, the apparent trend warrants consideration of plausible explanations that could be tested in future research. First, great horned owls are acoustic specialists and are particularly active at dawn and dusk.[36] High noise levels from commuting traffic in urban areas during twilight could impair hunting, as has been shown in several owl species,[37,38] and force urban owls to shift from foraging during dawn and dusk to other times of the night that are less noisy, but also darker, favoring improved dim light vision. Shifts in activity toward deeper times of night have been documented in other taxa; for instance, human disturbance has caused broad scale shifts to increased nocturnality among small mammals.[39] Moreover, many mammalian predators are known to shift hunting activity to align with activity patterns of their main prey.[40–42] If urban owls exhibit the same temporal prey tracking patterns, selection for better dim light vision could reflect an epiphenomenon of tracking prey activity patterns. Finally, it is also plausible that increases in dim light vision reflect a trade-off across sensory modalities. Increased reliance on visual surveillance when auditory surveillance is impaired by noise has been documented in mammals and birds,[43–46] and these consequences typically come at the cost of foraging. Because noise can drastically reduce owl prey detection[38] and hunting success,[37] it is possible that selection could act upon urban owl visual systems to compensate for the decreased reliance on hearing. These cross-modality effects should be the focus of future work, especially given that artificial night lighting can covary strongly with noise pollution in urban areas.[6]

The negative trends between dim light vision and collection year for red-tailed hawks and American crows provide support for the protection hypothesis. Exposure to artificial light at night can disrupt sleep and circadian rhythms,[12,47] imparting negative physiological consequences in humans and wild animals, spanning increased rates of metabolic disease to decreased immune function.[12,48–50] At present, key data on whether these physiological responses to light exposure relate to lifetime fitness are scant and limit our understanding of the full fitness costs of artificial night lighting. Nevertheless, if these physiological responses do impact fitness and are disproportionately borne by individuals in populations with better dim light vision, limiting light stimulation via the visual system could mitigate the physiological harm individuals experience when exposed to elevated levels of light and drive decreases in dim light vision.

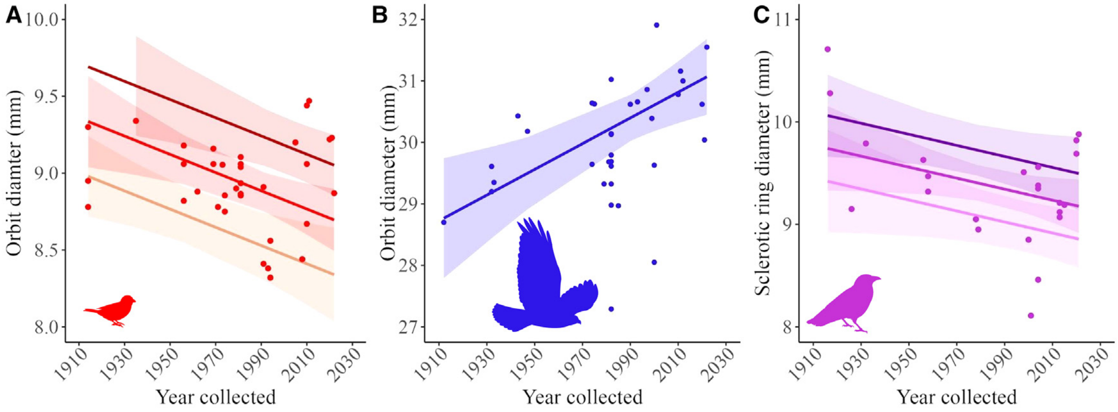

Figure 5. Relationship between individual eye geometries used to approximate dim light vision and collection year

Orbit diameter declined over time for (A) house sparrows and increased over time for (B) red-tailed hawks. Change in sclerotic ring diameter over time for (C) American crows. Trend lines represent marginal effects and shading represents 95% confidence interval (95% CI) of the estimated effect. In (A), different colors for trend lines and 95% CIs reflect estimates at three human population densities (light, medium and dark reflect 82, 260, and 829 people per km^2, respectively). In (C), different colors for trend lines and 95% CIs reflect estimates at three tarsus lengths (light, medium and dark reflect 49.72, 53.27, and 56.81 mm, respectively).

For American crows, we found strong trends that are outwardly in conflict; dim light vision increases with population density, but decreases over time. There was also weak evidence for a similar conflict with house sparrows, but the precision of the negative influence of human population density was low. Although the exact mechanisms responsible for these patterns are unknown, some likely explanations emerge that could be formally tested in the future. A previous study found that great tits exposed to bright night lighting conditions suffered sleep disruption, but exposure to relatively dim lighting conditions did not result in sleep disruption.[47] If intensity-specific responses are similar among free living urban bird populations, high intensities of artificial night lighting could favor reduced dim light vision in birds in the densest urban areas because the physiological costs of nocturnal light exposure outweigh the benefit of a widened temporal niche via improved vision in dim light conditions. It is also possible that the benefits of increased dim light vision are asymptotic with respect to artificial night lighting; under very bright conditions dim light vision may not be necessary to maintain activity at night and the physiological costs predominate. Additionally, although dim light vision appears to vary just as much in Northern flickers and American robins as in the other four species, this variation was not explained by any of our predictors. This pattern could be driven by the partially migratory nature of some American robins resulting in exposure to a variety of light environments and Northern flickers being obligate cavity nesters, thus sheltering them from some of the selective pressures of artificial night lighting. Alternatively, these two species could be pre-adapted to bright night lighting conditions or selection on other dimensions of their ecology outweighs any influence of artificial night lighting. Although large comparative analyses that better capture variation in traits, niches, and life histories will be necessary for a more rounded understanding of why dim light vision appears to increase, decrease, or fail to change with proxies of artificial night lighting, our analyses provide the first indication that anthropogenic nighttime lighting is likely a source of contemporary evolution of sensory systems. The prospect of microevolution of eye geometries across light regimes is complemented by new macroevolution evidence linking across-species variation in eye geometries to foraging ecology and lighting conditions created by different habitats.[34,35]

Increases or decreases in dim light vision among our study species appears to be linked to changes in orbit diameter in two species (red-tailed hawks and house sparrows) and sclerotic ring diameter in one (American crow). In others, changes in dim light vision appear to be an emergent property of more subtle changes in these skeletal features. The changes in orbit diameter are supported by a recent study finding a decline in lateral eye width in Carolina Wrens (*Thryothorus ludovicianus*) and Northern cardinals (*Cardinalis cardinalis*) with increased exposure to artificial night lighting,[51] which also is consistent with the protection hypothesis. However, because body size was not included in the models that showed this pattern, it is unclear whether this relationship between eye width and artificial night lighting is independent of variation in body size, especially given recent evidence of widespread changes in avian body size over relatively short time periods[52] and the evidence in our study where orbit diameter was strongly linked to tarsus length for two species. Because we also explicitly controlled for body size in our analyses, we can exclude the possibility that shifts in dim light vision simply reflected variation in body size for two reasons. In all cases, tarsus length was an uninformative predictor in all models explaining variation in dim light vision. Additionally, a *post hoc* analysis of tarsus length as the response variable in the previously selected best performing models did not reveal any relationships with collection year or human population density (Tables S3 and S4). These results conflict with previously documented avian body size changes over relatively short time scales,[52] potentially because we used tarsus length as a measure of body size rather than body mass, we did not restrict analyses to only adult males, or because our sample size was much smaller, albeit over longer periods of time. Regardless, not finding relationships between tarsus length and time or human population density indicates that the documented changes in eye geometries reflect selection acting on the visual system independently from overall body size.

Collectively, our results suggest that avian responses to artificial night lighting are variable among species and provide strong evidence that artificial night lighting may be an important agent of selection, driving contemporary human-induced evolution in wild birds. The wide range of responses exhibited by all six urban-adapted bird species in this study highlights the need to broaden this analysis with more species to shed light on what traits could drive species-specific patterns. Doing so while also analyzing changes in orbit or sclerotic ring sizes will reveal which morphological features drive variation in dim light vision and whether the visual geometries of some clades are particularly constrained or labile. Another natural continuation of this work includes investigating whether the species with dim light vision that improved with proxies of artificial night lighting are in fact shifting their temporal niches, and whether temporal niches vary along an urban gradient where the influences of noise, light, human activity, and other variables could be teased apart. Finally, although this work shows that evolutionary responses to altered light regimes may be possible, it also suggests that dim light vision may be an important trait in explaining ecological responses to human development in an increasingly urbanized world.

Limitations of the study

An important limitation to our study is that there are no direct artificial night lighting measures from the early 20th century, making it impossible to know artificial night lighting exposure for each historical sample. However, to still capitalize on the unique opportunity afforded by historical specimens, we used collection year and county population density as proxies, based on the knowledge that artificial light levels are increasing each year[1,3] and that bigger cities are brighter.[30] While this is effective in detecting patterns in our data, there are drawbacks to using proxies. Though artificial night lighting is generally increasing every year, the rate of increase over time and across locations may not always be consistent. Additionally, artificial night lighting is typically highest where there are the most people, but there are some areas characterized by high artificial night lighting conditions and lower human population densities. It is also true that artificial night lighting covaries with other macroscale changes that have taken place in the world over the past hundred years, climate change and its cascading effects being of the most notable. One could argue that with evidence that climate change is advancing avian breeding phenology,[53] temperate birds that are breeding earlier in the year and coping with shorter day lengths could require compensation in their dim light vision. While this is possible, the unnatural extension of day length due to artificial night lighting is more pronounced than those produced at different times of year in most latitudes, making it more likely that artificial night lighting is driving the changes we have documented.

RESOURCE AVAILABILITY

Lead contact

Requests for additional information should be directed to and fulfilled by the lead contact, Clinton D. Francis (cdfranci@calpoly.edu).

Materials availability

This study did not generate new or unique reagents.

Data and code availability

- Original data have been deposited on Mendeley Data. These data are publicly available. The DOI is listed in the key resources table.
- Original code has been deposited on Mendeley Data. The code is publicly available. The DOI is listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Both authors designed the research; M.M.W. led the data collection with contributions from C.D.F.; M.M.W. analyzed the data with supervision by C.D.F.; M.M.W. led manuscript preparation with contributions from C.D.F.; both authors gave final approval for publication.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2025.112039.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Museum specimens	Museums & collection identifiers available with original data	
Deposited data		
Original data deposited for this study	This study	Mendeley Data https://doi.org/10.17632/pdpbszdv2n1
Software and algorithms		
Code for model building, evaluation, and plotting (R code)	This study	Mendeley Data https://doi.org/10.17632/pdpbszdv2n1
R software v. 4.4.1	Core Team[54]	https://www.r-project.org
spaMM	Rousset and Ferdy[55]	https://onlinelibrary.wiley.com/doi/full/10.1111/ecog.00566
MuMIn	Bartoń[56]	https://CRAN.R-project.org/package=MuMIn
performance	Lüdecke[57]	https://doi.org/10.21105/joss.03139

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We collected data on 181 specimens from six species with divergent responses to artificial night lighting (see below). Species were chosenbecause they frequently occur in or near urban centers (high urban adaptedness),[58] were relatively common in museum collections, and they captured variation in foraging habits, ecosystem roles and represented unique avian families (Table S1). The selected species were American crows (*Corvus brachyrhynchos*, n = 23) and Northern flickers (*Colaptes auratus*, n = 30), both of which have been documented to decline in abundance with increased artificial night lighting[59]; house sparrows (*Passer domesticus*, n = 20 [16 additional records lacking tarsus length measurements]), which have been shown to increase in abundance with light at night,[59] but also experience increased rates of clutch failure and lower survival following West Nile Virus infections when experimentally exposed to dim light at night[9,15]; red-tailed hawks (*Buteo jamaicensis*, n = 34) and great horned owls (*Bubo virginianus*, n = 26), both of which do not change in abundance with nocturnal light exposure[59]; and American robins (*Turdus migratorius*, n = 32), which sing more often at night in areas influenced by artificial night lighting[60] and increase in abundance at bird feeders with higher exposure to artificial night lighting during longer nights.[59]

METHOD DETAILS

Specimen measuring techniques

We took measurements from museum specimens collected from 1912 to 2022 (Figure S1), sourced from the Natural History Museum of Los Angeles, Museum of Vertebrate Zoology at UC Berkeley, California Academy of Sciences, Burke Museum of Natural History, Denver Museum of Nature and Science, and the Field Museum of Natural History in Chicago. Light sensitivity in dim conditions was approximated by the ratio of the corneal diameter to the transverse diameter within an eye, with larger ratios corresponding to increased dim light vision.[15,22–24] The inner diameter of sclerotic rings (Figure 1A) reflects corneal size.[18,19] Rings with variance in diameter were measured to produce the largest diameter, except when there was an obvious but localized chip or deformation; in those cases, the measure that would produce the next largest diameter was taken. Any rings that were clearly misshapen or had missing or broken oscillates were eliminated from the sample. The transverse diameter within the eye was measured from the middle of the quadratojugal, at the point that represents the furthest edge of the orbital rim, to the point on the orbit rim directly opposite (Figure 1A).[18] We transformed the resulting cornea to orbit diameter ratio by multiplying values by 100 to facilitate interpretation of effects and visualization of the results.[24]

We also measured tarsus length to control for potential variation in individual body size, measuring from the protrusion directly below the cotyle to the longest accessible trochlea, which was the trochlea of the 4th digit for all species but owls and flickers, which we measured to the 2nd digit trochlea (Figures 1B and 1C). For orbit and sclerotic ring measurements, most specimen measures (n = 143) were taken 3 times, except for 3 that were taken more than 3 times and 38 that were measured once. Repeatability analysis suggests that these measurements are highly repeatable and that the values obtained from the 38 individuals with single measurements are reliable (Table S2). For subsequent analyses, we used mean values for measurements that were taken 3 or more times. All measurements were taken with Mitutoyo ABSOLUTE digimatic calipers or Fortis digital 150 calipers, both sensitive to 0.01 mm. One individual performed almost all of the measurements, but were occasionally assisted by two other team members.

Environmental data

Human population density per km^2 was calculated from county population and area data. We matched the specimen collection date to the US census record from 1910 to 2020[61,62] to acquire county human population density and obtained county area from the 2010 US census.[63] These values were used to calculate a human population density per km^2, which we logarithmically adjusted to meet model assumptions in subsequent analyses. Specimens were collected from 17 US states with county population densities ranging from 0.27–1496.13 individuals per km^2 and spanning 1912 to 2022 (Figures 2, S1, and S2).

QUANTIFICATION AND STATISTICAL ANALYSIS

We used species-specific models to explain variation in dim light vision (estimated by the ratio of the corneal diameter to the transverse diameter within the eye) based on collection year, county human population density from the decade of collection, and their interaction. We also included tarsus length in all models to account for the potential influence of intraspecies variation in body size. We began by considering spatially explicit linear mixed-effect models with an exponential spatial correlation function using the fitme function in the spaMM R package.[55] However, for all species, model comparisons based on AIC suggested that models with spatial components had less support from the data than non-spatial models. Therefore, we used multiple linear regression for all subsequent analyses.

We ranked models with the above-described fixed effects; simplified versions of those models that considered additive effects of the two artificial night lighting proxies and tarsus; models with one or the other proxy and tarsus; and models with tarsus alone, or the null. Models were ranked using AICc within the MuMIn package in R and were considered when within 2 AICc as supported by the data.[56] We used diagnostic plots from the performance package in R[57] for model diagnostics and to test for potential multicollinearity (VIF >5) among predictors. We report apparent trends from the best-supported model and use 95% confidence intervals (95% CIs) to reflect the precision of estimated effects. Where necessary, we qualify the interpretation of trends based on the presence, magnitude and precision of estimated effects in other supported models (ΔAICc $\leq$2). Finally, to better understand the underlying morphological drivers of changes in the dim light vision ratio, we substituted orbit and sclerotic ring diameter as response variables in the top-ranked models for each species where dim light vision was related to one or more predictor variables.