

More than mortality: Consequences of human activity on migrating birds extend beyond direct mortality

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ABSTRACT

Birds must contend with an array of anthropogenic threats during their migratory journeys. Many migrants are killed due to encounters with artificial light, introduced species, pollutants, and other anthropogenic hazards, while survivors of these encounters can suffer longer-lasting negative effects. The nonlethal effects of anthropogenic threats on migrating birds are less well understood than direct mortality, yet both potentially contribute to population declines. For example, building collisions frequently kill migrating birds, but the numbers of migrants that survive with an impaired ability to fly, refuel, or navigate to their destination on time is not well understood. Though not immediately fatal, such injuries can lead to delayed mortality and, ultimately, reduced lifetime reproductive success. Furthermore, migrants are likely to encounter multiple threats on their journeys, which can interact synergistically to further reduce fitness. For instance, light pollution attracts and disorients migrants, increasing the likelihood of window strikes, and surviving birds may be more vulnerable to predation from introduced predators. While considerable attention has focused on the lethal effects of anthropogenic threats, here, we review nonlethal effects of eight types of threats during migration, their interactions, and the pathways through which they can exert fitness costs. In doing so, we identify knowledge gaps and suggest areas for future research. In the absence of more information, we propose that the greatest reduction in the cumulative lethal and nonlethal impacts of anthropogenic hazards will be achieved by addressing threat types, like artificial light at night, that interact with and compound the impact of additional threats. Direct mortality from anthropogenic sources is recognized as a key driver of population declines, but a full understanding of the impacts of human activity on migrating birds must include the cumulative and interacting effects that extend beyond immediate mortality en route to influence overall migration success and lifetime fitness.

Keywords: anthropogenic mortality, anthropogenic stressors, anthropogenic threats, avian conservation, bird migration, demographic impacts, fitness costs, indirect effects, nonlethal effects

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LAY SUMMARY

- Migrating birds around the world face a wide variety of threats from human activity and many species are declining significantly.
- Many migrants are killed by these threats, while those exposed but not immediately killed may experience changes in their condition, migration timing, orientation, or route.
- Nonlethal effects of threats during migration, such as sensory pollutants and introduced species, have not been well-studied but are likely contributing to population declines by lowering future survival or reproduction.
- We review support for the nonlethal impacts of eight anthropogenic threats, describe how they can cause nonlethal fitness costs for migrating birds, and identify knowledge gaps.
- Reducing threats that compound the impacts of other threats, such as artificial light at night, will help to minimize the cumulative impacts on migratory birds.
- Fully capturing the costs of human activity on migratory birds requires understanding both lethal and nonlethal impacts of encounters with anthropogenic threats during migration.

Más que mortalidad: Las consecuencias de la actividad humana en las aves migratorias se extienden más allá de la mortalidad directa

RESUMEN

Las aves deben enfrentarse a una variedad de amenazas antropogénicas durante sus viajes migratorios. Muchas aves migratorias mueren debido a encuentros con luz artificial, especies introducidas, contaminantes y otros peligros antropogénicos, mientras que las aves sobrevivientes de estos encuentros pueden sufrir efectos negativos de larga duración. Los efectos no letales de las amenazas antropogénicas en las aves migratorias son menos comprendidos que la mortalidad directa, pero ambos pueden contribuir potencialmente a la disminución de las poblaciones. Por ejemplo, las colisiones con edificios matan frecuentemente aves migratorias, pero no se comprende bien el número de migrantes que sobreviven con una capacidad deteriorada para volar, reabastecerse o navegar a tiempo hacia su destino. Aunque no sean fatales de modo inmediato, estas lesiones pueden conducir a una mortalidad posterior y, en última instancia, a una reducción del éxito reproductivo a lo largo de la vida. Además, es probable que las aves migratorias encuentren múltiples amenazas en sus viajes, las cuales pueden interactuar sinérgicamente para reducir aún más su aptitud biológica. Por ejemplo, la contaminación lumínica atrae y desorienta a las aves migratorias, aumentando su probabilidad de colisionar con ventanas, y las aves que sobreviven pueden ser más vulnerables a la depredación por especies introducidas. Si bien se ha prestado considerable atención a los efectos letales de las amenazas antropogénicas, aquí revisamos los efectos no letales de 8 tipos de amenazas durante la migración, sus interacciones y las vías a través de las cuales pueden ejercer costos en la aptitud biológica. Al hacerlo, identificamos lagunas de conocimiento y sugerimos áreas para investigaciones futuras. A falta de más información, proponemos que la mayor reducción en los impactos acumulativos letales y no letales de las amenazas antropogénicas se logrará atendiendo aquellas amenazas, como la luz artificial durante la noche, que interactúan y agravan el impacto de otras amenazas adicionales. La mortalidad directa debido a fuentes antropogénicas se reconoce como un factor clave en la disminución de las poblaciones, pero para comprender completamente los impactos de la actividad humana en las aves migratorias, es necesario considerar los efectos acumulativos e interactivos que van más allá de la mortalidad inmediata en ruta y que influyen en el éxito general de la migración y la aptitud biológica a lo largo de la vida.

Palabras clave: amenazas antropogénicas, conservación de aves, costos de aptitud, efectos indirectos, efectos no letales, estresores antropogénicos, impactos demográficos, migración de aves, mortalidad antropogénica

INTRODUCTION

Migration is the most dangerous period of the annual cycle for migratory birds (Sillit and Holmes 2002, Paxton *et al.* 2017). During journeys that may span months and cross continents, birds navigate unfamiliar and variable conditions in terrestrial, marine, and aerial environments. Migratory birds are well adapted to overcome the challenges of migration (Moore 2018) but human activities have increasingly modified the environments birds encounter en route, especially in the decades since the advent of the industrial revolution (Davis 1955). Urbanization, the most drastic transformation to the landscape, is highly concentrated in mid-temperate latitudes around the world, south of regions that harbor the greatest richness of breeding migratory bird species (Seto *et al.* 2011, Somveille *et al.* 2013, Zhou *et al.* 2015). Thus, regions traversed by migrating birds are increasingly sown with evolutionarily novel threats that can impose considerable costs on bird fitness (Lambertucci *et al.* 2015, Cabrera-Cruz *et al.* 2018, La Sorte *et al.* 2022). These changes may be inflating the costs of being a migratory animal (Wilcove and Wikelski 2008, Hardesty-Moore *et al.* 2018).

Research on anthropogenic threats to birds has frequently focused on direct mortality sources, defined as hazards such as window collisions and cat predation that are “characterized by relative clarity of cause and effect” (Loss *et al.* 2015). Other factors such as climate change are considered indirect mortality sources because they kill birds via intermediate mechanisms (Loss *et al.* 2012, 2015; Calvert *et al.* 2013). Both direct and indirect anthropogenic mortality sources can also produce nonlethal effects or “delayed fitness costs” that reduce an individual’s future survival probability or reproductive output (Klaassen *et al.* 2012, Schmaljohann *et al.* 2022). Threat effects may not always materialize at the source and are likely increasing the challenges of migration in ways that are typically unaccounted for in estimates of direct mortality. Despite their potential importance, the nonlethal effects of anthropogenic threats during migration have only recently begun to receive research attention (Ware *et al.* 2015, Seewagen 2020, Overton *et al.* 2022).

Although threats are often studied in isolation, they can interact with one another to produce synergistic effects (Dutta 2017, Mahon *et al.* 2019, Norris *et al.* 2021, Richard *et al.*

2021), which may be lethal or nonlethal (Kummer *et al.* 2016, Winger *et al.* 2019, Van Doren *et al.* 2021, Reboló-Ifrán *et al.* 2021). Synergistic effects of multiple anthropogenic threats during migratory periods remain understudied (Dutta 2017, Richard *et al.* 2021), yet the repetition, combination, and interaction of even seemingly minor threats can substantially increase the extinction risk of wildlife populations (Kimmel *et al.* 2022), demonstrating that these effects must not be overlooked.

A narrow focus on direct mortality from anthropogenic threats, ignoring nonlethal effects and interactions, substantially underestimates the total cost of human activity on migrating birds. In this review, we first identify the primary pathways through which anthropogenic threats can impose nonlethal fitness costs on birds during migration. These pathways include effects on a migrant’s (1) physiological condition or health, (2) timing of migration, (3) orientation and navigation ability, and (4) migration route (Figure 1). We briefly describe the lethal effects (i.e., mortality, both immediate and delayed) that eight anthropogenic threat types have on migrating birds before summarizing the current knowledge of their nonlethal effects (Table 1). We mainly consider threats to birds migrating through terrestrial (rather than marine) environments. In cases where nonlethal effects have only been documented during non-migration phases of the annual cycle or in non-migratory taxa, we draw from that literature to hypothesize potential impacts on migrating birds (as in Seewagen 2020). Next, we identify evidence for cumulative and synergistic effects and explore the mechanisms through which multiple threats interact to harm migrating birds. Finally, we highlight knowledge gaps and discuss the conservation implications and potential pitfalls of failing to consider other consequences of human activity on migrating birds beyond direct mortality.

ANTHROPOGENIC THREAT PATHWAYS LEADING TO FITNESS COSTS

The anthropogenic threats that migrating birds encounter en route can have lethal fitness costs (mortality) or nonlethal fitness costs that reduce reproductive success or survival during a future stage of the annual cycle (Senner *et al.* 2015) (Figure

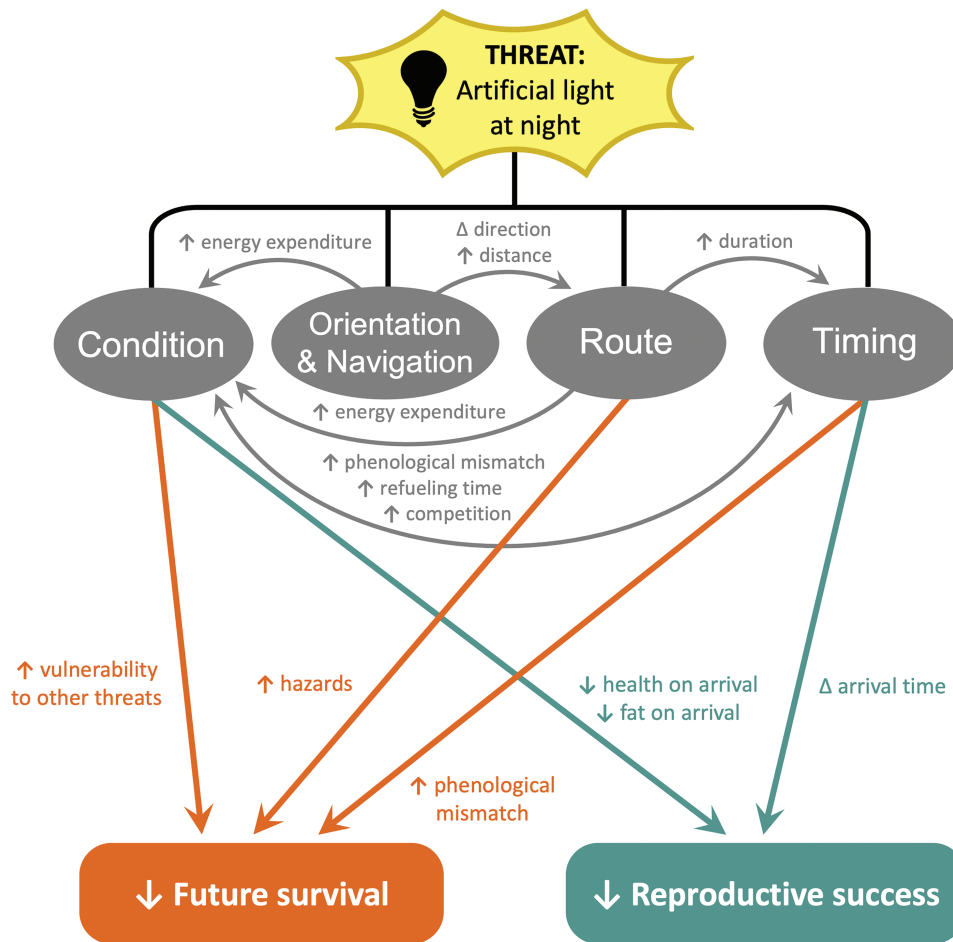


FIGURE 1. Conceptual diagram of the pathways through which a single anthropogenic threat, artificial light at night (yellow starburst), can influence the two components of a successful migration: future survival and reproductive success across the annual cycle (rounded boxes). Threats affect reproductive success and/or survival through intermediate pathways (gray ovals): by changing a migrant’s physical condition, orientation and navigation, route, or migration timing. Gray arrows are labeled with how linkages between pathways can occur: for example, artificial light at night attracts birds in flight (affecting orientation), which causes them to change direction and lengthen the distance traveled (affecting route), which leads to increased energy expenditure in flight (affecting condition). Colored arrows are labeled with the ways that artificial light at night can ultimately decrease survival probability (orange) and reproductive success (teal) via the four pathways.

TABLE 1. Glossary of terminology used in this article.

Term	Definition
Anthropogenic threats	Physical or sensory elements added to the environment, either intentionally by humans or unintentionally as a byproduct of human activity, that impose fitness costs on migrating birds.
Fitness costs	Increased mortality, reductions in reproductive success, and/or reductions in future survival probability
Lethal effects	Effects of anthropogenic threats that cause immediate or delayed mortality
Nonlethal effects	Effects of anthropogenic threats that cause a reduction in future reproductive output or survival probability, or that increase susceptibility to the effects of other threats through one or more intermediate mechanisms
Interacting effects	Anthropogenic threats that interact with one another to produce either lethal or nonlethal effects; these may be additive or synergistic

2). These costs are incurred through four non-mutually exclusive pathways that we describe here. An example of the pathways through which a single threat can affect fitness is shown in Figure 1.

Physiological Condition

We use “condition” to refer to both fuel stores (fat) and other components of health and vitality (Klaassen *et al.* 2012). Upon

arrival at their destination, migrants must find food, avoid predators and competitors, and/or seek mates. Their health and energetic condition at the end of the journey influences subsequent survival and reproduction (Klaassen *et al.* 2012, Halupka *et al.* 2017, Moore 2018). Encounters with anthropogenic threats can change a bird’s condition by reducing its energy stores through an impaired ability or motivation to forage (Jenni and Schaub 2003); by causing injury, illness,

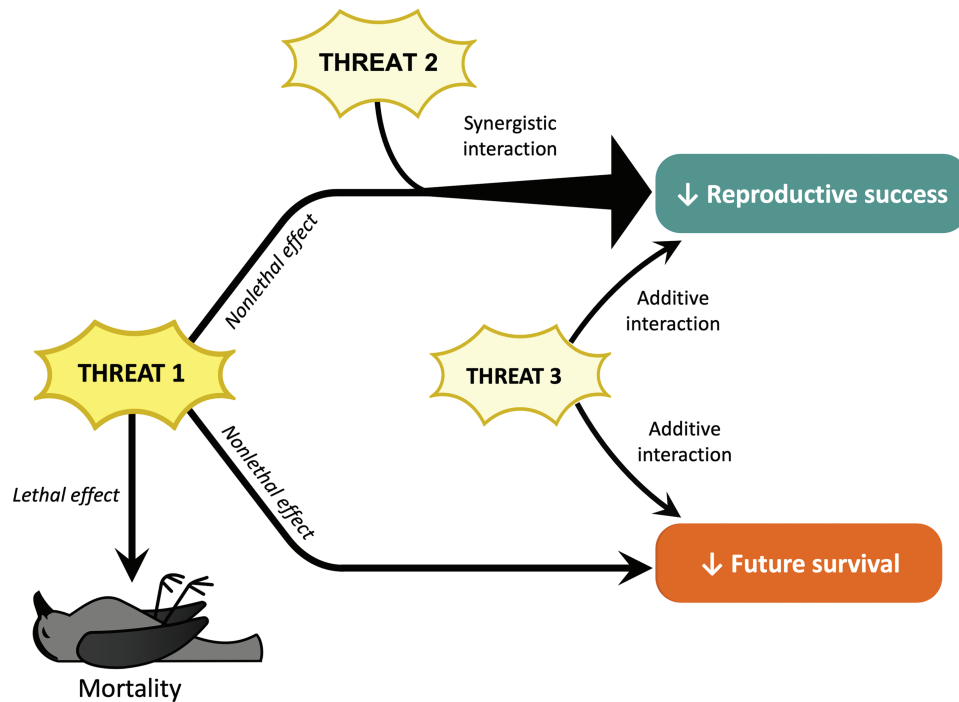


FIGURE 2. Anthropogenic threats (yellow starbursts) can affect migrating birds either individually or in combination with other threat sources. Lethal effects result in either immediate or delayed mortality. Nonlethal effects can reduce reproductive success or future survival probability (rounded boxes). Migrants can experience multiple threats en route that influence reproduction or survival independently of one another (additive interaction) or that interact to have a greater impact on reproduction and/or survival than they would in isolation (synergistic interaction).

or exhaustion (Van Doren *et al.* 2017, Linscott and Senner 2021); or by increasing disturbance and stress (Le Corre *et al.* 2009). Threats that reduce physiological condition, particularly fat stores, pose a potential fitness cost by delaying migration timing (Seewagen and Guglielmo 2010) or hampering reproduction upon arrival to breeding areas (Sandberg and Moore 1996).

Migration Timing

Appropriate timing of arrival to breeding, stopover, and stationary nonbreeding sites is critical for migratory birds to secure high-quality territories and mates, maximize reproductive potential, secure food resources for refueling, and avoid adverse weather (Kokko 1999, Smith and Moore 2005, Schmaljohann and Both 2017). Delays may arise via changes to a bird's physical state or route, environmental conditions, and other factors (Jenni and Schaub 2003, Åkesson and Helm 2020). En route conditions that delay a migrant's arrival to the breeding area may hinder its reproductive potential (Sandberg and Moore 1996, Smith and Moore 2005, Costa *et al.* 2021), while delayed arrival to nonbreeding areas in autumn can mean an individual spends the season in poor-quality habitat, delaying its departure in spring (Studds and Marra 2007, Cooper *et al.* 2015, but see González *et al.* 2020). Arrival timing at stopover sites is also important because both the needs of a migrating bird and the resources available at a given stopover site can vary within a season (Schaub and Jenni 2000, Linscott and Senner 2021, Cohen *et al.* 2022b, Schmaljohann *et al.* 2022). Thus, proper timing relative to environmental conditions is critical to a migrating bird's success, and any threat-related changes to the migration schedule (typically delays) that a bird would not have experienced otherwise may impose a fitness cost.

Orientation and Navigation

Migratory birds use an internal clock and compass mechanism coupled with a variety of external cues to orient themselves and navigate to their destinations (Alerstam *et al.* 2003, Åkesson and Hedenström 2007, Åkesson and Helm 2020). Although birds' navigation ability is remarkably flexible in the face of changing en route conditions (Åkesson and Helm 2020), anthropogenic threats can interfere with a bird's ability to correctly perceive or interpret environmental cues used for orientation and navigation. Disoriented migrants may deplete their energy reserves in flight (Ronconi *et al.* 2015), imposing fitness costs through reduced condition, delayed timing, or failure to reach the destination.

Migration Route

Migrating birds are expected to follow routes that minimize overall time, energy, or predation risk over the course of the journey (Alerstam and Lindström 1990, Alerstam 2001). Anthropogenic changes to the physical and sensory environment may cause migrating birds to alter or adjust their route, move to alternative stopover sites, or change their stopover frequency (McClure *et al.* 2013, Xu *et al.* 2020, Burt *et al.* 2023). Threat-related changes to the route presumably lengthen the duration of migration (i.e., timing) and can affect condition via increased energy expenditure or opportunity costs of using lower-quality stopover or airspace habitat, potentially leading to costly delays (Alerstam 2001, Overton *et al.* 2022).

ANTHROPOGENIC THREAT TYPES

In the sections below, we review the impacts of eight types of anthropogenic threats to migrating birds, whose lethal

effects we briefly describe before discussing their supported and hypothesized nonlethal effects through the pathways described above. These include (1) human-made structures (buildings, wind turbines, powerlines, etc.), which represent some of the largest sources of annual bird mortality during migration (Calvert et al. 2013, Loss et al. 2015), two sensory pollutants: (2) artificial light at night (ALAN) and (3) noise pollution; (4) environmental contaminants (focusing on insecticides and heavy metals); and (5) free-roaming domestic cats (*Felis catus*). We also included two additional threats caused or exacerbated by humans that are not typically considered to cause large-scale direct mortality but may nonetheless threaten migrating birds: (6) introduced plants and (7) wildfires. In addition, we consider the overarching effects of (8) anthropogenic climate change on bird migration. Increasing wildfire activity is one of many consequences of climate change, but we chose to discuss these threats separately due to their different pathways and effects on fitness. While hunting and trapping is a major threat to migrating birds globally, particularly in the East Asian-Australasian and Afro-Palearctic migration systems (Yong et al. 2015, Khelifa et al. 2017, Buchan et al. 2022), we did not find sufficient evidence of nonlethal effects of hunting during migration to include it in this review. We only briefly address stressors that are a consequence of the removal of elements from the landscape (e.g., habitat loss and fragmentation), though the importance of these factors in bird population declines cannot be understated. We demonstrate how many of these anthropogenic threats can cause functional habitat degradation, effectively reducing the availability of otherwise high quality or protected airspace and stopover habitats (Ware et al. 2015). It is possible that this synthesis will lead to discussion of additional nonlethal anthropogenic threats during migration beyond those we review here.

Anthropogenic Structures

Human-made elements in the airspace have become an increasingly common barrier to migratory movements, and birds collide with anthropogenic structures throughout the world's migration systems (Marques et al. 2014, Santiago-Alarcon and Delgado-V 2017, Hager et al. 2017, Bernardino et al. 2018, Pinto et al. 2020, Uddin et al. 2021, Mansouri et al. 2022). Not all collisions result in observed mortality: only a small percentage (approximately 6–7%) of collisions at residential buildings are estimated to be immediately fatal (Kummer and Bayne 2015, Samuels et al. 2022), but the long-term survival probability remains largely unknown (Klem 1990). Estimating the number of collision-related injuries and mortalities is therefore challenging because injured birds may move away from the point of impact (Drewitt and Langston 2008, Samuels et al. 2022).

In addition to delayed mortality, collisions during migration can have nonlethal effects that impose a fitness cost. The most frequent injury in birds surviving collisions is intracranial hemorrhaging (Klem 1990, Fornazari et al. 2021). In humans and model animals, traumatic brain injuries result in cognitive impairment (slowed reaction times), amnesia, balance impairment, and sleep/wake disturbance (McCrory et al. 2017). Symptoms can persist for days in animals (Giza and Hovda 2001), potentially impairing a bird's ability to refuel and migrate. Collisions may also reduce flight performance and affect a bird's ability to continue migrating (Orłowski and Siembieda 2005, Travers et al. 2021) or to properly orient itself. For in-

stance, a radio-tagged Gray Catbird (*Dumetella carolinensis*) that survived a collision in the midwestern U.S. migrated when it should have been breeding (L. DeGroot, unpublished data), suggesting that the collision affected the bird's ability to orient, navigate, and/or keep track of time. Ocular trauma, another common collision-related injury, can lead to infection or necrosis (Hudecki and Finegan 2018, Demir and Ozsemir 2021), causing vision impairments that leave birds vulnerable to predation and less efficient at foraging (Fernández-Juricic 2012). If they manage to reach the breeding grounds, collision survivors with broken or dislocated bones may have lower reproductive success compared to uninjured birds (Townsend et al. 2011). Nonlethal collision injuries can hence affect a bird's ability to evade other threats, reach its intended destination, and/or successfully reproduce.

Artificial Light at Night

Artificial light at night (ALAN) is an evolutionarily novel threat that alters the nocturnal landscape with myriad ecological consequences (Rich and Longcore 2006, Burt et al. 2023). Nocturnally migrating birds are attracted to light, whether it is emitted by artificial or natural sources (Gauthreaux and Belser 2006). Nocturnal migrants attracted to bright floodlights pointing upwards are unable to escape their influence (i.e., the entrapment effect) and fall to their death from exhaustion (Van Doren et al. 2017). Similarly, flares and artificial lights from oil and gas drilling platforms can attract and disorient birds that die of exhaustion, inhalation of toxic compounds, or incineration (Ronconi et al. 2015). ALAN increases migrating birds' risk of collisions with human-made structures (Winger et al. 2019, Van Doren et al. 2021), increasing the risk of immediate mortality.

Birds that manage to escape entrapment or burning may still suffer exhaustion or injury, reducing flight performance and possibly limiting a migrant's ability to reach a suitable stopover site for recovery. At the very least, deviation from the typical route is likely a waste of precious energy (Day et al. 2015). Light pollution typically attracts migrating birds (Gauthreaux and Belser 2006 and references therein), though there is some evidence of avoidance (McLaren et al. 2018). Attraction to and avoidance of lights may increase the tortuosity of birds' flight paths at the local scale (Cabrera-Cruz et al. 2021), or the circuitousness of their migration routes at broad spatial scales (Korpach et al. 2022), and energy expenditure in flight increases with path sinuosity (Amélineau et al. 2014). By traversing a nocturnal landscape scattered with ALAN (Cabrera-Cruz et al. 2018), birds are intermittently attracted to or repelled by lights along their entire migration route, with increased energy requirements accumulating throughout the migration season. Birds may require longer stopovers to compensate for the increased distance, and/or may have lower body condition upon reaching their destination.

ALAN can also directly influence a migrant's energetic condition. Both the perception of photoperiod and the production of hormones are disrupted by artificial lights (Liu et al. 2022). Fat deposition of migrating birds is regulated by photoperiod and hormones (Odum 1960, Cornelius et al. 2013) and melatonin production, the mechanism linking photoperiod to behavior, is reduced by ALAN (Dominoni et al. 2013a, Liu et al. 2022). The disrupted photoperiod of migrating birds stopping over in heavily light-polluted areas may affect their ability to rest and refuel, potentially leading

to delayed departure and late arrival to their destination. However, exposure to ALAN in captivity did not affect metabolic rate nor food consumption in two migratory sparrow species (Litt-Jukes 2023). Fat deposition rates of migrating birds stopping over in some, presumably light-polluted, urban parks are reportedly similar to those in more natural and presumably darker areas (Seewagen and Guglielmo 2010, 2011). On the other hand, artificial lights increase the production of testosterone in birds (Dominoni *et al.* 2013b, Ouyang *et al.* 2018), increased testosterone advances migratory departure in spring (Tonra *et al.* 2011, Owen *et al.* 2014), and ALAN-exposed birds depart and arrive earlier to their destination (Smith *et al.* 2021). While a direct link between testosterone, ALAN, and departure dates has not been established, the potential association warrants further investigation. Earlier departure could hypothetically increase competitive ability at the destination but might also increase phenological mismatches.

Noise Pollution

Human development is accompanied by noise from sources such as transportation, construction, and energy production (Shannon *et al.* 2016, Slabbekoorn *et al.* 2018). Human activity can generate low-frequency noise that propagates over long distances (Ortega 2012), and the extent and ubiquity of road and air travel networks means that even protected natural areas are not safe from noise pollution (Arévalo and Newhard 2011, Barber *et al.* 2011, Buxton *et al.* 2017). In North America, road networks extend for millions of kilometers and stopover sites are commonly surrounded by roads (Buler and Dawson 2014, Amaya-Espinel and Hostetler 2019).

Noise pollution is one of the few anthropogenic threats that rarely causes avian mortality. Instead, anthropogenic noise typically affects birds nonlethally by interfering with inter- and intraspecies communication, inducing stress, or causing birds to alter their behavior and habitat use (Patricelli and Blickley 2006, Herrera-Montes and Aide 2011, Ortega 2012). Many birds avoid noisy habitats altogether; those that remain may adjust their vocal behavior to compensate for chronically noisy environments, including vocalizing at higher frequencies, volumes, or at different times (Francis and Barber 2013, Shannon *et al.* 2016, Slabbekoorn *et al.* 2018).

Anthropogenic noise can reduce stopover habitat use by migrating birds. Broadcasting highway traffic noise from speakers at an autumn stopover site caused a reduction in bird abundance, and several species avoided this “phantom road” entirely (McClure *et al.* 2013). Noise pollution can mask acoustic cues that birds use to detect predators or prey, hindering their ability to escape or find food (Francis and Barber 2013). In noisy environments birds may increase vigilance to reduce predation risk, leaving less time for foraging (Francis 2015, Ware *et al.* 2015, McClure *et al.* 2017). Consequently, migrating birds that remain at noisy stopover sites may suffer lower body condition (Ware *et al.* 2015).

Noise pollution may also interfere with information that migrants use to assess habitat during both flight and stopover periods. Migrating birds may use anthropogenic noise to decide where and when to stop over: Cabrera-Cruz *et al.* (2019) found that birds increase flight altitude when migrating over urban areas and hypothesized that noise pollution can deter them from landing. Migrants in flight can use social informa-

tion from other birds, including acoustic cues, when deciding where to land (Chernetsov 2006, Mukhin *et al.* 2008, Németh and Moore 2014). Migrants also use social learning to assess the location of food resources, competitors, and predators at unfamiliar stopover sites (Németh and Moore 2007, Deakin *et al.* 2021, Aikens *et al.* 2022). Consequently, noise pollution that masks acoustic cues from avian communities, prey, or predators may reduce birds’ ability to quickly and safely refuel, affecting their condition and migration timing, and ultimately their fitness.

Environmental Contaminants

Humans’ production and use of toxic substances has increased dramatically over the past century (Bernanke and Köhler 2009; He *et al.* 2005). Migrating birds may be particularly vulnerable to toxicant ingestion since they must rapidly gain mass at unfamiliar stopover locations to replenish fat and lean mass catabolized during flight (Bairlein and Gwinner 1994, Klaassen *et al.* 2012, Seewagen *et al.* 2016, Seewagen 2020). While migrating birds may be exposed to a variety of contaminants (Tanabe *et al.* 1998, Henkel *et al.* 2012, Bianchini and Morrissey 2018, Richard *et al.* 2021, Ma *et al.* 2022), we focus on two widespread and well-studied classes—insecticides and heavy metals—as examples of the sublethal effects of environmental contaminants on migrating birds.

Insecticides have been estimated to kill millions of birds every year (Pimentel 2005) and include compounds in the classes of organochlorines, organophosphates, carbamates, and neonicotinoids (Richard *et al.* 2021). Organochlorines are the oldest class and infamously include DDT, the use of which has been banned or heavily restricted in many countries for decades (Jaga and Dharmani 2003). Neonicotinoids, the newest class, are currently the most widely used insecticide in the world (Goulson 2013). They are highly water soluble (Jeschke *et al.* 2011) and can accumulate in soil and aquatic ecosystems (Hladik *et al.* 2018, Huang *et al.* 2020), where they can persist and harm aquatic invertebrates (Morrissey *et al.* 2015). Insecticide overuse is contributing to steep insect population declines (Sánchez-Bayo and Wyckhuys 2019, van der Sluijs 2020, Barmantlo *et al.* 2021), reducing prey availability for insectivorous birds including during migration, and likely contributing to insectivore population declines (Nebel *et al.* 2010, Bowler *et al.* 2019, Spiller and Dettmers 2019).

All of the insecticide classes described here have the dose-dependent potential to be immediately lethal to birds, but sublethal effects can also occur depending on the exposure concentration, length of exposure, and other factors (Lopez-Antia *et al.* 2013, Mitra *et al.* 2011). Insecticide residues and metabolites can bioaccumulate in birds (Mora *et al.* 1987, Lopez-Antia *et al.* 2015, Kesic *et al.* 2021) and may be mobilized from the catabolism of tissues during physically rigorous activities like migration (Tanaka *et al.* 1986, Colabuono *et al.* 2012). Some insecticides may impact neurological development and function (Iwaniuk *et al.* 2006) or cause appetite suppression and anorexia (Grue 1982, Elliott and Bishop 2011, Lopez-Antia *et al.* 2013), potentially delaying migration through reduced refueling. Sublethal doses of a neonicotinoid caused significant decrease in food consumption, body mass loss (possibly due to appetite suppression), and delayed departure timing in White-crowned Sparrows (*Zonotrichia leucophrys*) during migration (Eng *et al.* 2019). Ingestion of

some organophosphates and neonicotinoids can also impair migratory orientation (Vyas et al. 1995, Eng et al. 2017).

Lead and mercury are two of the most common and harmful metal contaminants in the environment, though many others exist (Larison et al. 2000, Burger et al. 2015). Birds bioaccumulate both lead and mercury (Rimmer et al. 2005, Roux and Marra 2007, Burger et al. 2015), with lead toxicity observed in migrating vultures (Kenny et al. 2015) and waterfowl (Havera et al. 1992). Lead toxicity has also been observed in songbirds near contaminated areas (Beyer et al. 2013). Mercury exposure during the breeding season may decrease the probability of songbird survival during migration (Ma et al. 2018). Similar to certain pesticides, the physical exertion of migrating can mobilize tissue stores of methylmercury, the most bioavailable and harmful form of mercury, increasing its circulating levels (Seewagen et al. 2016). Methylmercury exposure can impair birds' navigation and ability to fly (Ma et al. 2018, Moye et al. 2016). Additionally, exposure to lead and methylmercury can hinder migration by interfering with refueling and reducing flight endurance and performance through a variety of effects that include altered metabolism (Seewagen et al. 2022), altered immune function (Lewis et al. 2013, Vallverdú-Coll et al. 2019), anorexia, lethargy, ataxia (Seewagen 2020, Pain et al. 2019) diarrhea, convulsions, and paralysis (Pain et al. 2019). Widespread environmental contaminants can thus negatively affect fitness by degrading the health, energetic condition, and orientation ability of migrating birds.

Free-Roaming Domestic Cats

Introduced mammalian predators pose a major threat to bird species worldwide, driving biodiversity declines and extinctions across taxa (Courchamp et al. 2003, Doherty et al. 2016, Lees et al. 2022). Although parks within the urban or agricultural matrix can provide important stopover habitat for migrating birds (Archer et al. 2019, Amaya-Espinel and Hostetler 2019), they may also host high numbers of novel predators (With 2002, Santiago-Alarcon and Delgado-V 2017). In this section, we focus on free-roaming domestic cats because of their global distribution, abundance, and documented impacts on birds throughout the annual cycle (Loss et al. 2022). Although other introduced predators also threaten birds (Kraus 2015, Doherty et al. 2016), we did not find sufficient evidence of their nonlethal effects on birds during migration to include them in this review.

Free-roaming domestic cats kill billions of birds annually (Blancher 2013, Loss et al. 2013, Li et al. 2021, Stobo-Wilson et al. 2022) and have been implicated in the extinctions of at least 40 bird species worldwide (Doherty et al. 2016). While there are few estimates of cat predation specifically during migration, 22% of observed mortalities at a stopover site in South Korea were attributed to domestic cats (Bing et al. 2012). The abundance of both unowned and owned free-roaming cats increases with human population density (McDonald and Skillings 2021, Cove et al. 2023), and birds migrating through urbanized regions may be more likely to encounter cats than in other phases of the annual cycle.

Nonlethal fitness costs of domestic cats likely arise from birds' antipredator responses (Cresswell 2008), which can include increased vigilance, flocking, foraging in closer proximity to cover, or avoiding risky habitats altogether (Lindström 1989, Lind and Cresswell 2006, Díaz et al. 2022). While there

are few published studies on migrating birds' behavioral responses to free-roaming cats during stopover (though see Nemes 2023), their responses to native predators can provide insights. For example, American Redstarts (*Setophaga ruticilla*) and Blue-gray Gnatcatchers (*Poliophtila caerulea*) on stopover used denser cover for foraging when migrating hawks were more abundant (Cimprich et al. 2005). During fall migration, birds were more abundant in habitat patches where there was no tradeoff between food resources and safety from hawk predation (McCabe and Olsen 2015). Migrants that have depleted their fat reserves, such as those that have newly arrived to a stopover site, take more risks when foraging (Cimprich and Moore 2006) and thus may be more susceptible to predation from cats (Dierschke 2003).

While antipredator behaviors increase short-term survival, they may come at the expense of migration speed or efficiency (Alerstam and Lindström 1990, Lind and Cresswell 2006). Behaviors such as vigilance and habitat switching can reduce risk, but migrating birds that reduce their foraging intensity or avoid locations with the best food resources may suffer lower fuel deposition rates or depart from stopover sites with less fuel (Alerstam and Lindström 1990, Lindström 1990). For example, migrating birds can reduce predation risk by carrying lower fuel loads because increased fat stores reduce take-off ability and maneuverability (Kullberg et al. 2000). However, departing from stopover with less fuel means flying a shorter distance before stopping, which may slow the migration rate and impose delayed costs in the form of lower reproductive potential (Lindström 1990). At the population level, the fitness costs of such "non-consumptive effects" can even outweigh the "consumptive effects" of predation (Preisser et al. 2005, Hamer et al. 2021). Based on migrating birds' responses to native predators, we expect them to exhibit antipredator responses to free-roaming cats as well (though see Hamer et al. 2021). Consequently, despite a lack of published research, we surmise that cats likely exert substantial fitness costs via non-consumptive fear effects that influence energetic condition and timing (Cresswell 2008, Loss and Marra 2017).

Introduced Plants

With more than 13,000 species of vascular plants naturalized beyond their native habitat (van Kleunen et al. 2015) and new introductions occurring regularly (Seebens et al. 2017), migrating birds are likely to stop over in habitats with introduced plants during their journeys. While not all introduced species are harmful, we specifically discuss species with negative ecological consequences. Migrants can suffer direct mortality from introduced plants through entanglement (Underwood and Underwood 2013, Arcilla et al. 2015) or overconsumption of toxic berries (Lincoln 1931); however, introduced plants are more likely to pose a nonlethal threat to migrants.

Introduced plants alter community structure and composition by replacing native species (McKinney 2004, Burghardt et al. 2009, Nelson et al. 2017) and reducing stopover habitat quality (McWilliams et al. 2004, 2021; Guglielmo et al. 2017). Important nutritional components in berries serve as antioxidants and immune stimulants in migrating birds (reviewed by Cooper-Mullin and McWilliams 2016), and native fruits often contain greater concentrations of energy, fat, or antioxidants than introduced ones (Bolser et al. 2013, Smith

et al. 2013, Oguchi *et al.* 2017, but see Cullen *et al.* 2020). As a result, fall migrants are more likely to settle into habitats with fewer introduced plants and preferentially consume native fruits (Bolser *et al.* 2013, Oguchi *et al.* 2017, 2018; Gallinat *et al.* 2020). Migrants that use stopover habitats with more introduced fruiting plants have lower concentrations of triglycerides in their bloodstream, indicating poorer refueling performance (Smith and McWilliams 2010, Smith *et al.* 2015). Despite the evidence that native fruits are nutritionally superior and preferred by migrating birds, the effects of introduced fruits on stopover duration and subsequent migratory performance have not yet been fully investigated.

Introduced plants can influence prey availability and migrant behavior at stopover sites (Burghardt *et al.* 2010, Narango *et al.* 2017, van Riper *et al.* 2018). Sedge Warblers (*Acrocephalus schoenobaenus*) in Iberia experienced lower fuel deposition rates and departed earlier from introduced saltbush (*Baccharis halimifolia*) habitats than native reedbeds (*Phragmites* spp.; Arizaga *et al.* 2013). Native cottonwood-willow habitat in the southwestern U.S. possessed more arthropod biomass during spring migration than non-native saltcedar (*Tamarix* spp.) habitat (Cerasale and Guglielmo 2010) and saltcedar-dominated riparian areas are avoided by most spring migrants (Fischer *et al.* 2015). However, complex interactions between or within trophic levels can sometimes result in migrants exploiting novel stopover habitats to their benefit (Besterman *et al.* 2020). For example, Wilson's Warblers (*Cardellina pusilla*) released from interspecific competition in cottonwood-willow habitat experienced greater refueling performance in saltcedar-dominated areas habitat (Cerasale and Guglielmo 2010). Introduced plants play an important role in migrant condition and possibly timing, potentially reducing reproductive success or future survival.

Wildfires

Humans have increased the frequency, severity, and spatial extent of wildfires by igniting fires (Pechony and Shindell 2010), through fire suppression and land use practices (Bowman *et al.* 2011), and by inducing climate change, which has intensified storms and altered temperature and precipitation patterns (Krawchuk *et al.* 2009, Jolly *et al.* 2015, Martinuzzi *et al.* 2016). For example, wildfire season in western North America starts earlier and lasts longer than in the past and now coincides with part or all of spring and fall migration for many birds (Westerling *et al.* 2003, Westerling 2016, Overton *et al.* 2022). Thus, we classify extreme wildfires as an “anthropogenic threat” while acknowledging the natural origin of many fires (Bowman *et al.* 2011), the dependence of many ecosystems on healthy fire regimes (McLauchlan *et al.* 2020), and the importance of Indigenous fire stewardship to conservation (Hoffman *et al.* 2021).

Severe wildfires in 2020 were estimated to kill over 1 million birds in Brazil (Tomas *et al.* 2021) and between 100,000 and 1 million migrating birds in the U.S. (Kittelberger *et al.* 2022). Wildfires can injure or kill birds via burning or smoke inhalation (Sanderfoot and Holloway 2017, Nimmo *et al.* 2021, Sanderfoot *et al.* 2021, Jolly *et al.* 2022). Migrating birds may be burned if they inadvertently fly too close to fires (Stone 1906); few studies have documented this phenomenon with wildfires, but gas flares at offshore oil and gas drilling platforms regularly kill migrating birds (Bjorge 1987, Ronconi *et al.* 2015; see also ALAN section above).

The efficiency of avian respiratory systems may increase their susceptibility to toxic compounds in wildfire smoke (Sanderfoot and Holloway 2017, Sanderfoot *et al.* 2021). Community scientists recently documented a mass avian casualty event coinciding with a period of intense wildfire activity across the western U.S. (Yang *et al.* 2021, Irannezhad *et al.* 2022) where the deaths of migrating passerines were correlated with proximity to both wildfires and poor air quality (Yang *et al.* 2021). Live birds captured during this period showed poor body condition and evidence of emaciation (Kittelberger *et al.* 2022), indicating that fires may have spurred them to migrate before they were ready or interfered with their ability to refuel en route (Yang *et al.* 2021, Irannezhad *et al.* 2022, Kittelberger *et al.* 2022).

Wildfires can influence the behavior of birds in flight. During a period of intense wildfire activity, migrating Tule Greater White-fronted Geese (*Anser albifrons elgasi*) landed prematurely, adjusted their flight paths, and attempted to fly over smoke plumes (Overton *et al.* 2022). Some individuals made inland stopovers that were far from their typical migration routes. Birds' efforts to circumnavigate smoke plumes increased the distances they traveled, doubling the time they spent on migration (Overton *et al.* 2022). The energetic cost of avoiding wildfires while migrating is probably substantial (Kittelberger *et al.* 2022); Greater White-fronted Geese would need to forage for an additional 4–6 days to compensate for the increased energy expenditure (Overton *et al.* 2022). While geese avoided wildfires, nocturnally migrating passerines are frequently attracted to and disoriented by bright light (see ALAN section above), and might be drawn towards wildfires (Stone 1906, Bjorge 1987). Either attraction to or repulsion from the light of wildfires could cause excess energy expenditure and changes to the migration route, requiring more time to refuel and increasing the total time spent on migration.

Climate Change

Human activities have dramatically changed the global climate in ways that impact biodiversity and biological processes across scales (Parmesan and Yohe 2003, Parmesan 2006, Rosenzweig *et al.* 2008). Climate change-related phenological shifts, species range shifts, and altered weather patterns throughout the annual cycle can modify ecological interactions and increase the challenges of migration (Robinson *et al.* 2009, Blois *et al.* 2013, Kharouba *et al.* 2018, Bateman *et al.* 2020), ultimately contributing to population declines (Northrup *et al.* 2019). While migrating birds have always had to contend with periods of adverse weather (Newton 2007), climate change may increase hazards during migration by increasing the frequency and severity of wildfires and extreme weather events (Dale *et al.* 2001, Martinuzzi *et al.* 2016), causing mass injury or mortality when birds in flight encounter heavy rain, snow, fog or mist, or high winds (reviewed in Newton 2007).

The nonlethal impacts of climate change on bird migration have been well studied. Climate change can alter the timing of migration, particularly in the pre-breeding (spring) season (Saino *et al.* 2011). Globally, birds are arriving increasingly earlier to their breeding areas (Gordo 2007, Usui *et al.* 2017), with average advances of 2–3 days per decade (Romano *et al.* 2022). Impacts on post-breeding migration timing are less consistent, with no clear global trends in departure timing (Romano *et al.* 2022) but an overall

increase in the duration of fall migration (Zimova *et al.* 2021, Horton *et al.* 2023). Birds might suffer from reduced food availability if their migration timing is out of sync with resource phenology (Carey 2009), a phenomenon called phenological or trophic mismatch. Mismatch between migrants' arrival timing to breeding areas and peak food availability for their offspring has been suggested as a driver of population declines in the Afro-Palearctic migration system (Both *et al.* 2006, Saino *et al.* 2011). Phenological mismatches with food sources on stopover can reduce refueling ability (Bairlein and Hüppop 2004, Kellermann and van Riper 2015) and potentially migration rate. In some regions climate change has decreased annual rainfall, reducing food availability during migration. For example, low precipitation at an important stopover site impaired the ability of Eurasian Reed-warblers (*Acrocephalus scirpaceus*) to refuel prior to crossing the Sahara Desert, reducing their annual survival (Halupka *et al.* 2017). Conditions during stopover carry over to affect reproductive timing and success: three species of Afro-Palearctic migrants bred earlier in years when migratory passage areas were warmer, and one species bred earlier in response to higher rainfall on passage (Finch *et al.* 2014), presumably due to increased insect prey on stopover. Birds that encounter extreme weather en route may be forced to make more frequent stops, which reduced subsequent reproductive success in Black-bellied Plovers (*Pluvialis squatarola*; Clements *et al.* 2022).

For temperate-breeding birds, warming temperatures may enable some species to spend the stationary nonbreeding season closer to their breeding areas, reducing the distances they must migrate (Visser *et al.* 2009, Curley *et al.* 2020). Other species show the opposite pattern, with proportionally larger northward shifts in breeding latitude resulting in longer average migration routes (Curley *et al.* 2020). Increases in migration distance due to climate change (Huntley *et al.* 2006, Robinson *et al.* 2009, Zurell *et al.* 2018) may necessitate longer or additional stops for birds to refuel (Schmaljohann and Both 2017, Howard *et al.* 2018) and could expose them to additional threats or reduce time available for reproduction and molt (Carey 2009). Organisms differ in their range shifts and phenological responses to climate change (Blois *et al.* 2013, Kharouba *et al.* 2018), reshuffling ecological communities and potentially influencing food sources (Bairlein and Hüppop 2004) or migrants' interactions en route (Cohen and Satterfield 2020). By disrupting patterns of phenology, weather, and species distributions, climate change alters birds' migration timing, routes, and ability to exploit resources throughout the annual cycle.

INTERACTING THREATS

Consensus is emerging that anthropogenic threats act in combination to impact birds and overall biodiversity (Brook *et al.* 2008, Isbell *et al.* 2022, Kimmel *et al.* 2022). Migrating birds are exposed to multiple anthropogenic factors en route and often encounter several threats simultaneously (Figure 3). Many such factors abound in urban and industrial areas, effectively transforming these into hubs for the interaction of threats and facilitating negative effects (Richard *et al.* 2021). Similarly, agricultural intensification is a source of multiple threats such as environmental contaminants, habitat loss, noise pollution, and introduced flora and fauna (Stanton *et*

al. 2018), all of which can interact to harm migrating birds. Threats may be additive, where their combined effect is equal to the sum of the independent effects, or synergistic, where the combined effect is greater than the sum of the individual effects (Darling and Côté 2008). For example, noise pollution reduces bird abundance during stopover (McClure *et al.* 2013) but its influence is greater when ALAN is also present, and some species are affected only when light and noise co-occur (Wilson *et al.* 2021).

Threats interact in complex ways, and the effect of a single threat may expose birds to one or more other anthropogenic or natural stressors (Figure 3). For instance, attraction to ALAN can increase risk of collisions with structures (Gauthreaux and Belser 2006). The combination of ALAN and collisions increases mortality by introduced predators because free-roaming domestic cats and dogs prey on unconscious or stunned birds after window collisions (Rebolo-Ifrán *et al.* 2021). ALAN can also increase mortality from native predators that hunt nocturnally migrating songbirds that are attracted to or disoriented by city lights (DeCandido and Allen 2006). Birds' antipredator responses to free-roaming cats may draw the attention of native predators, a phenomenon documented during the breeding season (Bonnington *et al.* 2013, Greenwell *et al.* 2019), and chronic noise pollution may mask acoustic cues that migrating birds use to perceive predators or to warn other individuals (Francis and Barber 2013, but see Pettinga *et al.* 2015). Furthermore, attraction to artificial lights may increase migrants' exposure to air pollution and toxicants from urban areas (La Sorte *et al.* 2022) and oil flares (Bjorge 1987). The immunosuppressive effects of certain contaminants together with natural reductions in immune response during migration might render migrating birds especially vulnerable to disease (Gylfe *et al.* 2000, Owen and Moore 2006, Vallverdú-Coll *et al.* 2015).

Birds that are weak, ill, or disoriented from exposure to adverse weather or wildfire smoke may be more susceptible to predation during stopover. Both native and introduced predator species in fire-adapted ecosystems, including free-roaming cats, exploit fire to hunt fleeing prey or hunt more effectively in recently burned areas (Doherty *et al.* 2022). Similarly, birds experiencing neurological impairment, mass loss, or immunosuppression from ingestion of pesticides or heavy metals could be more susceptible to building strikes, extreme weather stress, vagrancy, or predation during migration (Galindo *et al.* 1985, Eng *et al.* 2017, 2019; Seewagen 2020). Although these interactions are not often studied explicitly, captive studies have demonstrated that birds dosed with pesticides are more susceptible to domestic cat predation (Galindo *et al.* 1985).

Anthropogenic climate change alters weather patterns, phenology, and species distributions in ways that can increase birds' exposure or susceptibility to other threats (Figure 3B). Introduced species show range expansions with climate change (Parmesan and Yohe 2003, Hellmann *et al.* 2008), which may increase migrants' probability of encountering these threats en route (Robinson *et al.* 2009, Bateman *et al.* 2020, Kubelka *et al.* 2022). Climate change could also affect availability of preferred foods during stopover by altering the phenology or distribution of introduced plant species (Gallinat *et al.* 2020). Thus, the combined effects of multiple interacting threats more accurately reflect their true level of impact on migrating birds.

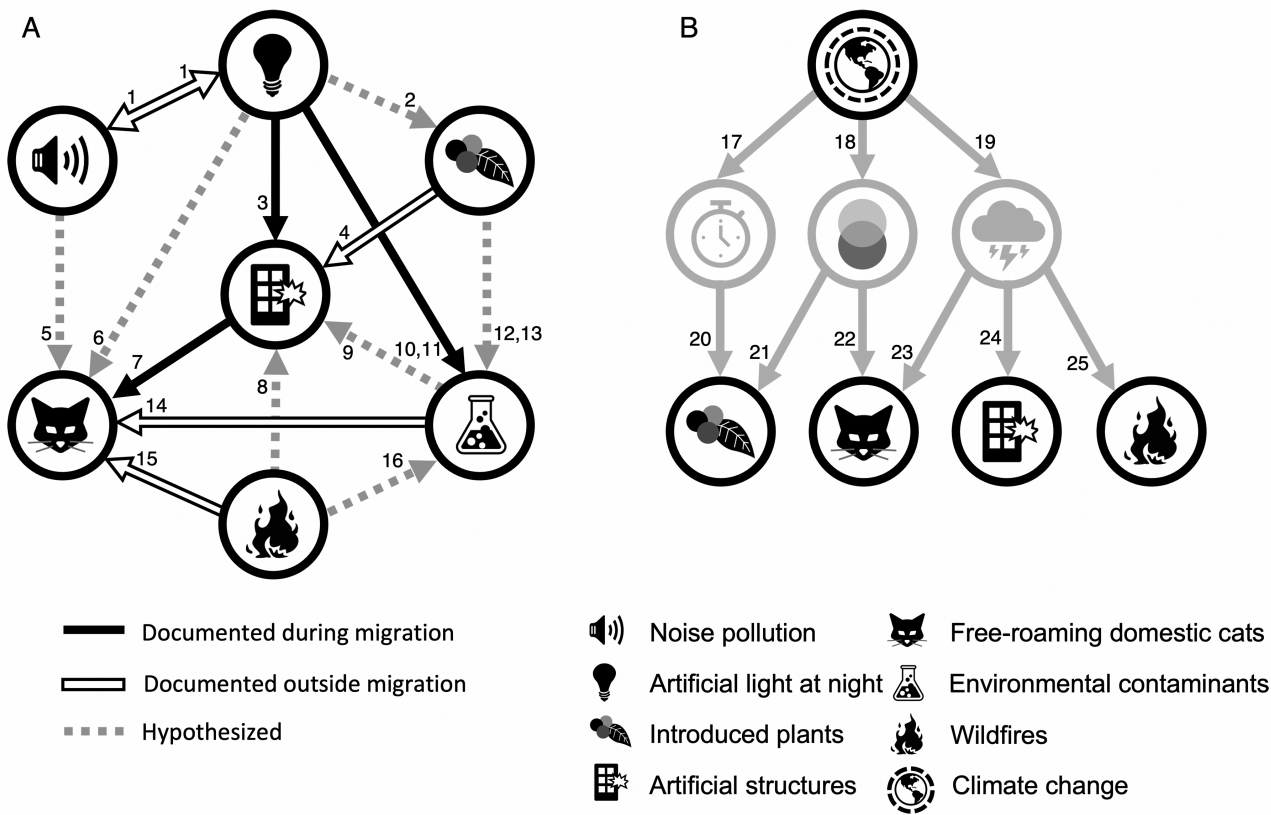


FIGURE 3. Anthropogenic threat sources can interact to produce cumulative or synergistic effects on migrating birds. **(A)** We found several published studies documenting interactions between pairs of threats during migration (black arrows), as well as studies that documented threat interactions affecting birds outside of the migration period (or affecting non-migratory species) that we imagine could also occur during migration (white arrows). We hypothesize that additional interactions between threats are possible but did not find published evidence for them (gray dashed arrows). Numbers at the head of each arrow denote the corresponding source(s); for hypothesized interactions, sources provide evidence for how expected interactions might arise. **(B)** By altering migration phenology (clock symbol), inducing range shifts (shaded circles symbol), and increasing the frequency of extreme weather events (lightning storm symbol), climate change may increase migrating birds’ exposure to introduced plants, introduced predators, collisions, and wildfires. For clarity, we only provide example citations in the figure rather than an exhaustive list of all sources relevant to a given interaction. Figure citations: (1) Wilson et al. (2021), (2) Dolan et al. (2011), (3) Gauthreaux and Belser 2006, (4) Kinde et al. (2012), (5) Quinn et al. (2006), (6) DeCandido and Allen (2006), (7) Rebolo-Ifrán et al. (2021), (8) Newton (2007), (9) Mineau and Tucker (2002), (10) La Sorte et al. (2022), (11) Russell (2005), (12) Shimeta et al. (2016), (13) Bautista (2007), (14) Galindo et al. (1985), (15) Doherty et al. (2022), (16) Vyas et al. (2009), (17) Robinson et al. (2009), (18) Bateman et al. (2016), (19) Martinuzzi et al. (2016), (20) Gallinat et al. (2020), (21) Blois et al. (2013), (22) Hellmann et al. (2008), (23) Hilton et al. (1999), (24) Loss et al. (2020), (25) Bateman et al. (2020).

KNOWLEDGE GAPS AND FUTURE DIRECTIONS

Arguably, the most critical unanswered question is the extent to which nonlethal effects during migration contribute to population declines. We have outlined potential ways that exposure to nonlethal anthropogenic hazards, singly or in combination, can impose fitness costs. In practice, nonlethal effects that occur during migration are extremely difficult to link to population trends; the same is true for even well-studied mortality sources (Loss et al. 2012, Rosenberg et al. 2019, though see Katzner et al. 2020). This knowledge gap is due to several critical limitations inherent to studying migratory animals. First, movements are difficult to track; populations differ in their migration routes and timing, and individuals of many species are too small to precisely monitor their entire journeys in real time. Second, as birds migrate, experiences at one location may carry over to reduce fitness at a later time and place (Finch et al. 2014, Grandmont et al. 2023), making it difficult to pinpoint the consequences of nonlethal stressors and their interactions. Finally, there is a geographic bias in migration research that makes it difficult to quantify the effects

of threats with variable occurrence throughout the migratory route. Below, we describe these limitations in further detail and suggest approaches to address these knowledge gaps.

A major challenge in linking en route anthropogenic threats to population declines is that populations vary in their migratory timing and routes, exposing them to different levels of risk (Kirby et al. 2008, Hewson et al. 2016, Pearce-Higgins et al. 2017). We have a poor understanding of migratory connectivity for most species (Cohen et al. 2018, Marra et al. 2019), further hampered by the difficulty of tracking the full migrations of small birds in real time. To identify where and when bird populations are exposed to threats during migration, further research on migratory connectivity (Webster et al. 2002, Cohen et al. 2019) together with spatially explicit threat maps that cover entire migration corridors (Tulloch et al. 2015, Bowler et al. 2020, Buchan et al. 2022) and extend upwards into the airspace (Davy et al. 2017, Cohen et al. 2022a) will prove invaluable. Incorporating a temporal component to create dynamic threat maps can more accurately capture the seasonal ebbs and flows in risk that birds experience as they move across continents (Runge et al. 2016, Bauer

et al. 2019). Mapping spatiotemporal patterns of risk as well as migration bottlenecks (Buehler and Piersma 2008, Bayly *et al.* 2018, Gómez *et al.* 2019, Horton *et al.* 2019) and important stopover sites (Buler and Dawson 2014, Cohen *et al.* 2021, Guo *et al.* 2023) can inform the design of dynamic rather than static protected areas that enable safe passage at the most critical times and places for migratory species (Runge *et al.* 2014, Johnston *et al.* 2015, Reynolds *et al.* 2017).

Over broad spatial scales, environmental conditions en route influence migration timing and survival (Tøttrup *et al.* 2012, Briedis *et al.* 2017), but less clear are any compounding effects of more localized threats or of repeated exposure throughout the migration period. We can imagine that a bird that sustains an injury at one stopover site presumably remains at increased risk of predation at subsequent stopover sites, unless and until it has fully recovered, but few studies have examined how long nonlethal effects persist. There is increasing evidence that conditions at a single stopover site can carry over to affect later survival and reproduction (e.g., Halupka *et al.* 2017, Clements *et al.* 2022, Grandmont *et al.* 2023). For instance, Snow Geese (*Anser caerulescens*) exposed to adverse conditions at a single spring stopover site have lower nesting success and may skip breeding altogether (Legagneux *et al.* 2012, Grandmont *et al.* 2023).

A variety of experimental and model-based approaches can help quantify the nonlethal effects of threats and their interactions. Researchers can couple individual migration tracking with manipulations of threat sources (Birnie-Gauvin *et al.* 2020, Nemes 2023), such as experimentally elevating noise or light pollution (McClure *et al.* 2013, Cabrera-Cruz *et al.* 2021), or can compare the performance of birds at sites with different levels or combinations of threats (Hewson *et al.* 2016, Sanderfoot *et al.* 2021). Increased bird banding and tagging efforts in urban and suburban habitats throughout species' nonbreeding ranges would provide useful comparisons of the physiology, behavior, and survival of populations exposed to elevated levels of anthropogenic disturbance during migration (Dunn 2016). Anthropogenic threats rarely occur in isolation in the real world, and single-factor experimental manipulations should be complementary to research on multiple interacting stressors during migration. Theoretical models of behavior, including individual-based models, offer opportunities to investigate how individuals' responses to threats during migration carry over to affect life history events such as reproduction (Bauer and Klaassen 2013). Full annual cycle population models that incorporate the influence of en route nonlethal effects on subsequent per capita reproduction and survival or population vital rates (Weber *et al.* 1999, Norris and Taylor 2006, Ratikainen *et al.* 2007) can be used to guide future research and inform spatial and temporal prioritization for reducing nonlethal anthropogenic threats (Sheehy *et al.* 2011, Hostetler *et al.* 2015).

Finally, although we did not conduct a systematic review, we noted clear bias in the geographic locations of studies on nonlethal effects. Within the Nearctic-Neotropical migration system, more research is needed on threats outside of the U.S. and Canada (Bayly *et al.* 2016, 2018). Likewise, while threats to migrating waterbirds within the East Asian-Australasian migration system have received increasing research attention (Amano *et al.* 2010, Szabo *et al.* 2016, Lei *et al.* 2019, Yong *et al.* 2021), threats and life history information for other taxa, particularly passerines, are less understood (Yong *et al.* 2015, 2018; Yamaura *et al.* 2017). Similarly, Afro-Paleartic

bird migration has been well studied within Europe and parts of the Middle East, but the ecology of many species during migration and nonbreeding seasons in sub-Saharan Africa remains poorly documented (Vickery *et al.* 2014, Marcacci *et al.* 2022). These patterns reflect a well-established Global North bias in conservation research and publication (MacGregor-Fors *et al.* 2020, Maas *et al.* 2021, Soares *et al.* 2023) that undermines efforts to protect migrating birds and the ecosystems upon which they rely across the annual cycle (Wilson *et al.* 2016). Threats can vary across migration corridors and between populations based on socioeconomic, geographic, ecological, cultural, and policy differences (Runge *et al.* 2014, Horton *et al.* 2019). For example, while organophosphate insecticides have been outlawed in the U.S. and Canada since the 1970s, Neotropical migrants may be exposed in parts of their nonbreeding ranges where these compounds remain legal (Maldonado *et al.* 2017). To design effective transboundary conservation measures that simultaneously benefit birds and people (Kark *et al.* 2015, Saunders *et al.* 2021), we must understand how the variable occurrence and timing of threats influence the success of migration through these regions (Runge *et al.* 2014).

CONSERVATION IMPLICATIONS

Why should researchers, conservation managers, and the public be concerned about nonlethal effects of human activity on migrating birds? Alleviating sources of en route mortality will undoubtedly reduce their nonlethal effects as well, but specifically addressing nonlethal effects will also lead to more robust protections. For example, environmental impact assessments that only evaluate direct bird mortality might underestimate the consequences of proposed development in migration corridors, which can degrade terrestrial or aerial habitat for migrating birds without killing them (Marques *et al.* 2020). Conversely, conservation efforts based on an incomplete understanding of if and how nonlethal effects influence fitness may waste limited resources with little benefit for populations (Fraser *et al.* 2018, Wilson *et al.* 2020). We surmise that a fuller understanding of how nonlethal effects impact migrants en route will help elucidate why some individuals and populations are more susceptible than others, which will guide targeted conservation measures (Bauer *et al.* 2019, Katzner *et al.* 2020).

Our review indicates that most nonlethal effects of anthropogenic threats during migration are even less well documented and quantified than direct mortality from anthropogenic threats. Furthermore, the magnitude of individual threat effects and their interactions on migrating birds depends on the local context as well as the species involved, meaning that a single ranking of relative threat level due to a particular source for all taxa and flyways may not be meaningful (Bellard *et al.* 2022). Consequently, we have not attempted to rank the importance or severity of nonlethal effects of threats en route, but we recognize that with increased knowledge such a ranking would be beneficial for prioritizing conservation action and raising awareness (e.g., Kirby *et al.* 2008). However, we suggest that threats exhibiting a higher number of interactions with other threats are likely having the greatest impact on migrating birds (Figure 3). As an example, ALAN produces documented or hypothesized interactions with five other threats, meaning that alleviating ALAN will concurrently reduce migrating birds' exposure or susceptibility to

other anthropogenic hazards. Similarly, multiple threats can increase migrants' vulnerability to free-roaming cats, and thus managing cat populations could reduce the total impact of these threats on migrating birds (Lepczyk *et al.* 2022).

A further reason to mitigate nonlethal effects of threats is that humans often experience negative effects from the same factors that harm birds, such as sensory pollution and environmental contaminants (Şekercioğlu *et al.* 2016, Liang *et al.* 2020). Thus, alleviating nonlethal effects on migrating birds will simultaneously benefit human health and well-being in ways that measures to reduce direct bird mortality, such as installing bird-safe windows, typically do not (Liang *et al.* 2020). This provides an opportunity for conservation practitioners to partner with stakeholders who might not otherwise support bird-friendly policies to achieve shared benefits for both migrating birds and public health (Sandifer *et al.* 2015, Şekercioğlu *et al.* 2016, Aronson *et al.* 2017). In all cases, understanding and successfully reducing both lethal and nonlethal effects of anthropogenic threats across the entirety of bird migration corridors will require international cooperation and input from partners across governments, institutions, and the public (Runge *et al.* 2017, Yong *et al.* 2018, Marcacci *et al.* 2022).

CONCLUSION

Simply surviving the migratory journey is of little use if birds arrive to their destination too late, unhealthy, or exhausted to successfully reproduce or survive the next season (Hedenström 2008, Senner *et al.* 2015, Moore 2018). Although challenging to study, understanding if and how threats encountered during migration impose fitness costs that scale up to influence migratory bird populations, and how the effects of those threats change or increase as they interact with other threat sources, will enhance conservation (Bowlin *et al.* 2010, Runge *et al.* 2014, 2016; Katzner *et al.* 2020). With migratory species facing steep declines (Vickery *et al.* 2014; Rosenberg *et al.* 2019), the impact of human activity on migrating birds should not be measured solely by mortality, but also in changes to a bird's migration timing, route, and physiological condition (Moore 2018). Focusing exclusively on immediate mortality risks underestimating the full costs of human activity on migrating birds and our responsibility to lessen the barriers that impede successful migration.

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The authors declare no conflicts of interest with this publication.

Author contributions

C.E.N. led the work including writing and submitting the initial proposal, finalizing the concept, and writing the first ver-

sion of the manuscript with input from S.A.C.-C. and E.B.C. The initial idea for the manuscript was a team (lab) effort by all authors. All authors contributed to the writing of individual sections and reviewed and revised the draft manuscript. C.E.N. and E.B.C. were supported by startup funds from the University of Maryland Center for Environmental Science to E.B.C.

Data availability

No new data were used in this work.

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