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Review

The effects of light pollution on migratory animal behavior

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Light pollution is a global threat to biodiversity, especially migratory organisms, some of which traverse hemispheric scales. Research on light pollution has grown significantly over the past decades, but our review of migratory organisms demonstrates gaps in our understanding, particularly beyond migratory birds. Research across spatial scales reveals the multifaceted effects of artificial light on migratory species, ranging from local and regional to macroscale impacts. These threats extend beyond species that are active at night – broadening the scope of this threat. Emerging tools for measuring light pollution and its impacts, as well as ecological forecasting techniques, present new pathways for conservation, including transdisciplinary approaches.

Highlights

Awareness of light as a pollutant is growing, and with emerging technologies our understanding of how light pollution uniquely impacts migratory species through mechanisms of negative or positive phototaxis, and at times physiological responses, has grown.

Extinguishing and dimming lights is a first priority to reducing ecological impacts, but light can be modified when needed across multiple dimensions, including correlated color temperature or more holistic color spectra. Responses to light color and intensity are not uniform across taxonomic groups.

Light pollution can affect nocturnal and diurnal animal migrants by disrupting their movements at various scales: at local scales through collisions with lit structures, at regional scales by altering stopover sites and the aerial connectivity of the night sky, and at macroscales through exposure to sky glow and altered phenology.

History and introduction to light pollution

For hundreds of years, and likely even millennia, humans have observed disruptions of animal behavior by light (e.g., fire) [1–4]. However, artificial light was only referenced as a pollutant and entered the lexicon of peer-reviewed scientific literature in the past 50 years (Figure S1 in the supplemental information online). It was not until 1985 that the term 'photo pollution' was examined with reference to the effects of light on wildlife [5]. Yet, for decades **light pollution** (see Glossary) and similar terms primarily occupied studies of astronomy [6,7]. Eventually this term evolved, and **astronomical light pollution** was defined in relation to specific effects on the night-time viewing of celestial bodies. In 2004 Longcore and Rich set out to define light pollution with regard to ecology, coining the term **ecological light pollution**. Their landmark review amplified the importance of studying the effects of light pollution on wildlife and the need to distinguish it from astronomical light pollution [8].

At the intersection of light pollution and ecology, some of the first examples of the impacts of artificial light, before the use of the term light pollution, date as far back as the late 1800s – many of these early observations relate to migratory animals, often birds. Events that were hard to miss often included the fatal collisions of birds with lit lighthouses, illuminated ships, oil platforms, and other prominently lit structures – yielding some of the most gripping and grave examples of these impacts [1,9–14]. The iconic Washington Monument, a 169 m marble obelisk that defines the night-time skyline of Washington DC, USA, claimed 576 birds on 12 September 1937, including 17 warbler species [10]. This staggering event occurred in only an hour and a half, killing an average of 6.4 birds per minute. We can jump forward 80 years in time and see that, tragically, strikingly similar instances still occur. In the spring of 2017 nearly 400 birds were killed when they collided with a single brightly lit high-rise in Galveston, Texas, USA [15]. Again, in fall of 2021, 226 migratory birds were killed in window collisions near One World Trade Center in New York City, USA, sparking outcry [16].

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It is estimated that as many as a billion birds die each year due to collisions with buildings – with artificial light acting as an amplifying agent [17]. However, light attraction is not only a problem for birds: mammals, reptiles, amphibians, fish, and invertebrates face some of the same pressures [8], yet light may have differential impacts across taxa or even species [18–20]. Although animal migration has been studied for centuries [21], and light pollution more recently [22–25], studies at the intersection of these two topics are sparse, particularly for non-avian taxa. Given rising awareness of the anthropogenic impact of ecological light pollution on migratory wildlife, we review the effects of light pollution during migration to outline the current state of knowledge and identify gaps.

Defining migration

We have adopted the following four criteria to center our review on an objective definition of migration that could be systematically applied (adapted from [26]): migration is a movement that is (i) persistent, (ii) of a greater scale and greater distance than a movement during daily activities, (iii) spurred by seasonal conditions or restraints such as movement between nonbreeding and breeding grounds, and (iv) leads to a redistribution of populations. Using these criteria, it was clear that the movements of some species would be excluded from our review. For example, we excluded the diel movements of aquatic invertebrate species, such as *Daphnia*, that make regular movements up and down through the water column. Although these movements are stimulated by light [27], and more recently impacted by artificial light [28,29], they fail to fulfill the second and third criteria of our adopted definition.

There are many examples of lights impacting migratory species during non-migratory phases of their life cycle, including sea turtles [30], mule deer [31], salmon [32], and moths [33]. For example, seabirds (including Procellariiformes), the majority of which are migratory, display positive phototaxis to land-based light pollution which has been shown to cause mass mortality [34]. In 1963, McFarlane described the positive phototaxis of hatchling Atlantic loggerhead sea turtle (*Caretta caretta*) to a nearby roadway lit by mercury vapor lights, resulting in 90 hatchings being crushed by traffic and only 18% making it to the sea [35]. Although these examples and others like it contextualize our understanding of ecological light pollution, they do not directly shape our understanding of the impact light pollution has on individuals or populations during migration.

Rate of light pollution growth and research

Across the past 100 years, much of the globe has seen a steady increase in artificial lighting. Over the past half-century light pollution has grown at 3–6% per year [36] and has continued to grow at ~2.2% per year over the past 10 years [37]. Although much of the world was lit by oil lamps until transitioning to gas lamps in the 19th century, rural and urban centers remained relatively dark compared to current standards [38]. The first major increase in light use and light pollution began with the advent of the light bulb and electric streetlamps in 1879 [38]. From there, we saw continued developments in the lighting industry and continued brightening of the night sky. The invention of light-emitting diodes (LEDs) in 1962 spurred ultra-efficient lighting, whereby almost all the supplied energy could be converted to light [38]. By 2001, two-thirds of the global human population lived with light pollution [39], and by 2016 the Milky Way was not visible to one-third of the population worldwide [40].

With the development of new lighting technologies, lighting has become more energy efficient and more cost-effective. However, as affordability increased, light consumption and associated light pollution increased to a greater extent – thus the cost savings are not entirely realized [126]. By extension, this rapid growth leads to an ever-increasing amount of light pollution and its deleterious effects on both human health [42] and wildlife [25,43,44]. This principle is not

Glossary

Astronomical light pollution: artificial lights that impede the view of stars and other celestial bodies caused by light that is either directed or reflected upward.

Ecological forecasting: a tool that predicts changes in ecosystems, behaviors, or organismal movements in response to environmental drivers such as climate variability, weather conditions, pollution, and/or habitat change and phenology. Forecasts can be developed to predict phenomena in near-term (seconds to days) or long-term (months to years) future intervals.

Ecological light pollution: artificial light that disrupts the natural pattern of light and dark in ecosystems, whether through chronic or periodically increased illumination, unexpected changes in illumination, and direct glare.

Light pollution: artificial light that shines where it is neither wanted nor needed.

Sky glow: brightening of the night sky through natural and anthropogenic causes. Natural causes include sunlight reflected off the Moon and Earth, auroras, zodiacal light, starlight scattered in the atmosphere, and background light from faint, unresolved stars and nebulae. Anthropogenically caused sky glow can be greatly magnified by specific atmospheric conditions such as low cloud ceilings, fog, and mist.

unique to light pollution and is an example of what is known in economics as a Jevon's paradox [41]. More importantly, it likely suggests that technological advances in lighting alone will not be effective in reducing impacts on wildlife, and could have the opposite effect.

Approaching this problem with three spatial domains

Light pollution acts as an attractant, and in some instances as a repellent, that can negatively affect wildlife migration by disrupting, disorienting, and at times reshaping the timing of their journey – this disruption occurs across multiple spatial scales. For this reason we examine the effects of light pollution on migration at the local, regional, and macroscales (Figure 1).

Local scale effects

At the local scale, the negative effects of light pollution on migration have been most prominently measured by bird collisions with windows, communication towers, offshore vessels, and countless other built structures around the globe through data collected by collision monitoring, surveys, and citizen science programs [9,17,45–47]. Collisions abound, particularly in well-lit cities in the USA, such as Chicago, Dallas, Houston, and New York City [48,49]. Across 6 years, the Post Tower, a colorfully lit 41-story skyscraper, in Bonn, Germany, was found to be responsible for >900 night-time bird causalities [50]. Similarly, in Argentina, Rebolo-Ifrán *et al.* measured bird collisions with built structures through the use of citizen science data both at national and local scales [47]. These data are important because 10% of bird species inhabit Argentina alone, and collision data outside North America are crucial [47]. On the campus of the National School of Higher Studies (ENES) of the National Autonomous University of Mexico located in León, Mexico, Uribe-Morfín *et al.* led a citizen science study that measured the number of collisions on campus, and migratory birds accounted for 59% of collisions [51].

One of the most data-rich examples of bird collision monitoring occurred at McCormick Place Convention Center in Chicago, Illinois, USA, located on the shore of Lake Michigan (Figure 1). Because mortality data on bird collisions are typically lacking, particularly long-term data [45], the unique collections conducted at McCormick Place Convention Center offer crucial insights [52]. Since 1978, daily and consistent bird collision monitoring has been conducted around the building in spring and fall seasons, and resulted in the recording of more than 40 000 dead birds. Importantly, in addition to these crucial collections documenting where and when species of migrants collided, since 2000 detailed records describing interior window illumination were gathered. It was clear that mortality was highest when the lights were turned on, particularly during large nocturnal migration events associated with winds that concentrated birds along the Chicago lakeshore. All told, it was estimated that bird mortality could be reduced by ~60% at this site by decreasing window illumination to the minimum levels recorded [49]. This study showed strong support for a relationship between nocturnal migration magnitude and urban bird mortality mediated by light pollution and local atmospheric conditions [49]. At 21 buildings in Minneapolis, Minnesota, USA, the area of lit glass on a building was the largest predictor of bird mortality [53,54]. This research highlights not only that the external artificial lighting of built structures affects migratory species but also that illumination from interior lighting can have a dramatic effect.

Although lights do not directly cause mortality in avian migrants, they can dramatically alter the behaviors of in-flight migrants – this is particularly apparent at the annual Tribute in Light memorial hosted every September 11th in lower Manhattan, New York City, USA (Figure 2A). With a total of 88 spotlights sculpted to represent the Twin Towers (44 lights per tower), on some autumn nights thousands of migrants can be seen circling, calling, and appearing and vanishing in and out of the bright lights [55]. What these pictures do not show is the magnitude of the impact. Using radar remote sensing across 7 years, it was estimated that flight behaviors of 1.1 million

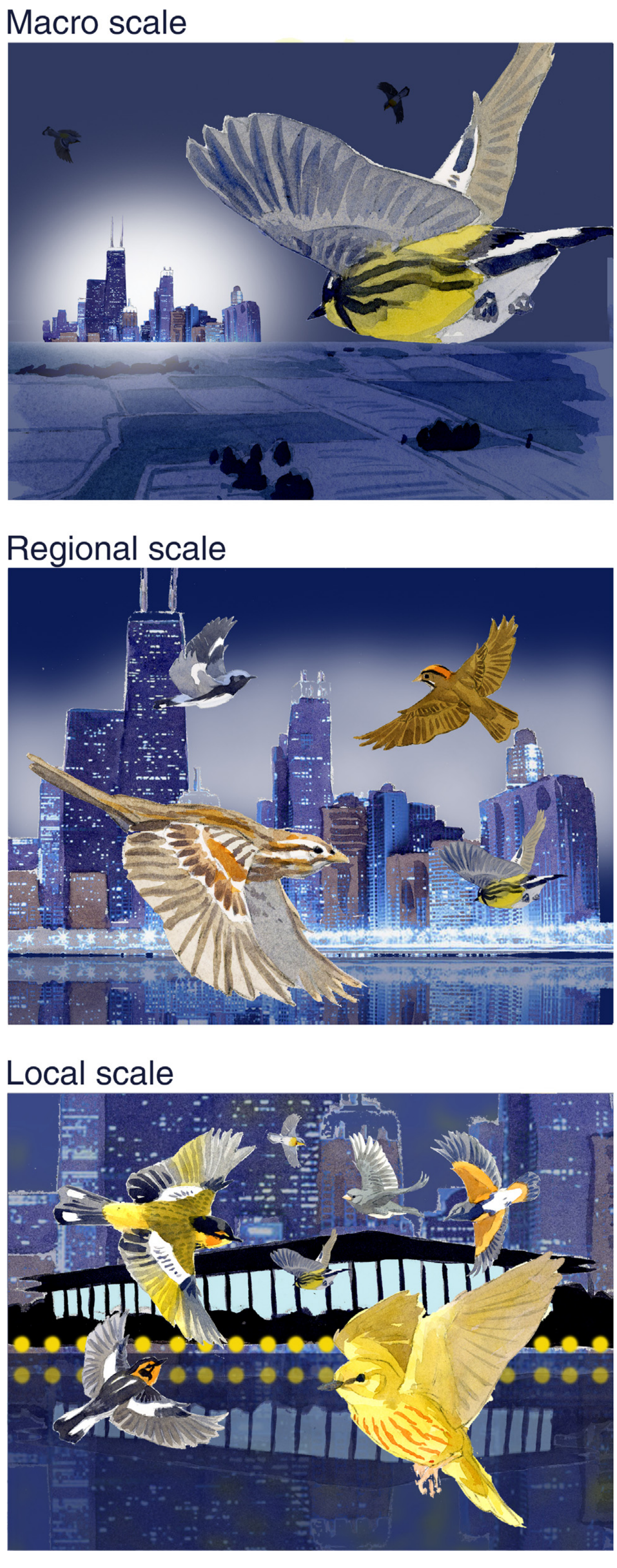

Figure 1. Effects of light pollution on migratory birds at local, regional, and macroscales, using Chicago, Illinois, USA, as a case study. Light pollution can negatively affect migrants across multiple scales throughout their journey at the local (e.g., collisions with windows and building structures), regional (e.g., the distribution and abundance of migrants in the air and on the ground, decreased connectivity), and macroscales (e.g., sky glow and potential exposure to light pollution). What are the costs at each scale? Although we present our review of these scales from finest to broadest in the text, disruptions for migrants may logically occur from broadest to finest spatial scales. The illustration depicts how light pollution disrupts behavior, using Chicago, Illinois, USA, as an example, for nocturnally migrating birds. At the macroscale, the sky glow from the city acts as an attractant that draws migrants away from their migratory routes. At the regional scale (offshore from Chicago over Lake Michigan), the migrants become disoriented from the light pollution and continue to be pulled into the city. Finally, at the local scale, there is a risk of collision with McCormick Place because its large glass windows are illuminated, and even reflect off the surface of the lake, thus exacerbating their impact [49]. Illustrated by Debby Kaspari.

Figure 2. Examples of the negative effects of light pollution on migratory behavior across taxa. (A) Nocturnal songbirds are attracted to the September 11th Tribute in Light Memorial in New York City, USA [55]; (B) grasshoppers flock to the glow of Las Vegas, USA, disrupting their multigenerational movements [74]; (C) reduced light pollution in urban and rural areas improves the connectivity of migratory bats [76]; and (D) light trespass can interrupt diurnal migration in monarch butterflies (*Danaus plexippus*) [86]. Illustrated by Debby Kaspari.

migrants were altered by these spotlights [55]. Nevertheless, mortality, by comparison with McCormick Place, was minimal. This can largely be attributed to actions taken to mitigate the negative impact. At the Tribute in Light, the lights are extinguished each time 1000 birds are visually detected. The result is a dramatic shift in flight activity – during illumination, peak densities regularly reached more than 20-fold those of surrounding baselines, and at times 150-fold. More startling, these disruptions all occur in one of the most photo-polluted cities in North America, demonstrating the capacity for disruption, even in already bright areas.

Turning lights on and off is not necessarily a new practice. Instead, it is one of the oldest and most straightforward tools for mitigation [56]. Reports from lighthouses throughout the early 1900s documented, at times, tens of thousands of migrants circling the glowing and revolving beams of light designed to warn sailors. As lighthouses shifted towards strobed beacons, reports of fewer migrant attraction events soon followed [57]. Although the need for lighthouses has largely passed, other high-rise towers have sprung up over the past century, namely communication towers. Mandated under aviation safety guidelines per the International Civil Aviation Organization (ICAO) obstacle light requirements, structures greater than 45 m must be marked with lights or sometimes paint. It is estimated that 7 million birds die annually in North America [17] owing to communication towers, with lights serving as a local attractant – where the tower, or often the guy wires of the tower, delivers the fatal blow [9]. Lighting patterns play an important role in mitigating this impact [58]. Lighting also elevates the vocal activity of migrating birds [55,59,60], and this flight calling behavior predicts vulnerability to light pollution via fatal collisions [52]. With communication towers firmly implanted on the global landscape, understanding how light color, intensity, and flashing pattern influence attraction is crucial, especially given the complex effects that differing atmospheric conditions can have on these patterns [49,61,62].

Threats are not limited to terrestrial habitats. Globally, light pollution along coastlines can have negative impacts on reef and coastal ecosystems as well as on local sessile and migratory species. The Mediterranean Sea, Red Sea, Persian Gulf, and seas of South-East Asia include some of the most photo-polluted coastlines [63]. Even offshore, migratory species may face the threat of light pollution through fisheries, energy production platforms, and cruise ships [46,63,64]. Attraction to these sources can create episodic mortality events through bird collisions with built structures or exhaustion through endless circling, or even cause indirect effects through changes in prey density and greater risk of predation [46,63].

Regional scale effects

For birds, urban parks and urban green spaces, surrounding and within urban centers, unequivocally provide important habitat for migrants [65] and often yield high species richness [66,67], but is their use higher than expected? This is precisely what Zuckerberg *et al.* found, showing novel use of anthropogenic habitats [68]. In North America, ~71% of terrestrial birds are considered to be migratory, and of the migratory species, 80% migrate at night [48]. Examining those that migrate at night, ~49% are passerines, and 76% of those passerines breed in forest habitats [48,69]. Why were so many forest species residing in seemingly suboptimal forested habitats? La Sorte *et al.* set out to address this question using community science observations (eBird) from 40 long-distance migrants [70]. By pairing these data with visible infrared imaging radiometer suite (VIIRS) day/night band (DNB) measures of upward radiance (section on Methods for quantifying light pollution), they found that the diurnal abundance of nocturnal migrants was higher in and around urban areas, and concluded that urban light sources broadly shape migrant distributions across the landscape. The evidence suggests that nocturnally migrating passerines are more strongly affected by light pollution compared to other nocturnally migrating bird species [71].

Using a wholly different sensing platform (weather surveillance radar), McLaren *et al.* similarly found that migrant densities increased with increasing proximity to bright areas in the northeastern USA (as measured by ratio of zenith artificial sky luminance to natural sky brightness), but densities decreased at more local scales [72]. These impacts may extend into airspaces above urban areas, but potentially in unexpected ways, and migrants typically fly higher over urban areas than over more rural areas [73]. These opposing relationships suggest broadscale attraction, but potential local scale repulsion for stopover, which may suggest that brightly lit areas are perceived as suboptimal stopover habitats by migrants.

However, not only birds flock to urban centers – insects are also drawn to city lights. In 2019 massive waves of grasshoppers (primarily *Trimerotropis pallidipennis*) were observed leaving vegetated areas as the sun set and taking flight in the direction of the brightest US city, Las Vegas, Nevada, USA [74]. More than 45 million grasshoppers were on the move on a single night, and city lights acted as a broad ecological trap that reshaped the regional distribution of biomass (Figure 2B). In Canberra, Australia, plagues of Bogong moths (*Agrotis infusa*), a species that makes an upwards of 1000 km journey, can become entrapped en route by brightly lit buildings, including the capital's Parliament House, thus delaying or ending migration for some individuals altogether [75].

In the case of bats, light pollution was shown to have a negative impact on the spatial connectivity of several migratory or partially migratory insectivorous bats in Lille, France, including species in the genera *Pipistrellus* and *Myotis.* Laforge *et al*. found that reduction in the radiance of an area increased the connectivity among bat populations in both natural and urban areas, and highlighted that light pollution can exacerbate regional fragmentation and reshape the movement of populations across the landscape [76] (Figure 2C). Conversely, Korpach *et al.* found, by tracking the Eastern whip-poor-will (*Antrostomus vociferus*) with global positioning system (GPS) units during migration, that their en route stopover locations were primarily in darker areas (e.g., near rural areas), and they avoided brightly lit urban centers [77]. Light pollution from urban centers can fragment the dark skies, imposing additional challenges during an already energy costly process such as migration. The transformation of the night sky through light pollution may not fit the natural paradigm of habitat loss, but it may have similar ecological consequences for some organisms, particularly at large scales.

Macroscale effects

Given that migrants traverse a diversity of habitats and geographies, is the migratory phase in fact the period of greatest concern with regard to exposure to light pollution? Examining 298 bird species spanning six continents, Cabrera-Cruz *et al*. used range maps of species breeding and nonbreeding ranges and regions of passage where species only occur during migration. They found higher exposure to light pollution during the migratory phases, particularly in the western hemisphere [78]. Satellite remote sensing layers [e.g., VIIRS and the Defense Meteorological Satellite Program (DMSP); section on Methods for quantifying light pollution for more information] deliver global coverage that enables quantification of areas of greatest light pollution, and more recently reveal how it is changing [79,80]. Integrating measures with commensurately broad ecological datasets is crucial for mapping threats. When considering migratory birds, it is clear that geography and seasonality are the crucial dimensions that drive the spatial distribution of migrants [81]. Regarding light pollution and migratory birds, not only the amount of light is important but also where that pollution is located relative to the passage of migrants. Pairing VIIRS measures and one of the first continental uses of weather surveillance radar data, Horton *et al.* ranked the 125 largest cities in the USA to quantify the seasonal exposure of passing migratory birds to light pollution, and demonstrated that the level of threat reflects a combination of size, brightness, and migration intensity [48]. This catalog of cities ranked by exposure threat has already served as a guide for light pollution mitigation, and has concentrated efforts in areas of high light pollution exposure (e.g., Lights Out Texas) – but more research, beyond the USA, is imperative.

Not just a nocturnal problem

It may seem obvious to focus on nocturnal migratory species when exploring the impacts of ecological light pollution, but recent evidence suggests this may underestimate the growing effects of light pollution. Light pollution can disrupt daily and seasonal movements that rely on the natural light cycle. This anthropogenic change can affect cues for the arrival times of migrants (phenology), change behavior (i.e., foraging, reproduction, daily movements), alter hormone production, and produce changes in circadian rhythms [82,83].

Purple martins (*Progne subis*), a long-distance diurnal migratory species, spend their nonbreeding phase in South America, and many individuals roost at night in urbanized areas.

Using small, lightweight geolocators [84], devices designed to log and measure environmental light-data, Smith *et al.* found that greater exposure to lights at night shifted migration phenology, and individuals exposed to the most light pollution advanced their spring initiation by up to 8 days [85]. These migrants subsequently arrived 8 days earlier to their breeding sites – a migration that spans upwards of 3000 km. Of the 155 birds studied, 31% were exposed to light pollution on their wintering grounds. Similarly, monarch butterflies (*Danaus plexippus*), another diurnal migrant, had their circadian rhythms altered by simulated light trespass – light that falls or emanates beyond its intended purpose (Figure 2D). Rhythms were altered so severely that they could be stimulated to migrate at night in the presence of light pollution [86]. Light pollution has also been found to shift the emergence of primary resources (e.g., bud formation, leaf-out dates) on which the timing of migration may crucially depend, potentially resulting in a phenological mismatch between arrival and resources [87]. Clearly, the impacts of light pollution do not only alter the behaviors of those moving under the cover of 'darkness'.

Methods for quantifying light pollution

Light pollution itself is not a uniform problem. Variation in lighting intensity, color, duration, and whether the source is static or pulsing, can vary the extent to which wildlife are impacted by light pollution at the local, regional, and macroscales [82]. Quantifying light pollution requires tools that can be applied to an enormous range of scenarios, from individual lamps to continental maps. Although some studies deliver compelling results from 'lights on' versus 'lights off' contrasts [49,55], predictive models and syntheses require quantitative characterization of stimuli [88]. Sky quality meters (SQMs) [89] have been widely applied to measure the zenith luminance (Figure 3) of the night sky, but this practice may be inappropriate for studying migratory responses to light pollution. Zenith luminance is an insensitive measure of light pollution and it does not localize light sources. The broad aperture of SQMs is problematic for quantifying light pollution near the horizon. Imaging sensors are more expensive, but they provide thousands of localized luminance measurements per image.

Scene luminance can be measured with consumer digital cameras; published methods enable radiometric calibration of these sensors [90–92]. However, the Bayer color filters in consumer cameras require additional effort for spectral calibration and pixel interpolation. Monochromatic astronomical cameras offer excellent radiometric sensitivity, and each pixel provides the same measurement. Precision optical filters can be added to deliver measurements with standardized spectral characteristics. Interchangeable lens systems enable selection of the field of view and light-gathering capacity. With fisheye lenses, cameras can characterize the entire celestial hemisphere in a single image (e.g., Sky Quality Camera) [93–95]. Cameras flown on drones can characterize scene luminance from the perspective of a bird, bat, or insect [96]. At a considerably higher price, spectrometers can be used to more acutely parse light pollution beyond simple measures of correlated color temperature (CCT) and can be used to evaluate the composition of light pollution across wavelengths [97], which is important in assessing differential species or taxonomic responses to light pollution (e.g., [62,98–101]).

Satellite data have characterized the global footprint of light pollution. The DMSP provided annual measures of visible and near-IR light from 1992 to 2013 at 3000 m spatial resolution [102]. The VIIRS DNB sensor provides daily, global measurements of nocturnal visible and near-IR light at a native resolution of 740 m [102]. Although satellites measure upward radiance, models have been developed to translate these data into estimates of **sky glow** and light trespass [40,103,104]. There have been calls for specialized multispectral satellite sensors optimized for light pollution studies [105], and potential tools are emerging to fill these additional needs [106].

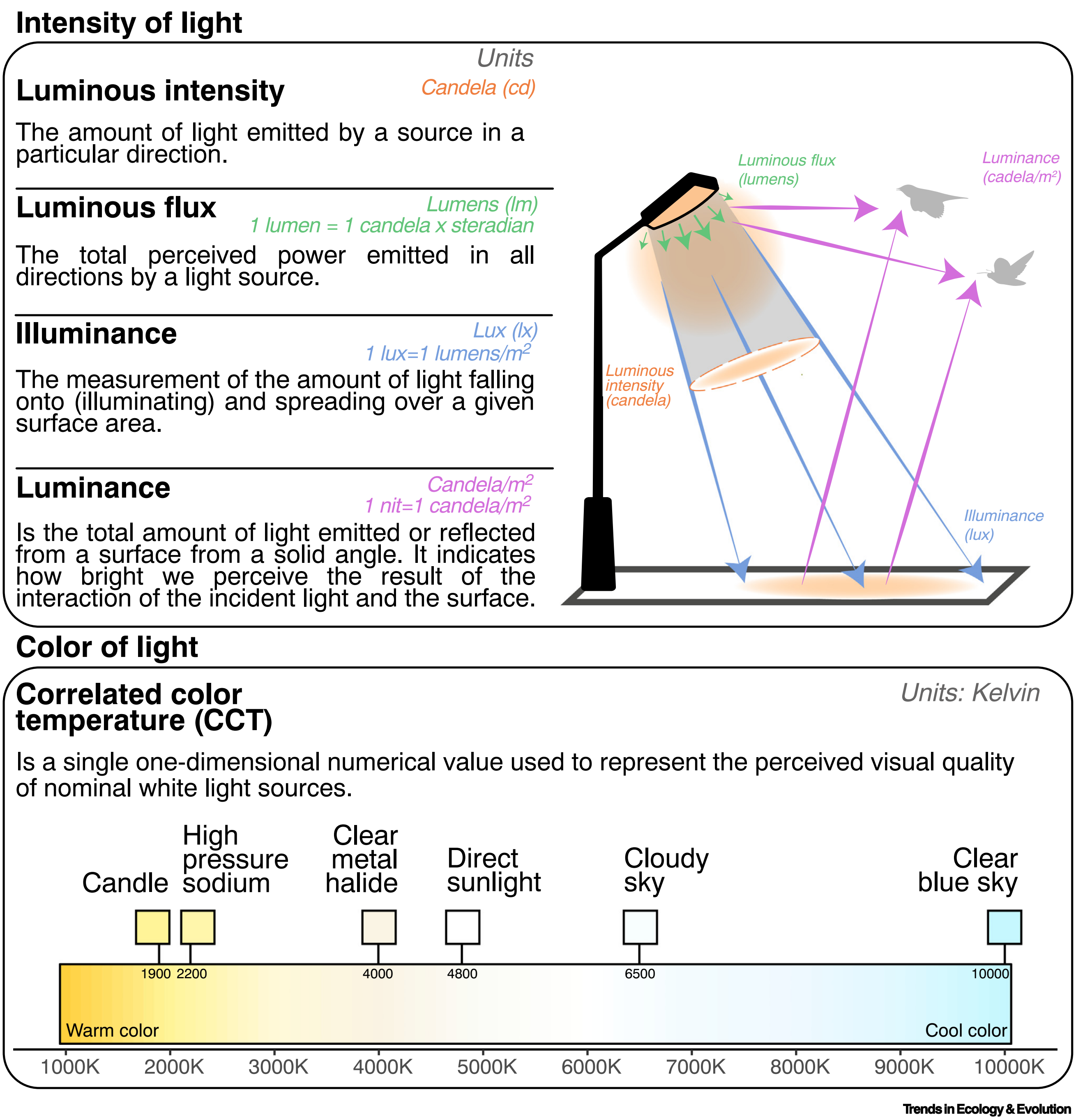

Figure 3. Overview of light measurement terminology with international system (SI) units of light intensity and color for use in wildlife research. Whether measures are collected at local or macroscales, researchers should consider whether measures of illuminance or luminance are best suited for the taxa and migration events of interest. For instance, luminance is likely the relevant measure for active avian migration attraction, orientation, or disruption (depicted by the migratory bird and moth silhouettes), whereas illuminance may be most appropriate for understanding shifts in migration connectivity, foraging, phenology, among other behaviors shaped by light densities [88]. It is imperative that these distinctions are understood in the early development of essential studies on the impacts of light pollution on animal migration. We have included common units of measure, definitions, and a visual representation of how wildlife may interact with or perceive these lighting elements in the intensity of light box (above). In addition to measuring illuminance or luminance, it is important to understand and measure the composition of correlated color temperature (CCT) because species may have differential responses to different colors. We show a spectrum of white light on a scale from warm (1000 K) to cool (10 000 K) for simple comparison in the color of light box.

Ecological forecasting as an emerging tool for action

Biodiversity and ecosystem crises driven by climate and land-use change have pushed ecologists to embrace a more predictive approach to data–model integration for the purpose of forecasting ecological patterns and processes [107,108]. In the scope of light pollution, near-term **ecological forecasting** tools create a pathway for targeted action. However, such forecasts must match the temporal and spatial scale of the phenomenon. In the case of avian migration, mass movements may span hundreds of kilometers, where activity levels vary tremendously at the local scale and from night to night – and by extension the interactions of migrants with light pollution also vary tremendously. Similarly, the rapid emergence of millions of insects, such as the synchronous emergence of up to 88 million mayflies (*Hexagenia*) from aquatic environments, can place vast swarms of organisms in proximity to light pollution [109]. Understanding their physiology and environmental conditions that cue their development can provide a predictive framework for understanding this intersection [109]. Van Doren and Horton showed that nightly bird migration could be predicted across the contiguous USA, matching the scale needed for dynamic action [110]. Predictive performance was largely driven by atmospheric conditions, and air temperature, barometric pressure, and wind speed and direction, among other variables of geography and seasonality, led the way. Estimates of hundreds of millions of birds forecast at a continental scale were not uncommon, demonstrating the scope and potential benefit of undertaking lights-out actions. Expanding this application and potential conservation actions, Lippert *et al*. used similar datasets to design a forecasting system to predict bird migration across western Europe using 22 weather radars from the European weather radar network across Belgium, France, Germany, the Netherlands, and Switzerland [111].

From large-scale measures of bird migration in North America, we have come to understand that nocturnal migration is not evenly distributed across space and time. Although migration seasons may span months in any one area, the bulk of migration occurs during only a few nights – on

Box 1. Convergent research: addressing this societal problem with transdisciplinary collaborations

How can new technical knowledge (such as ecological forecasting) be translated into effective public policy and behavioral change to address a societal problem such as light pollution? Scholarship on theories of the policy process has a robust literature that has grappled with this problem for decades [118–120]. Of primary relevance to the interaction of light pollution and migratory wildlife is how coalitions of policy actors (such as advocates and decision-makers) who focus on policy within ecological domains can incorporate new knowledge to facilitate policy change [121]. Migration forecasts have the potential to alter the belief systems of policy actors by making the negative impacts of light pollution more evident and accessible, thus changing the understood benefit/cost ratio of efforts to decrease the overall impact by targeted light reductions, and broadening stakeholder and policymaker appreciation for the impact of light pollution on migratory species.

Effective utilization of convergent research for improving public policy requires that we better understand how, when, and why participants in the policy process respond to new technical information. In part, this response depends on whether the new information has an impact on the shared belief systems of the coalitions of actors who advocate for policies and outcomes, thereby stimulating policy learning and effective advocacy for policy change [122]. The adoption and learning from technical innovations such as ecological forecasting is contingent on alignment with the goals and values of the relevant policy actors within an issue domain (i.e., are the implications of the forecasting consistent with the values and interests of policy actors?), and is independent of the technical accuracy of the forecasts. One notable example of the impacts of technical knowledge in an ecological policy controversy concerns the effects of forestry practices and wildfires on the turbidity of Lake Tahoe in California, USA [123]. However, examples of specific impacts of new technical knowledge on policy learning and change are rare [121], in part because the beliefs of policy actors tend to be anchored in deeply held values that are resistant to change [124,125].

The case of light pollution provides an important opportunity to engage in transformational research that involves a wide array of stakeholders in the co-design, selection, and development of data products that are useable by decision-makers, policy activists, and the broader public [107]. By gathering systematic data on individuals and stakeholder organizations, scientists can learn more about how beliefs, perceptions, decisions, and behaviors can influence the adoption of ecological forecasting in ways that lead to sustainable public policy.

average ~10.0 nights in spring and 10.9 in the fall [112]. Horton *et al*. show that real-time forecasts can capture these high-intensity periods, thus offering a reliable and dynamic approach for recommending lights-out warnings with 1–3 day lead times [112]. However, although the strength of such forecasts comes from their dynamism, it may also be a detriment. Subscribing to forecast alerts may require additional personnel, technology, and infrastructure to automate action. Although forecasting bird migration is technically possible, among other taxa, it remains to be seen whether it is feasible to evoke appropriate and effective human action in response to those forecasts (see Box 1 for pathways forward).

Concluding remarks

The remarkable efforts of community and professional scientists have yielded extensive evidence of the impacts of light pollution on migratory animals, particularly birds, over the past two decades. Nonetheless, significant data gaps remain across all spatial scales and especially for non-avian migratory species (see Outstanding questions).

There is a pressing need for more small-scale and large-scale datasets that quantify the mortality of migrating animals caused directly and indirectly by light pollution. At the local scale, a coordinated and standardized monitoring effort to quantify the impacts of light pollution is needed. Without these data, it is difficult to know to what extent light pollution contributes to the ongoing precipitous declines in the populations of migrants [113]. Given the weight of evidence regarding the impacts of light pollution, public policy changes that curtail the impacts of nocturnal lighting might be expected to be forthcoming. However, we know from models of public policy formation (Box 1) that evidence of an ecological problem will not inevitably lead to new policy. A concerted effort to create transdisciplinary convergence targeted at achieving policy outcomes requires expertise in political science and an understanding of the social systems that create those policies [114].

It is important to note that light pollution does not affect migration in isolation. Light pollution originates from anthropogenic activities that generate other forms of environmental pollution such as air pollution, airborne toxic chemicals, water pollution, noise pollution, and increased human development [71,115–117]. Light pollution can interact with each factor, adversely affecting migration, and can even intensify the effects of airborne pollutants during and even beyond migration through a broad array of behavioral and physiological effects that can hinder survival and reproductive success during the breeding season [117]. In addition, all these factors can be exacerbated by climate change and land-use change, two of the largest threats impacting on biodiversity globally. However, one difference with light pollution is that, theoretically, it could be fully and quickly reversed – lights can be turned off.

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Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

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Outstanding questions

- Why are organisms attracted to light? Although the evidence is unequivocal that some nocturnal animals are attracted to light, we still lack a complete mechanistic understanding to explain the cause. Such an understanding could help to guide mitigation strategies.
- How much could be learned about the ecological impacts of lights at night through studies of animal perception of brightness and spectrum? As lights are becoming both brighter and often bluer, which dimensions of lighting should be prioritized to mitigate disruption of nocturnal migrants? As it stands, recommendations for mitigation leverage an incomplete understanding of these factors – factors that may show strong species-to-species or habitat-to-habitat variation.

Are there thresholds or trigger points at which increases in the brightness of lights at night non-linearly increase the impacts on a breadth of animal taxa?

- What is the fitness consequence of attraction to light pollution beyond mortality? Although our most salient measures of the toll of light pollution come in the form of monitoring fatal collisions, the effects may penetrate well beyond instantaneous events. Attraction may carry additive deleterious effects throughout full annual cycles – our estimates of the adverse effects may be woefully inadequate.

If data were available for a wider range of taxa, would they show similar patterns of mortality at local scales and behavioral effects at regional and macroscales?

- Are the few existing studies of carry-over effects of light pollution during migration indicative of general impacts across phases of the annual cycle and on different taxa?
- Is animal migration changing in fundamental ways due to artificial light?
- What are the impacts of light pollution on animal migration when measured in conjunction with other environmental pollutants such as air pollution?

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