The effects of artificial light on bird movement and distribution

by

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Abstract

Artificial light is one of the fastest growing pollutants worldwide and conveys biological effects from molecular to ecosystem levels on many taxa, including birds. Birds flying at night sometimes collide with illuminated structures, but artificial light can have other effects that are less lethal or even beneficial for birds. I created a systematic map of the evidence that artificial light affects bird movement and distribution. I located evidence through a systematic search and I built a database of studies with metadata about their populations, interventions/exposures, comparators, and outcomes. I identified relevant evidence for four secondary topics: aggregation and mortality during flight, attraction and disorientation as mechanisms for these aggregations, efficacy of light-based deterrents, and habitat selection when not in flight. The search produced 490 studies. I found relevant evidence for each of my secondary topics, though evidence of bird attraction and disorientation was lacking. My database of these studies and their metadata could support several subsequent reviews of research and management questions by others. I identified a particular need for experiments using light sources similar to those that birds encounter in built environments.

I explored species-specific effects of artificial light with two field studies that targeted species in the nightjar (*Caprimulgidae*) family. These insectivorous birds forage at low light levels. Nightjars may benefit from foraging on insects aggregating at light sources, but may experience higher predation risk if artificial light makes their camouflaged ground nests more visible. I tested these hypotheses using data from the Canadian Nightjar Survey in British Columbia. I modeled the association between artificial light and the relative abundance of Common Nighthawks (*Chordeiles minor*) and Common Poorwills (*Phalaenoptilus nuttallii*). The relative abundance of extra-territorial Common Nighthawks, which are likely to be foraging,

showed a positive association with artificial light only at low levels of urban land cover. Relative abundance of territorial Common Nighthawks and of Common Poorwills, which nest and foraging within their territories, were both negatively associated with artificial light. These results suggest that Common Nighthawks may benefit from foraging on insects at artificial lights, but only in areas with very little urban development. Breeding nightjars may experience disadvantages in lit environments, perhaps through greater predation at their nests.

A final component of my dissertation was to assess subtle behavioural changes associated with artificial light, which may affect temporal patterns of habitat use across the daily light cycle with effects that differ by latitude. I studied the effects of artificial light on both spatial and temporal habitat use by Common Nighthawks and compared these effects in a northern and southern region of Alberta. I collected acoustic recordings in the southern Grassland region and northern Boreal region and I measured spatial intensity of territorial and extra-territorial habitat use. At sites where I detected Common Nighthawks, I tested for differences in daily patterns of vocal activity between lit and unlit sites. I found a negative association with artificial light for intensity of both territorial and extra-territorial spatial habitat use in the Grassland region and no association in the Boreal region. I found no effect of artificial light on temporal patterns of habitat use. Artificial light may be more likely to affect spatial habitat use by crepuscular birds at lower latitudes where natural illumination is lower during the breeding season. Artificial light does not appear to affect circadian rhythms or extend foraging activity for Common Nighthawks in my study areas.

Taken together, the results of my dissertation increased the available information about the effects of artificial light on birds. The evidence in my systematic map showed diverse and widespread effects of artificial light on bird movement and distribution that are difficult to

generalize among species, contexts, and locations. Some topics have enough evidence for quantitative analyses and my systematic map can provide evidence relevant to particular contexts using metadata searches. My research on nightjars showed effects that differed across urban land cover, behavioural context, and region. My research suggests that artificial light is unlikely to provide widespread foraging benefits for these species, and negative effects may be greater at southern latitudes. Both systematic reviews and further taxa-specific research are needed to support broader generalizations about biological consequences and potential mitigation of artificial light for birds.

Preface

This thesis is an original work by Carrie Ann Adams (CAA).

Chapter 2 of this thesis has been published as Adams CA, Blumenthal A, Fernández-Juricic E, et al. (2019) Effect of anthropogenic light on bird movement, habitat selection, and distribution: a systematic map protocol. Environ Evid 8:13. All authors collectively identified the topic for the systematic map and developed the search and data extraction strategies. CAA wrote the manuscript with significant contributions from Arden Blumenthal, Colleen Cassady St. Clair (CCCS), and Esteban Fernández-Juricic (EFJ). Erin Bayne (EB) also edited the manuscript.

Chapter 3 of this thesis has been published as Adams CA, Fernández-Juricic E, Bayne EM, St. Clair CC (2021) Effects of artificial light on bird movement and distribution: a systematic map. Environmental Evidence 10:37. CAA conducted the search and metadata coding, with assistance from a research assistant and volunteers (see acknowledgements in Chapter 3). CAA and EB designed the relational database in Microsoft Access. CAA conducted the analyses and wrote the manuscript under the advice of CCSC, EB, and EFJ.

Chapter 4 of this thesis will be submitted for publication to Landscape Ecology. This article will include CCSC, Elly Knight (EK), and EB as co-authors. CAA developed the research questions, with significant contributions from EK. The data from the Canadian Nightjar Survey were provided through the Nature Counts portal by Andrew Coughlin. Data processing and analysis were conducted by CAA, who also wrote the first draft of the manuscript. Andy Crosby helped CAA learn the statistical methods. All authors edited and commented on subsequent versions of the manuscript and read and approved the final manuscript.

Chapter 5 of this thesis will be submitted for publication to a journal, with the specific journal yet to be decided, with EK, CCSC, and EB as co-authors. CAA developed the research questions, in consultation with CCSC and EB. CAA conducted the analyses with assistance from EK and feedback from CCSC and EB. CAA wrote the manuscript, with comments and edits from all authors.

Dedication

I dedicate my thesis to the health care, grocery, and food service workers that risked their own health to care for the sick and fulfill our society’s basic needs during the Covid-19 pandemic that began in 2019. I owe the privilege of collecting data and writing this thesis in the safety of my home or tent to your sacrifices and dedication to your work.

Acknowledgements

Thank you to my supervisors, Erin Bayne and Colleen Cassady St. Clair, who invested the time and resources in my projects and my growth as a scientist. Colleen encouraged and challenged me as writer and ecologist. Erin supported my ambitious field work and analysis plans, and taught me to separate the signal from the noise statistically and ecologically. Andy Crosby helped me learn find the relationships between bird counts and landscape features. I am so grateful for the mentorship and collaboration of Elly Knight, an inspiring ecologist and dear friend. Thank you for providing invaluable feedback on my nightjar chapters and encouraging me to follow my curiosity.

My family loved, encouraged, and bolstered my resolve through the ups and downs of my PhD. To my sisters, Elizabeth and Kathryn Adams: our group texts and shared streaming passwords maintained my sanity over the past five years. To my Godmother, Mary DeByl: thank you for buying me my first birdfeeder over twenty years ago and encouraging my love for the natural world. Mom and Dad (Lyn Gracie and Jim Adams), your emotional and financial support during my many years of education have made all the difference. Thank you for believing in me when I doubted myself. Finally, my niece Grace has brought me so much joy during the last months of my degree. I hope she reads this someday.

I have been blessed with friendships in both the Bayne and St. Clair labs, as wells as the 2022/23 Biology Graduate Students' Association executive team. I particularly thank Cat Bannon, Justin Johnson, Claire Edwards, Elene Haave-Audet, Austin Zeller, and Michael Foisy for sharing these years with me in both joy and commiseration. Many, many friends remain unnamed but very much appreciated. I've also had the friendship and assistance of three very competent, supportive, and fun field partners: Wendy Margetts, Jac Curry, and Kyle Field.

Many volunteers contributed to the data collection for this thesis. In Chapter 3, I acknowledge the 25 undergraduate volunteers who contributed to that chapter. I particularly thank Cala Jorgenson, Fares Mandour, and Lucas Wessner for working with me on multiple projects. Chapter 4 would not be possible without the commitment and generosity of the volunteers of the Canadian Nightjar Survey and the organizers at Wild Research and Birds Canada. Chapter 5 relies on data collected by many students of the Bayne lab for various projects over the past eight years and I am proud to have contributed to this collective effort.

I appreciate the support and encouragement of my many mentors before my Ph.D., especially during my time working at Teton Raptor Center. Amy McCarthy and Meghan Warren encouraged my love for birds, and Bryan Bedrosian helped me find the excitement and joy in applied wildlife research. I will be forever grateful for the time I spent under your wings. During my Masters degree, Terry Root encouraged my first research project and inspired me to return to graduate school to study the effects of energy development on birds, which eventually led this thesis. Thank you for investing your time and effort in my career development.

I am extremely grateful for the financial support for my graduate degree and research. The Alberta Conservation Association funded the collection of acoustic data for my thesis. Funding for my graduate degree was provided by the Government of Alberta through the Alberta Graduate Excellence Scholarship, the National Science and Engineering Research Council of Canada through the Bios2 program, and the Department of Biological Sciences at the University of Alberta through teaching assistantships. The Department of Biological Sciences also administered two endowed awards to support my degree: the Bill Shostak Wildlife Award and the McAfee Estate Scholarship. I am very grateful to the Shostak and McAfee families for supporting me and other students in our academic pursuits.

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Chapter 1. Introduction

People have long recognized the power of artificial light, including firelight, to affect bird movement. Even before the widespread use of electricity, there are records of people using torches to immobilize and capture roosting birds, including Indigenous peoples on Vancouver Island (MacPherson 1897), Europeans in the 16th century (MacPherson 1897), and 19th century hunters in the southern United States. Similar methods are employed today to capture birds for wildlife research (Cummings and Hewitt 1964). Humans have also unintentionally harmed birds with artificial light at lighthouses, where birds have suffered collision injuries and death since at least since the 19th century (Allen 1880), and likely since the first lighthouses were erected in ancient Egypt (Trethewey 2018).

Since the invention and widespread use of electric lighting, birds' exposure to artificial light has dramatically increased (Kyba et al. 2017; Cox et al. 2022). The power of global light emissions that can be observed by satellite increased by at least 49% from 1992 to 2017, but the true increase is likely higher because many regions have transitioned to LED lights that include wavelengths that are not observed by satellites (Sánchez de Miguel et al. 2021). Satellite-based estimates with a grain size of 1.6 x 2.1 km^2 detected direct illumination over 26.5% of the land surface between 59°N and 55°S (Cox et al. 2022). Skyglow, created when artificial light is reflected by particles in the atmosphere and back towards earth, was detected on 46.9% of this land surface.

For migratory birds, exposure to artificial light is typically highest during migration (La Sorte et al. 2022). The most obvious effects of artificial light on birds also occur in this context, with mass mortalities of migrating birds concentrated in areas populated by humans (Van Doren et al. 2017; Winger et al. 2019). Artificial light affects bird movement and distribution in other contexts with varying effects. For example, lasers and spotlights are used to protect crops from birds (Blackwell et al. 2002), and to protect birds from hazards like tailings ponds in mining operations (Read 1999; Cassidy 2015). During the non-breeding season, artificial light can affect the timing of spring migration (Smith et al. 2021). It can also alter the onset of reproduction and daily timing of activities during the breeding season (Dominoni et al. 2013, 2014). For activities like nesting, roosting, and foraging, bird species' associations with artificial light have been found to be positive in some cases (Gorenzel and Salmon 1995; Jaggard et al. 2015; Daoud-Opit and Jones 2016; Rodríguez et al. 2020; Wang et al. 2021) and negative in others (de Molenaar et al. 2006; Yorzinski et al. 2015; Sierro and Erhardt 2019; Simons et al. 2021). Responses to artificial light can depend on the intensity (Syposz et al. 2021), spectral composition (Evans et al. 2007a; Longcore et al. 2013), and polarization of light sources (Horváth et al. 2009).

Thesis objectives

The goal of my thesis is to describe the effects of artificial light on bird movement and distribution over multiple behavioural and landscape contexts. In chapters 2 and 3, I synthesize the existing literature about artificial light's effects on birds into a database and describe the availability of evidence for four inter-related topics that are relevant to bird conservation or management. My fourth and fifth chapters used those insights to explore the effects of anthropogenic light on nightjars (*Caprimulgidae*), a bird family of crepuscular, aerial insectivores that may be particularly sensitive to artificial light. I compared the effects of artificial light on two different species of nightjars and varying behavioural, spatial, and temporal contexts. I organized this dissertation around two broad objectives.

Objective 1. Document the diverse effects of artificial light on bird movement and distribution

For birds, artificial light can disrupt migration (Gauthreaux and Belser 2006; Van Doren et al. 2017), alter orientation (Gauthreaux 1982; Wiltschko and Wiltschko 2019), deter from areas of human-wildlife conflict (Blackwell et al. 2002), warn of obstacles in their flight path (Dwyer et al. 2019), and influence habitat selection at both small and large spatial scales (de Jong et al. 2016; McLaren et al. 2018). Existing literature syntheses typically consider only one of these diverse responses of birds to light. The objective of my systematic map was to combine this evidence into a single synthesis using the ROSES protocol (Haddaway et al. 2018) that identifies relevant evidence based on the study population (birds), intervention/exposure (artificial light), and outcome (bird movement and distribution), expanding both the quantity of evidence available and the diversity of populations and interventions in the associated database.

In the second chapter of this thesis, I provide a protocol for the systematic map by outlining a search strategy for finding as much evidence for the effects of artificial light on bird movement and distribution as possible (Adams et al. 2019). I identified government, industry, and non-profit sources of evidence. Within Web of Science, I created a search strategy to maximize the number of articles found while reducing manual screening in the search process. This protocol was reviewed by experts in systematic reviews, and published prior to conducting the search and creating the systematic map.

Chapter 3, the systematic map, is a narrative description of this evidence and an associated database of 490 studies (Adams et al. 2021). I organized the evidence from diverse sources to describe the full range of bird responses to artificial light and provided a practical tool for answering conservation and management questions. I selected four of these questions as the secondary questions for the systematic map and identified relevant evidence for each based on study population, intervention/exposure, comparator, and outcome. In doing so, I expanded the evidence base for each secondary question to include relevant research that was not necessarily conducted for the purpose of answering that question. I also identified subtopics within each secondary question that have enough evidence for quantitative review and others that require more field or laboratory research, chosen based on their conservations and/or management importance.

Objective 2. Document how artificial light affects habitat use by nightjars across behavioural, spatial, and temporal contexts

One knowledge gap identified in the systematic map was the effects of artificial light on habitat selection in non-passerine species and beyond the directly illuminated area. This gap is logically addressed with crepuscular, aerial insectivores (i.e., birds that eat insects while in flight) because they are sometimes observed foraging under artificial lights where insects aggregate (Bharos 1992; Vernon 2003; Ortiz Z 2012). Hereafter, I refer to this possibility as the foraging benefit hypothesis. It is not yet known whether this behaviour benefits aerial insectivores enough to consistently change their habitat use over large spatial extents or whether this behaviour changes with natural light levels. Conversely, light pollution over large spatial extents may harm populations of aerial insectivores by negatively affecting insect populations (Owens and Lewis 2018; Kalinkat et al. 2021) or increasing predation risk, especially for bird species that nest on the ground (Troscianko et al. 2016). Hereafter, I refer to this as the predation risk hypothesis. The potential foraging benefits and predation risks associated with artificial light could be illuminated by studying nightjars of the family *Caprimuligidae* because these birds eat flying insects, nest on the ground, and are most active during twilight and night, when lights turn on and are brighter than background illumination.

In Chapter 4, I tested the foraging benefit and predation risk hypotheses by studying how artificial light affects the relative abundance of two nightjar species in British Columbia with different life history strategies: Common Nighthawks (*Chordeiles minor)* and Common Poorwills (*Phalaenoptilus nuttallii*). Using data from community science point counts conducted as part of the Canadian Nightjar Survey, I compared the effects of artificial light on their relative abundance across two behavioural contexts and at varying levels of urban landcover, which correlated with artificial light. Common Nighthawks may respond differently to artificial light when nesting on territories (detected with a characteristic wingboom) or foraging extra-territorially (detected with vocalizations without wingbooms), whereas Common Poorwills forage and nest within the same territory. I also identified the spatial extent at which artificial light best explained nightjar abundance to study whether the effects of artificial light extended beyond the directly illuminated area.

In my fifth chapter, I compared the effects of artificial light on Common Nighthawks between a southern and northern population in Alberta, including both spatial and temporal habitat use. I used acoustic recordings units to detect nighthawk wingbooms and vocalizations. I compared the association between spatial habitat use and artificial light in the southern Grassland region to the northern Boreal region, where natural illumination remains brighter throughout the breeding season. I also compared the effects of artificial light on temporal activity patterns in these two regions to determine if it altered the circadian rhythms or timing of foraging behaviour of Common Nighthawks.

I conclude my thesis by summarising how I fulfilled these two objectives and showed how bird responses to artificial light vary among species, but also across behavioural, spatial, and temporal contexts. I describe how the systematic map can be used to answer many questions regarding the effects of artificial light on bird movement and distribution. I discuss the contexts in which artificial light is most harmful for nightjars, and those in which it may have a neutral or beneficial effect. I also consider how the results of my systematic map and my research on nightjars can help motivate public support for policies and individual actions to reduce light pollution.

Chapter 2. The effects of anthropogenic light on bird movement, habitat selection, and distribution: a systematic map protocol

Abstract

Background

Anthropogenic light is known or suspected to exert profound effects on many taxa, including birds. Documentation of bird aggregation around artificial light at night, as well as observations of bird reactions to strobe lights and lasers, suggests that light may both attract and repel birds, although this assumption has yet to be tested. These effects may cause immediate changes to bird movement, habitat selection and settlement, and ultimately alter bird distribution at large spatial scales. Global increases in the extent of anthropogenic light contribute to interest by wildlife managers and the public in managing light to reduce harm to birds, but there are no evidence syntheses of the multiple ways light affects birds to guide this effort. Existing reviews usually emphasize either bird aggregation or deterrence and do so for a specific context, such as aggregation at communication towers and deterrence from airports. We outline a protocol for a systematic map that collects and organizes evidence from the many contexts in which anthropogenic light is reported to affect bird movement, habitat selection, or distribution. Our map will provide an objective synthesis of the evidence that identifies subtopics that may support systematic review and knowledge gaps that could direct future research questions. These products will substantially advance an understanding of both patterns and processes associated with the responses of birds to anthropogenic light.

Methods

The protocol describes the steps taken to ensure the search for evidence is comprehensive, transparent and replicable. We will find relevant studies in the grey and peer-reviewed literature using publication databases, Google Scholar, stakeholder suggestions, and organizational websites. We will select studies for inclusion in the map by identification of relevant: (i) population including any species of bird; (ii) intervention or exposure to anthropogenic light; and (iii) outcomes including changes in bird movement, habitat occupancy, population density, or distribution. We will extract and organize metadata into a systematic map that can support subsequent search by interested individuals. The quantity of evidence on particular topics will be characterized through heat maps and narrative syntheses, but subsequent work will be needed to evaluate evidence validity.

Keywords

Light pollution; artificial light; wildlife conservation; evidence synthesis; human-wildlife conflict; behaviour; wildlife deterrents; bird strike; nocturnal migration; avian mortality

Background

Artificial light has been increasing globally at a rate of 2.2% per year (Kyba et al. 2017), with a high diversity of documented effects on wildlife, including birds. Man-made objects (buildings, vehicles, power lines, street lighting, etc.) have spectral properties (e.g. wavelength, intensity) that differ from natural light present in avian evolutionary history. In many contexts, birds aggregate near artificial lights at night, with documented cases dating back to the nineteenth century (reviewed by Gauthreaux and Belser 2006) that are assumed to stem from attraction to light. Paradoxically, light is also sometimes used to deter birds from zones of human-wildlife conflict (reviewed by Bishop et al. 2003). There is evidence that both the potential attractant and deterrent effects of light can cause immediate changes to bird movement (Day et al. 2015) and alter habitat selection and settlement at a local (Read 1999; Glahn et al. 2000) and regional spatial scale (McLaren et al. 2018). The potential of light as a management tool has generated interest in a wide variety of disciplines, from pest management to bird conservation (Read 1999; Blackwell and Fernandez-Juricic 2013). Despite being applicable in many contexts, there has been no attempt to unite the evidence showing attraction, deterrence, and neutral responses of birds to light. Integrating knowledge related to how birds respond to anthropogenic light could contribute substantially to our basic understanding of relevant physiological and behavioural mechanisms. In turn, this understanding has tremendous potential to minimize bird mortalities and sublethal effects resulting from illuminated structures and regional light pollution, and also maximize bird deterrence in zones of human-wildlife conflict.

Despite high diversity of light effects on birds and large variation in their temporal and spatial scales, there has been no broad synthesis of this literature. Existing peer-reviewed syntheses have tended to emphasize specific effects of light, such as disruption to migration (Gauthreaux and Belser 2006). Similarly, existing reviews in the grey literature target particular contexts for bird control, such as agriculture (Bishop et al. 2003), poultry (Atzeni et al. 2016), mining (Marsh et al. 1991) and aviation (Ross and Davis 1998). Such specific contexts are also targeted by some reviews in the peer-reviewed literature, such as offshore oil and gas (Ronconi et al. 2015), wind turbines (Kerlinger et al. 2010), and communication towers (Longcore et al. 2008). The most comprehensive review of night lighting to date (Gauthreaux and Belser 2006) synthesizes evidence from the grey and peer-review literature, but it is now over 10 years old and did not consider the deterrent effects of light. There is both opportunity and need for a comprehensive synthesis of the effects of anthropogenic light on birds.

Such a synthesis is necessary to develop new insights into how to mitigate the disruptive effects of light on birds, which most often applies to steady-burning lights (i.e. lights with constant luminous intensity) and nocturnally-migrating birds. Anthropogenic light has been associated with all major sources of collision mortality (Ogden 2002; Longcore et al. 2008; Calvert et al. 2013; Rodríguez et al. 2014; Ronconi et al. 2015): buildings and windows (Ogden 2002), transmission lines (Longcore et al. 2008), roads (Rodríguez et al. 2014), and communication towers (Longcore et al. 2008). Light may increase bird numbers and non-linear flight paths at illuminated structures (Ogden 2002; Longcore et al. 2008; Rodríguez et al. 2014; Ronconi et al. 2015) and affect both movement and distribution at large spatial scales (Van Doren et al. 2017; McLaren et al. 2018). Even sub-lethal effects of aggregation and disruption to flight paths may ultimately reduce survival during migration by reducing energy stores and delaying arrival at breeding or wintering grounds (Gauthreaux and Belser 2006). Despite documented effects of light, some studies show no significant effect of light on bird flight behavior, density, or mortality at illuminated man-made structures (Jones 1980; Day et al. 2017). Describing the numbers of studies and contexts associated with different kinds of light effects is a necessary first step toward potential mitigation.

Reducing the disruptive effects of artificial light requires an understanding of the contexts, light characteristics, and species involved in which bird aggregation is most likely to occur. A map of the types and correlates of light effects on birds will advance subsequent studies of mechanisms. For example, a subsequent review may reveal that aggregation is more likely for some bird species, spectral characteristics of lights source, weather, and ambient light conditions. Such factors may explain why one study reported that red lights are less likely to cause aggregation of nocturnal migrants (Evans et al. 2007b), while another study found that green and blue lights were less disruptive to birds than red ones (Poot et al. 2008). Similarly, ambient light may explain why migrating eiders (*Somateria mollissima* and *S. spectabilis*) exposed to artificial light increased flight velocity during the day, but decreased velocity at night (Day et al. 2017).

Bird aggregation and mortality is often documented during nights of low cloud cover (Larkin and Frase 1988; Poot et al. 2008), but sometimes occurs in clear weather as well (Van Doren et al. 2017). Comparison of all available evidence and further primary research is needed to understand the many factors that contribute to bird aggregation around artificial light sources. Current context-dependent reviews of light effects are likely to overlook promising explanatory factors that may be revealed from broader syntheses.

The deterring effects of light are similarly scattered in the existing literature. Many industrial contexts now employ flashing lights, rotating beams, and lasers to deter birds from hazards, but there has been no synthesis of their efficacy. Such a synthesis would be relevant to applications that include agricultural lands, aquaculture facilities, airports, urban structures, industrial ponds, and other contexts in which birds cause damage, pose a danger to humans, or may be harmed by associated anthropogenic activity (reviewed by Bishop et al. 2003 and Read 1999). Light deterrents potentially offer a significant advantage over chemical and acoustic deterrents because they (a) are non-lethal, (b) can target a specific area, (c) can be used around other man-made structures, and (d) are silent, avoiding disruption to wildlife and neighboring humans associated with noise pollution (Blackwell et al. 2002). However, the way these studies have measured avoidance has been recently questioned, emphasizing the need for choice tests to establish whether birds are indeed avoiding lights in the true behavioral sense (Goller et al. 2018).

As for the literature associated with bird aggregation and attraction to light, there are few generalizations with which to predict or evaluate the effect of light as bird deterrents. For example, a particular light-based treatment may effectively deter some bird species and not others (Read 1999; Blackwell et al. 2002), a deterrent that was initially effective may no longer induce a reaction after birds habituate (Blackwell et al. 2002), and small scale movements by birds as pests may simply relocate them to nearby areas (Andelt et al. 1997; Avery et al. 2006). The literature reflects a general consensus that *some* types of lasers and strobes can deter (Verheijen 1960) *some* bird species in *some* contexts (Harris and Davis 1998; Bishop et al. 2003; Atzeni et al. 2016), but no systematic comparison has been applied to understand when and why particular treatments are effective. There is similarly no synthetic evaluation of the risk to the eyes of people and wildlife posed by using lasers, which can cause temporary or permanent damage to vision (Gunduz and Arden 1989; Barkana and Belkin 2000; Harris et al. 2003).

Incorporating laboratory and controlled field studies in our Systematic Map will provide evidence for understanding the physiological, ecological and evolutionary mechanisms governing bird responses observed in field studies. Understanding these mechanisms will in turn support better design of lighting and illuminated structures. The physiological and cognitive basis for avian responses to light remains elusive (Verheijen 1960; Gauthreaux and Belser 2006; Blackwell and Fernandez-Juricic 2013), but laboratory studies offer some insight into how anthropogenic light may disorient birds. Early laboratory studies suggested that bright lights in dark environments often disorient birds by decreasing their ability to see the environment surrounding the light source (reviewed by Verheijen 1960), and lights of particular wavelengths or intensities disrupt their ability to sense the earth's magnetic field (Rappl et al. 2000; Wiltschko et al. 2010). Disorientation in response to loss of night vision or magnetoreception has been referenced by authors of field studies as an explanation for aggregation around anthropogenic light (Verheijen 1960; Poot et al. 2008; Van Doren et al. 2017), but the mechanism by which disoriented birds are attracted to fly towards and remain within the illuminated area is unclear. The systematic map will integrate relevant evidence from field and lab studies necessary to support inferences about how potential mechanisms of disorientation demonstrated in controlled settings may influence bird behaviour in field studies where aggregation is observed.

The mechanisms associated with the deterring effects of light on birds are also obscure and could benefit from better integration of lab and field studies. Predicting bird behavioural response to light-based deterrents requires both an understanding of what the bird is seeing, based on the target species' visual system, and how the bird is likely to respond once the stimuli is perceived (Fernandez-Juricic 2016). Bird perception is difficult to predict because the avian visual system differs in several ways from that of humans (Cuthill 2006; Jones et al. 2007; Fernández-Juricic 2012; Tanaka 2015) and visual perception varies across bird species (Fernandez-Juricic 2016). Given that a bird perceives the light deterrent, it may respond with movement to prevent collision with an approaching object (e.g. airplane or vehicle) or avoid a novel stimuli (e.g. moving laser) (Conover 2001). This systematic map will include empirical evidence from laboratory and field studies documenting bird reaction to deterrents across a range of species and deterrent type. The resulting evidence base will support review questions about deterrent efficacy for particular target species or populations, light characteristics, contexts, and intended behavioural responses.

There is a tremendous need for systematic review of many aspects of light effects on birds to inform evidence-based lighting policy and wildlife management. As an example of the link between evidence and policy, research on the disruptive effects of steady-burning light on nocturnally-migrating birds caused changes to regulations set by the US Federal Aviation Administration for obstruction lighting, eliminating non-flashing lights (Gehring et al. 2009). Substantial voluntary changes in light use were encouraged by Audubon's *Lights Out* programs at cities across North America (National Audubon Society). Our systematic map will deepen the evidence base for these programs and encourage development of new ones by documenting effective interventions. Others have shown how regulation is limited by inadequate information. For example, the U.S. Bureau of Ocean Energy Management evaluation of lighting schemes identified inconsistency in research addressing the reaction of birds to light of varying wavelengths (i.e. color), demonstrating a need for systematic review of the evidence (Orr et al. 2013). Bird management at airports, tailings ponds, urban areas, and agricultural fields would benefit from systematic review of light-based deterrents.

The secondary questions of our systematic map include three main subtopics of interest to bird management and conservation: a) bird aggregation around artificial light sources, b) bird deterrence by light-based interventions, and c) avian habitat use and distribution in artificially illuminated landscapes. These three subtopics are linked by overlapping evidence bases, with many studies applying to more than one subtopic, and mechanistic explanations. For example, a study may document both aggregation and dispersal effects if comparing flashing and steady-burning light treatments. The evidence base for dispersal and habitat selection overlaps where the efficacy of light-based deterrents affects bird habitat use in landscapes where deterrents are employed (Holevinski et al. 2007). Similarly, changes in flight path induced by bright light sources may affect migratory stopover habitat use (McLaren et al. 2018). In all cases, bird response is likely to depend on light characteristics as perceived by the bird and the ambient light conditions, life history stage and taxa of the bird, and the spatial and temporal scale of the intervention. The systematic map will provide a comprehensive database of all the available evidence, with metadata on the sources of heterogeneity across studies, with the dual goals of a) providing a comprehensive list of light-based interventions and evidence of their efficacy in various contexts and b) identifying subtopics that may support a systematic review.

Stakeholder Engagement

Informal conversations with stakeholders from industries, government agencies, and non-profit organizations confirmed that this topic is relevant in many fields. We developed a questionnaire for stakeholders to expand our literature search, identify secondary questions of particular importance, support map interpretation, and guide subsequent systematic reviews and primary research (Appendix A, Additional File 1). To date, we have received responses from four stakeholders. We will continue to target individuals with expertise in the fields of bird conservation and management, including human-avian conflict, aiming for a total of 12 responses. Stakeholders include leaders and researchers at universities or non-profit organizations associated with bird conservation or management, in addition to wildlife managers at federal, provincial, and civic authorities. We will search grey literature sources suggested by stakeholders for relevant articles and listed in the published map. We will also provide the opportunity for stakeholders to review the final map and request that they share the resulting database with relevant decision makers.

Objective of the Review

The objective of this systematic map is to provide an overview of the evidence of the effects of anthropogenic light on bird movement, distribution and habitat selection. The map will integrate light effects associated with attraction and aggregation as well as deterrence and dispersal of birds. We will include studies documenting the effects of multiple light sources and identify covariates of effects that may contribute to variation in bird responses to light. Possible covariates include light characteristics (e.g. wavelength, intensity, direction, and flashing pattern), environmental variables (e.g. weather variables, temporal variables, moon phase, land/freshwater/ocean), and population characteristics (e.g. species, bird activity during intervention, domestication status, migratory status). The map will describe the quantity of evidence available on each subtopic, without evaluating the validity of the evidence presented. The map will identify areas of primary concern for managers, topics for further primary research, and potential subtopics for systematic reviews.

Primary Question:

What is the evidence that anthropogenic light affects bird movement, habitat selection, and distribution?

Secondary questions:

- What information is available documenting that artificial illumination is associated with bird aggregation or attraction?
- What information describes the effect of light as a means of deterring or dispersing birds?
- What are the contexts in which anthropogenic light is associated with changes (either increase or decrease) in bird habitat use and/or density?
- What documentation is available concerning how the effects of light on birds change over time or space, which may occur as a function of prior exposure, weather conditions, light characteristics, or other factors?

Components of the primary question

(P) Population	All bird species
(I or E) Intervention or Exposure	Anthropogenic light sources
(C) Comparator	Similar habitats, structures, or landscapes that are unlit or lit with different types of light; same study site before or after intervention
(O) Outcome	Changes in bird movement, habitat occupancy, population density, or distribution

See *Article Screening and Eligibility Criteria* for more detailed descriptions of each component

Methods

This systematic map follows CEE guidelines (Pullin et al. 2018) and ROSES reporting standards (Haddaway et al. 2018).

Searching for Articles

Database and Citation Indexing Service Search Strategy

The databases outlined in Table 2.1 will be searched for articles relevant to our primary question. We chose Web of Science Core Collection as our primary tool for its comprehensive coverage of the published literature. We determined that the maximum number of articles we can screen is 20,000, which made it feasible to add only one other comprehensive citation indexing service. We chose Web of Science Zoological Record because it indexed six of the fourteen benchmark articles that were not indexed in the Web of Science Core Collection (Appendix A, Additional File 2). We found all six of these articles using the proposed search string in the Web of Science Zoological Record (Table 2.2). Only three of the benchmark articles not indexed in Web of Science Core Collection were available in Scopus and none were available in JSTOR. Additionally, we will search Proquest Dissertations and Theses and Open Access Theses and Dissertations to find relevant graduate theses that may not be indexed in Web of Science.

Table 2.1 Details of database and citation indexing service searches

Database/Citation Indexing Service	**Institutional Subscription**	**Search Fields**	**Search String**	**Screening platform**
Web of Science Core Collection	University of Alberta	Topic (includes Title, Abstract, Author Keywords, and Keywords Plus)	TS=(*Bird* OR Avian OR Ave$) AND TS=(Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$) *	Zotero/ Microsoft Excel
Web of Science Zoological Record	University of Alberta	Topic (includes Title, Book Title, Abstract, Broad Terms, Descriptors Data, Super Taxa,		Zotero/ Microsoft Excel

		Systematics, Taxa Notes)		
Conservation Evidence	Open Access	NA	Screen all articles in “Bird Conservation” category	Microsoft Word
Crop Protection Compendium	University of Alberta	All fields, organism descriptor	od:bird* AND (Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$)	Microsoft Word
Proquest Dissertations and Theses Global	University of Alberta	Anywhere except full text	noft(Bird* OR Avian OR Ave$) AND noft(Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$)	Zotero/ Microsoft Excel
Open Access Theses and Dissertations	Open Access	Any field	(Bird* OR Avian OR Ave$) AND (Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$)	Microsoft Word
Artificial Light at Night (ALAN) Research Literature Database	Open Access	Title, abstract, and keywords	Bird*, Avian, and Aves searched one-at-a-time in each field	Zotero/ Microsoft Excel
Tethys Knowledge Base (for renewable energy)	Open Access	Receptor, Stressor	Receptor: Birds Stressor: Lighting	Microsoft Word

* We will also search the Web of Science Core Collection using the expanded population search string (Appendix A, Additional File 3). Using a Microsoft Excel macro, we will extract from these results and screen only articles which a) lack an abstract or keywords and b) do not contain “bird*”, “avian,” or “ave$” in their title.

Search String

The mapping team developed a list of search terms for the population and intervention components of the primary question based on terms used in a list of “benchmark articles”

(Appendix A, Additional File 2). We describe the search strings for Web of Science Core Collection below. Modifications to this search string for other databases and citation indexing services are listed in Table 2.1.

Intervention/Exposure**:** The search terms for the relevant interventions/exposures were consistent across the test articles. In additional to the terms outlined in Table 2.2, the terms "reflect" and "LED" were also considered for inclusion in the intervention/exposure search string, but removed because of they were commonly used in unrelated contexts. Our search strategy will find all benchmark articles that used these terms to describe an intervention because these studies also included the word "light" in their titles or abstracts. We considered including an additional intervention/exposure string including terms similar to "anthropogenic," but found that some benchmark studies did not include any such terms in their titles, keywords, or abstracts.

Population**:** During scoping, we developed the population string "*bird* OR avian OR ave$" to search the Web of Science Core Collection (Table 2.2). Because we were concerned that some relevant articles in the Web of Science Core Collection may not be found using this population string, hereafter called the "proposed search string," we tested a search string that included all of the common family names listed by the International Ornithological Conference World Bird List 2018 (Gill and Donsker 2014a), hereafter called the "expanded search string" (Appendix A, Additional File 3). Using the expanded population string and the intervention/exposure string described above, Web of Science Core Collection returned 35,767 results. CAA screened the first 4000 articles from this search (sorted by date) and an additional 2000 papers selected randomly from all search results, identifying 37 eligible articles. These eligible articles were added to the benchmark articles list. The benchmark articles list contains 64 known eligible articles that are contained in the Web of Science Core Collection, hereafter called the “known eligible articles.” We searched the Web of Science Core Collection using the proposed search string (*bird* OR avian OR ave$), generating 10,846 results. We searched within these results for each of the 64 known eligible articles and found 59 of these articles with the proposed population search string.

All five of the eligible articles that were not found by the proposed search string lacked an abstract in the Web of Science Core Collection. When using the proposed population search string instead of the expanded population search string, we may fail to find eligible articles that do not contain “bird,” “avian,” or “aves” in their title and do not have an abstract in the Web of Science Core Collection. To ensure that we find such articles, we will download all of the search results returned using the expanded population string as a text file, import them into Microsoft Excel, and use a macro to extract all articles that a) lack abstracts or lack keywords and b) do not contain “*bird*,” “avian,” or “ave$” their titles. These articles will be added to the other Web of Science Core Collection search results for eligibility screening. Every step of this process will be carefully documented and published as a supplement to the Systematic Map, including Microsoft Excel macros.

We will search the Web of Science Zoological Record using only the proposed search string (Table 2.2). All benchmark articles indexed in the Zoological Record were found using the proposed search string. Even articles that lacked an abstract or keywords and did not contain “*bird*,” “avian,” or “ave$” in their title were found because the Zoological Record “Topic” field includes Super Taxa, Systematics, and Taxa Notes. The proposed search string found these articles because they contained “Aves” in at least one of the taxa fields.

Outcome**:** During scoping, the mapping team determined that the terms used to describe outcomes in relevant articles were too numerous and unpredictable to include in the search string.

Table 2.2 Population and Intervention search strings for Web of Science Core Collection and Zoological Record.

Population	*Bird* OR Avian OR Ave$
Intervention/Exposure	Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$

Increasing Specificity: During scoping, we found that many of the articles in Web of Science Core Collection search results did not address relevant interventions/exposures, but were found because they contained the phrases, "in light of," "sheds light on," and other iterations of these phrases. We developed a strategy to eliminate from the Web of Science search results any articles that contain an intervention/exposure term within one of these phrases, but do not contain an intervention/exposure term anywhere else in the title, abstract, keywords, or category. We will export our results from Web of Science as comma-delimited text files and open them in Microsoft Excel. We will use an Excel macro to automatically find and replace these phrases with synonyms in capital letters that do not contain an intervention/exposure term (Table 2.3). This Macro will be published as a supplement to the Systematic Map. After these replacements have been made, we will use a macro to search within the Web of Science search results for articles that contain one of the intervention/exposure search terms in any of the following categories: title, abstract, author keywords, Web of Science keywords, journal name, or Web of Science category. We will exclude from further screening any articles that do not contain an intervention/exposure search term after the irrelevant phrases have been replaced. All search results excluded through this process will be reported in the search records. We will screen ten percent or 200 (whichever is greater) of the excluded articles to ensure that this process did not exclude relevant articles from screening. We will eliminate duplicate articles using Microsoft Excel Remove Duplicates feature by identifying articles with identical authors, titles, and journal names.

Web-based Search Engines

Table 2.3 Irrelevant phrases containing search terms in intervention/exposure search string

Find	**Replace**
in light of	CONSIDERING
in the light of	CONSIDERING
come to light	REVEAL
comes to light	REVEALS
in this light	FROM THIS PERSPECTIVE
lightweight	NOT HEAVY
shed light on	SHOW
shed some light on	SHOW
sheds light on	SHOWS
sheds some light on	SHOWS
light-level geolocator	LL GEOLOCATOR
light level geolocator	LL GEOLOCATOR
light-logging geolocator	LL GEOLOCATOR
light-logger	LL GEOLOCATOR
light-based geolocator	LL GEOLOCATOR
light rail	L RAIL
light-rail	L-RAIL

Irrelevant phrases are listed in the "find" column. In the Web of Science search results, these phrases will be replaced by the text in the "replace" column using a Microsoft Excel macro.

We will search Google Scholar for relevant literature using two search strings:

- Bird AND (Light* OR Laser* OR Streetlight* OR Headlight* OR Spotlight$ OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$)
- Avian AND (Laser* OR Strobe* OR Light* OR Streetlight* OR Headlight* OR Spotlight$ OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$)

We will search the full text, rather than the title, because several benchmark articles do not include "bird" or "avian" in their titles. We will export and screen the first 1000 results of each Google Scholar search to identify articles that might have been missed with our other search methods.

Organisational Websites

To avoid introducing bias in our map associated with bird type, light contexts, or other factors, we have attempted to create a list of relevant organizations, including NGOs, government agencies, and for-profit companies interested in a diversity of effects of light on birds (Table 2.4). We will also search additional organisational websites suggested by stakeholders.

Table 2.4 Organizational websites included in search

Organization	**Type**	**Context**	**Website**
Bird Control Group	For-profit	Bird Deterrent Manufacturer	https://birdcontrolgroup.com/
Bird-X	For-profit	Bird Deterrent Manufacturer	https://bird-x.com/
Accipiter	For-profit	Bird Deterrent Manufacturer	https://www.accipiterradar.com/
Bird Avert	For-profit	Bird Deterrent Manufacturer	http://www.birdavert.com/
DeTect	For-profit	Bird Deterrent Manufacturer	http://detect-inc.com/
Merlin Environmental	For-profit	Bird Deterrent Manufacturer	http://www.merlinenvironmental.co.uk/bird-control/
USDA/APHIS	Government	Agriculture	https://www.aphis.usda.gov/aphis/home/
Department for Environment, Food & Rural Affairs (UK)	Government	Agriculture	https://www.gov.uk/government/organisations/department-for-environment-food-rural-affairs
Transport Canada	Government	Aviation	http://www.tc.gc.ca/eng/menu.htm
USFWS	Government	Energy/Aviation/Buildings	https://www.fws.gov/birds/bird-enthusiasts/threats-to-birds/collisions.php
Bureau of Ocean Energy Management	Government	Energy	https://www.boem.gov/
USDA National Wildlife	Government	Agriculture	http://digitalcommons.unl.edu/icwdm_usdanwrc/

Research Center-Staff Publications			
Bird Strike Association of Canada	Government/Industry Partnership	Aviation	http://www.canadianbirdstrike.ca/en
British Trust for Ornithology	Non-profit	Bird Conservation	https://www.bto.org/
Bird-Life International	Non-profit	Bird Conservation	http://www.birdlife.org/
FLAP	Non-profit	Bird/window collision	http://www.flap.org/who-we-are.php
International Dark Skies Association	Non-profit	Conservation	http://darksky.org/
Internet Center for Wildlife Damage Management	Non-profit	Human-wildlife conflict	http://digitalcommons.unl.edu/icwdm/
IUCN SSC Human Wildlife Conflict Task Force	Non-profit	Human-wildlife conflict	http://www.hwctf.org/resources/document-library
Proceedings of the Vertebrate Pest Conference	Academic	Human-wildlife conflict	http://www.vpconference.org/Proceedings_of_the_Vertebrate_Pest_Conference/

Document/file formats

The search will not have any document type restrictions. If software to open a file is not available, we will request an alternative format from the authors.

Computer settings

To inhibit the narrowing of searches that could result from learning algorithms built into internet browsers, we will disable browser history and cookies when conducting searches. The search team will use “incognito mode” in Google Chrome and not access any electronic accounts during the search session.

Language Restrictions

Searches will not be restricted by language, but only articles written in or translated to English will be included in the systematic map.

Search Records

For each database or citation indexing service search, the date, search string, license used, and number of results will be recorded and reported in the final systematic map. When possible, the search results from each database will be exported and saved in a Zotero library. The search results from each database will be made available in an .RIS and BibLaTex format as a supplement to the Systematic Map. The Web of Science Core Collection search results will be imported into Excel as described above in the "Increasing Specificity" section. The search results of all other exportable searches will be exported from Zotero to a Microsoft Excel spreadsheet and will be combined with the search results from the Web of Science Core Collection Search. All articles with the same title, authors, and journal name will be considered duplicates and one of the duplicates will be removed from the spreadsheet. The final spreadsheet of search results will be included as a supplement in the Systematic Map.

Some databases and most websites lack options to export search results. When possible, we will copy and paste the search results into a Microsoft Word document. We will record search dates and save relevant articles in a Zotero library. The Microsoft Word documents showing all search results and the Zotero library of relevant articles will also be published as a supplement to the Systematic Map.

Assessing Search Comprehensiveness

We developed the search strategy to ensure that all benchmark articles (Appendix A, Additional File 2) will be found in the search. Benchmark articles include articles known to the authors, articles found in relevant reviews, and additional articles found during scoping. After all searches are complete, we will confirm that the search strategy finds all benchmark articles.

We will further assess the search comprehensiveness through bibliographic checking of a review pertaining to each secondary question. For each secondary question, if at least one review is identified in our search, we will randomly select one review for bibliographic checking. We will record the bibliographic details for the review, the number of references assessed as relevant in the review's reference list, and the number of relevant references missed by our searches. We will add additional components to the search strategy until all relevant references are found.

Article Screening and Study Eligibility Criteria

Screening process

Articles will be screened for relevance in Microsoft Excel using the eligibility criteria outlined in Table 2.5. The screening process will occur in two stages: title/abstract and full text. If at the title/abstract stage the relevance of the article cannot be determined, it will be included in the full text stage of screening. The full text of all articles not excluded at the title or abstract stages will be accessed using the licenses of the University of Alberta and Purdue University. Any full texts that are not available through these licenses will be obtained through Google Scholar or will be requested from the authors. The number of articles excluded at each stage will be listed in a PRISMA flow chart (Moher et al. 2009). For each article excluded at the full text stage, the reasons for exclusion will be recorded in Excel and reported.

One article may contain multiple studies, and the same study may be reported in multiple articles. During title/abstract and full text screening we will screen for eligibility at the article level. The systematic map will include a Microsoft Access database with two separate tables: Articles and Studies (see *Data Coding Strategy*). We will include any article that contains at least one eligible study in the Articles table. If an article containing an eligible study also contains ineligible studies, we will exclude the ineligible studies from the Studies table. Study eligibility will be determined during data coding, and reasons for exclusion of the ineligible studies will be recorded in the Articles table.

Table 2.5 Eligibility Criteria

	Eligibility Criteria	**Exclusion Criteria**
Population	● Any bird species, including domesticated species	
Intervention/ Exposure	● Anthropogenic light sources, including, but not limited to, point sources of light, illuminated habitat, and skyglow	
Comparator	● Same site under different lighting conditions ● Nearby site with similar habitat type, anthropogenic activity, migration density (jf applicable) and weather as the treatment site, at the same time of day ● Documentation of aggregation, mass landing, mortality, or other bird behaviours near artificial light sources without comparator will be included in the map and categorized as incidental reports	
Outcome	● Bird density, including (but not limited to radar observations, visual counts and vocalization counts ● Bird mortality ● Resource consumption (such as crop damage or aquaculture predation) ● Behavioural outcomes directly involving movement through space, including (but not limited to) orientation, flight path, flight initiation, diving and foraging ● Behaviours known to precede movement: overt reaction distance, alert response (e.g. moving head laterally or vertical, crouching) ● Temporal shifts in behaviours involving movement through space or habitat use (e.g. migrating, foraging, reproduction)	● Responses that are not conventionally associated with movement (e.g. hormonal responses) ● Behavioural responses that do not include movement through space (e.g. preening)
Study Design	● BA, CI, BACI, RCT, time-series, post-hoc surveys, or description / anecdote (e.g. documentation of mass mortality event)	

Articles containing eligible studies will be included in the map. Studies must meet one of the eligibility criteria in each category to be included in the map, and studies that meet any of the exclusion criteria will not be included in the map.

Screening Consistency Checking

Two members of the mapping team (CAA and AB) will screen and evaluate the same random subset of 200 articles at the title/abstract level and 20 articles at the full text stage. We will complete the consistency checking exercise at the title/abstract level before beginning screening and repeat the process after 7,000 articles have been screened to maintain confidence in comparable judgement. Although greater consistency might be achieved if two researchers screened every article (Frampton et al. 2017), screening by single authors is necessary to screen such a high number of expected search results (>15,000). We will measure consistency of eligibility decisions between the researchers with the Kappa test. After consistency checking, the mapping team will discuss discrepancies and clarify the eligibility criteria. If the Kappa score is <0.6, CAA or AB will use the new eligibility criteria to repeat the consistency checking exercise on an additional random subset at both screening stages. Changes to the eligibility criteria will be reported in the map. Consistency checking for eligibility screening at the study level will be performed during consistency checking of the data coding strategy (see below).

Study Validity Assessment

We will not critically appraise overall study validity. The heterogeneity in study design, populations, interventions/exposures, and outcomes included in the scope of the map does not support consistent criteria for evaluating studies. However, study design will be categorized as BACI, BA, CI, CI-rotating, behavioural assay, habitat/resource selection, or incidental report. Description of the study methods and replicates will be recorded to aid in identifying subtopics that may support systematic review.

Data Coding Strategy

The systematic map will include a Microsoft Access database with metadata about each article and study, as outlined in Table S2.1 (Appendix A, Additional File 4). We will extract a broad range of metadata, including treatments, effect modifiers (e.g. weather, ambient light, habitat, temporal variables etc.), outcomes measured, and outcome measurement methods. Table S2.1 (Appendix A, Additional file 4) lists the metadata that will be included in the Articles table in the database, and Table S2.2 (Appendix A, Additional file 4) lists metadata included in the Studies table. Changes to these categories and variables will be reported in the systematic map. The database will have search and filter functions to identify studies with any combination of category values.

During full text data extraction, any metadata that cannot be obtained will be coded as "UA" (unattainable). Any metadata category that is not applicable to a study will be coded as "NA" (not applicable). Studies for which full text is not available after contacting the author will be included in the database, with the category *Full Text Available* coded as "No" and all metadata which is not available in the abstract will be coded as "UA."

Data Coding Consistency Checking

To ensure that data are being extracted in a consistent and repeatable manner, data for at least ten studies will be extracted by two researchers (AB and CA) and compared to check consistency. If any inconsistencies occur, the mapping team will discuss the discrepancies and provide additional specifications in the *Description* columns of the Articles and Studies tables if necessary. These additional specifications will be recorded and reported in the systematic map.

Study Mapping and Presentation

We will publish the database generated by the systematic map as an additional file to the published manuscript in the form of a Microsoft Access database. Both the Articles and Studies tables will also be available as Microsoft Excel files. We will present the data so that users that have basic familiarity with Microsoft Excel can use simple filters to explore the product of the systematic map.

The narrative report, supported by heat maps, will describe the volume and key characteristics of the evidence base. The report will identify subtopics that require further primary research (knowledge gaps) and subtopics that may have been sufficiently studied to allow a systematic review (evidence clusters). We will describe the number and study design of studies pertaining to the following three subtopics:

- How does artificial light associated with illuminated anthropogenic structures affect bird movement or aggregation?
- Are light-based deterrents effective at deterring birds?
- How does artificial light affect bird density or habitat use?

Additional subtopics may be identified through the course of producing the systematic map. We will describe the following sources of heterogeneity among studies within each subtopic: light characteristics (e.g. wavelength, intensity, direction, and flashing pattern), environmental variables (e.g. weather variables, temporal variables, moon phase, land/freshwater/ocean), and population characteristics (e.g. species, bird activity during intervention/exposure, domestication status, migratory status).

By identifying knowledge gaps evidence clusters, describing the comparability of outcomes measured within each subtopic, and identifying stakeholder interest, we will provide critical information that we and other authors may use to identify systematic review topics and guide primary research. The relative number of studies, excluding incidental reports, for these subtopics and sources of heterogeneity will be visualized as heat maps and narratively described. Subtopics investigated by relatively few studies will be listed as knowledge gaps, while those represented in the greatest number of studies will be listed as evidence clusters. We anticipate that a lack of comparable outcomes across studies will be a barrier to systematic review. Within each of the subtopics, we will characterize the outcomes measured (e.g. bird density, mortality, qualitative flight path, alert response) to provide information on whether studies can be systematically compared and encourage greater standardization of measurement in future. This narrative report, together with feedback from surveyed stakeholders, will help inform the choice of subsequent subtopics for systematic review and/or meta-analysis.

Declarations

Ethics approval and consent to participate

The authors consulted with the University of Alberta Research Ethics Office and determined that no ethics approval is required for this study.

Consent for publication

Not applicable.

Availability of data and materials

Not applicable.

Competing interests

The authors declare that they have no competing interests. No member of the mapping team will be involved screening or extracting data from a study on which he or she is an author.

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Authors' Contributions

CA, AB, CCS, and EFJ collectively identified the topic for the systematic map and developed the search and data extraction strategies. All authors contributed to the development of the stakeholder engagement strategy. CA wrote the protocol manuscript with significant contributions from AB, CCS, and EFJ. EB also edited the protocol and advised in the development of the database. All authors agreed on the final version of the protocol.

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Chapter 3. The effects of artificial light on bird movement, habitat selection, and distribution: a systematic map

Abstract

Background

Artificial light is ubiquitous in the built environment with many known or suspected impacts on birds. Birds flying at night are known to aggregate around artificial light and collide with illuminated objects, which may result from attraction and/or disorientation. In other contexts, birds are repelled by light-based deterrents, including lasers and spotlights. Artificial light can also change birds' perceptions of habitat quality, resulting in selection or avoidance of illuminated areas. Studies documenting aggregation, deterrence, and habitat selection are typically considered separate literature bodies, but they actually study a common set of populations, interventions/exposures, and responses. Our systematic map provides a comprehensive, searchable database of evidence of the effects of artificial light on bird movement and distribution, increasing both the quantity and diversity of studies that are accessible for further comparison and synthesis. We identify and describe the evidence available for four secondary questions relevant to conservation or management: aggregation/mortality at structures with artificial lights, evidence that light attracts and/or disorients birds, light-based deterrent efficacy, and the influence of continuous illumination on habitat selection.

Methods

Using the principles of systematic reviews and methods published in an earlier protocol, we conducted an extensive and interdisciplinary literature search. We searched multidisciplinary citation indices as well as databases and websites specific to conservation, pest management, transportation, and energy. In our map, we included all studies reporting eligible populations

(birds), interventions/exposures (artificial light), and outcomes (movement through space, behaviour preceding movement, or distribution). We evaluated the quantity of available evidence based on meta-data fields related to study context, population traits, light source characteristics, and outcome variables. We used these meta-data to identify relevant evidence for each secondary question and describe aspects of our secondary questions that may support reviews (evidence clusters) and others that require more research (knowledge gaps).

Review Findings

We manually screened 26,208 articles and coded meta-data for 490 eligible studies in a searchable database, organizing the literature to facilitate future reviews and evidence-based management. Much of the evidence was concentrated in particular locations (Northern hemisphere), taxonomic orders (*Passeriformes, Charadriiformes*, and others), and light wavelengths (red and white). We identified 56 distinct response variables and organized them into 3 categories (behaviour, distribution, and avian community), showing the diversity in bird responses to light.

Conclusions

Our database can be used to answer the secondary questions we identified and other questions about the effects of artificial light on bird movement and resulting changes to distribution. There may be sufficient evidence for a review of the weather and lunar conditions associated with collisions, which could help identify nights when reduction of artificial light is most important. Further experiments should investigate whether specific types of light can reduce collisions by increasing the detectability of structures with artificial lights. The efficacy of lasers as deterrents could be evaluated through systematic review, though more studies are needed for UV/violet lasers. To reduce the impacts of outdoor lighting on birds, research should investigate how spectral composition of white light influences bird attraction, orientation, and habitat selection.

Introduction

Artificial light is growing worldwide (Kyba et al. 2017), with diverse biological and ecological impacts (Sanders et al. 2020). Electric light sources have different spectral properties and higher intensities than celestial light, and both electric lighting and anthropogenic flames change the daily, monthly, and annual light cycles under which most organisms evolved (Gaston et al. 2014). Artificial light at night (ALAN) can alter daily activity patterns and affect organismal physiology, particularly hormone levels and stress responses (Sanders et al. 2020). In some species, ALAN elicits positive phototaxis (Voigt et al. 2017; Kim et al. 2019) or interferes with orientation and navigation (Wiltschko et al. 1993; Price et al. 2018), limiting dispersal (Degen et al. 2016) and changing broad scale distributions (McLaren et al. 2018). Phototaxis can lead directly to mortality in sea turtles (Stanley et al. 2020), insects (Kim et al. 2019), and fledgling seabirds (Rodríguez et al. 2017), and may have sublethal impacts that are more difficult to quantify (McLaren et al. 2018). ALAN can also affect habitat selection (Santos et al. 2010; Price et al. 2018; Ditmer et al. 2020) and population metrics including abundance (Hölker et al. 2015; Davies et al. 2017; Grubisic 2018) and reproduction (Kim et al. 2019), potentially affecting population trajectories (Yoon et al. 2010; Wilson et al. 2018; Boyes et al. 2020). The strength and direction of the effects of ALAN varies widely among species, creating imbalances that disrupt trophic relationships and pollination networks (Davies et al. 2012; Minnaar et al. 2015; Bennie et al. 2015; Knop et al. 2017; Parkinson et al. 2020). Most research has focused on artificial light at night, but daytime artificial lighting can also have ecological impacts and management applications if it: (a) illuminates places that are otherwise dark (Mann et al. 2002);

(b) uses wavelengths that are lethal or harmful to particular species (Hori et al. 2014); or (c) creates a novel stimuli that may act as an attractant or activate an organisms' anti-predator response (e.g. light-based deterrents) (Blackwell 2002).

For birds, most well-known effects of artificial light occur during nocturnal migration, when birds are frequently observed aggregating around or colliding with structures with artificial light, such as communication towers and their associated guy wires (Gauthreaux and Belser 2006; Longcore et al. 2013). Birds aggregate around beams of light projected into the sky, as seen at ceilometers and at the September 11th Memorial, diverting, delaying, and sometimes grounding them during migration (e.g. Greene 1962; Van Doren et al. 2017). Groundings have been documented extensively for fledgling seabirds at coastal light sources (Rodríguez et al. 2017). These aggregations present a conservation concern because artificial light has been associated with all major sources of collision mortality: buildings and windows, transmission lines, roads, and communication towers (Loss et al. 2015).

The proximate and ultimate causes of these aggregations remain unclear. Many authors attribute these aggregations to birds preferentially flying towards light sources, which would suggest attraction to them (Troy et al. 2013; Van Doren et al. 2017). Even if they do not preferentially fly towards light sources, birds may be unwilling to leave an illuminated area once they encounter it in their flight path, a phenomenon called capture (Graber 1968; Larkin and Frase 1988; Gauthreaux and Belser 2006). Attraction could be caused by an overstimulation of the visual system (Verheijen 1985). Artificial light becomes polarized when reflected off of asphalt surfaces, which may attract waterbirds who mistake the asphalt for water and become injured or stranded (Horváth et al. 2009). This interpretation assumes that birds see polarized light, which is controversial (Muheim 2011). Additionally, birds may fly towards light sources to increase visibility during flight or enhance the chances of detecting predators.

Most authors agree that birds aggregating around light sources are disoriented; they have lost the ability to select and maintain a certain direction (Chernetsov 2016). Artificial light has the potential to disrupt each of the three primary mechanisms of compass orientation in migratory birds: solar, stellar, and magnetic. Birds use the position of the sun to orient during the day and at dusk, taking the time-of-day and day-of-year into account (Helbig 1991; Chernetsov 2016). Clock-shift experiments have shown that some birds orient in the wrong direction when exposed to daylight periods shifted by several hours, even when daylength matches the local photoperiod (e.g. Helbig 1991; Wiltschko and Balda 1989; Baldaccini and Bezzi 1989). It is unknown whether outdoor lighting causes birds in the wild to perceive clock-shifts of sufficient magnitude to disorient them. Artificial light may also interfere with the stellar compass, which forms when young birds identify the center of celestial rotation during their first spring and learn to use constellations to orient north and south (Emlen 1970; Chernetsov 2016; Foster et al. 2018). There is individual variation in which and how many stars they require to orient (Emlen 1967). The night sky birds encounter during migration could be very different than the stellar patterns they learned if skyglow levels change or increasing numbers of satellites move across the night sky, as is expected within the next decade (McDowell 2020; Lintott and Lintott 2020; Venkatesan et al. 2020). During magnetic compass orientation, a radical-pair process in the retina allows birds to detect the inclination of the earth's magnetic field and specific types of artificial light interfere with this ability (Wiltschko and Wiltschko 2019). If artificial light bleaches the rhodopsin in their retina, birds could lose their ability to see relatively dim light coming from the stars and the reflection of dim celestial light off of landmarks (Daw 2012).

Disorientation can explain the loss of a linear flight path, though it is unclear why disoriented birds remain near the artificial light sources.

In contrast to the examples of apparent attraction, light has also been used to deter birds from zones of human-wildlife conflict. A better understanding of deterrent efficacy is necessary to prevent millions of dollars in damage to crops and aircraft (Allan and Orosz 2001; Montràs-Janer et al. 2019). Birds are assumed to respond to approaching vehicles as they would to a predator (Frid and Dill 2002), and artificial light is used to increase the detectability and perceived risk of the vehicle, increasing detection, alert and flight initiation distances (Blackwell and Fernandez-Juricic 2013; Blackwell et al. 2016). To elicit an avoidance response without an approaching object, light-based deterrents must create the illusion of risk that outweighs the benefits of using a resource (e.g. food). Deterring birds can be especially challenging when there is no immediate risk to the bird (e.g. roost trees in cities), the birds may not perceive the risk (e.g. toxic tailings ponds), or there are significant attractants (e.g. aquaculture ponds). If non-lethal deterrents fail, continued conflict may result in lethal management strategies. Ultimately, interventions to reduce bird attraction to artificial light or increase bird deterrence using light-based interventions have the same goal – to change bird movement and distribution.

Understanding how light changes bird distributions is important because it is often the goal of interventions using or reducing artificial light, but it is also sometimes the metric by which the ecological impacts of exposure to artificial light are measured. Bird distributions result from habitat selection, the process of choosing resources through a series of innate or learned behavioural decisions (Hutto 1985). Studies of bird distributions, including population density or locations of individuals, are often used to infer habitat selection and identify important habitat components in conservation planning under the assumption that species have evolved to select higher quality habitat (Jones 2001; Johnson 2007). Artificial light can influence habitat quality in diverse ways that include changes to diel activity patterns (Dominoni and Partecke 2015; Amichai and Kronfeld-Schor 2019), hormone production (Zhang et al. 2019), cognitive function (Taufique et al. 2019; Moaraf et al. 2020), and nestling development (Raap et al. 2016b, a; Grunst et al. 2020). Artificial light can also change the relative abundance of bird prey and predators (Canário et al. 2012; Borchard and Eldridge 2013; Owens and Lewis 2018), affecting the chances of survival and reproduction. Even when artificial light seems to increase bird abundance or use of illuminated areas, there may not be corresponding increases in reproductive success, particularly in human-modified landscapes (Bock and Jones 2004). Habitat selection may also be driven by innate attraction to or avoidance of light (Gilroy and Sutherland 2007). Birds may adequately perceive some impacts of artificial light on habitat quality (e.g. changes to prey abundance) and respond with selection decisions that improve fitness, while other impacts could be more difficult for both birds and human researchers to perceive (e.g. increased stress hormone levels in nestlings under artificial illumination; Grunst et al. 2020). Each of these elements of habitat selection – attraction, deterrence, and perception of habitat quality – involves a series of cognitive processes that cannot be directly observed as outcome variables but may be inferred based on changes to movement or distributions. Providing the evidence for these inferences drives the primary question in our systematic map: *How does artificial light affect bird movement and distribution?*

Large bodies of research address two aspects of how artificial light affects bird movement and distribution: collision mortality of nocturnal migrants (e.g. Poot et al. 2008; Gehring et al. 2009; Van Doren et al. 2017) and bird deterrence from zones of human-wildlife conflict (e.g. Andelt et al. 1997; Blackwell et al. 2012; Cassidy 2015). More recent studies use bird distributions to estimate the ecological impacts of ALAN on birds (e.g. Arai et al. 2004; de Molenaar et al. 2006). These literature bodies are typically synthesized separately (e.g. Gauthreaux and Belser 2006; Gorenzel and Salmon 2008), despite shared emphases on bird movement and distribution. Evidence from each body of research is directly relevant to the others. For example, light-based deterrents that reduce the number of birds in zones of human-wildlife conflict could also reduce collision mortality of nocturnal migrants. Through our extensive literature search, we found and included in our map additional bodies of research that studied bird movement and distribution in response to artificial light. We sought to combine all the available evidence from multiple literature bodies to increase both the quantity of evidence available to inform review or management decisions and the diversity of species and light characteristics for which evidence is available.

Stakeholder Engagement

Informal conversations with stakeholders from industries, government agencies, and non-profit organizations confirmed that this topic is relevant in many fields. We developed a questionnaire for stakeholders to inform our search strategy, identify secondary questions of particular importance, support map interpretation, and guide subsequent systematic reviews and primary research (Appendix A, Additional file 1). Ten stakeholders responded to our questionnaire, helping us to expand our literature search and identify secondary questions of particular importance. Stakeholders included two academic researchers, four researchers or managers at government organizations, two non-profit leaders, and two industry stakeholders. The diversity of stakeholders was reflected in the broad range of topics identified as important, including the efficacy of deterrents, the contribution of ALAN to bird-building collisions, and the ecological impacts of artificial light in bird breeding and foraging habitat. All stakeholders were professional contacts of the authors, or were referred to us by other stakeholders who completed the survey, resulting in geographic bias, with nine of the ten stakeholders based in North America. We reached out to five additional stakeholders who did not respond. All stakeholders surveyed indicated that they were interested in how birds' behavioural responses to light are affected by light characteristics (e.g. wavelength, intensity, and direction). Future systematic reviews should engage in further stakeholder engagement to determine the level of interest in the evidence clusters we have identified.

Methods

This systematic map follows CEE guidelines (Pullin et al. 2018) and ROSES reporting standards (Haddaway et al. 2018) (Appendix B, Additional file 1 *ROSES form*).

Deviations from the protocol

We altered our secondary questions to identify relevant studies based on PE/ICO elements. In order to increase the number of unique search results in our Google Scholar search, we used four search strings instead of the two written in our protocol. We used the program Publish or Perish (Harzing 2017) to save our Google Search results as .csv files. We changed our method for selecting reviews for bibliographic checking to identify reviews that focused on birds, artificial light, and one or more of our secondary questions. We added details to our eligibility criteria to promote transparency and consistency. We altered some of our metadata fields and codes to accommodate the diversity of studies included in the map. Records of these alterations and the final coding fields are listed in Appendix B Additional file 11 (*Data coding fields)*. Volunteers assisted with data coding. We further explain these changes to our protocol in the relevant sections below.

Searching for Articles

We did not apply any document type restrictions to our search. All searches were conducted in English in Google Chrome using incognito mode. Although we did not include language restrictions in the database searches, we included only articles written in English. As described in our protocol (Adams et al. 2019), we compiled a list of 78 articles representative of the diverse studies that were eligible for inclusion in our map ("benchmark articles") and created a search strategy that found all of these articles.

Database, Citation Indexing Service, and Website Searches

We used a search string consisting of population and intervention/exposure components of the primary question to search databases and citation indexing services. In the Web of Science Core Collection and in the Web of Science Zoological Record, we used the search string (*TS = *Bird* OR Avian OR Ave$)* AND (*TS = Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$)*. As outlined in our protocol (Adams et al. 2019), when searching for articles indexed without abstracts or keywords in the Web of Science Core Collection we expanded our population search string to include all English common family names (Appendix B, Additional file 2 *WOS search strategy*). We pre-screened the Web of Science search results to exclude articles that only used our intervention/exposure search terms in common irrelevant phrases (e.g. in light of, comes to light, or light-level geolocator), listed in Appendix B Additional file 2. A complete explanation of this strategy and the macros used to implement it are provided in Appendix B Additional files 2 and 3 (*WOS search strategy* and *WOS search records*). This strategy ensured that we found all benchmark articles indexed in Web of Science Core Collection or in Web of Science Zoological Record.

We also searched the following additional databases: Proquest Dissertations and Theses Global, Open Access Theses and Dissertations, Conservation Evidence, Crop Protection Compendium, Tethys Knowledge Base, Artificial Light at Night (ALAN) Research Literature Database, NWRC Staff Publications, and Internet Center for Wildlife Damage Management, and Environmental Studies Program Information System (Appendix B, Additional file 4 *Database search records*). We modified our search string to fit the format of each database (Appendix B, Additional file 4). Finally, we searched the 18 websites that we identified in our protocol, using a combination of hand searching and built-in search functions on the website (Table S3.1, Appendix B, Additional file 12 *Supplementary tables and figures*). We used Google to search within the websites that were too large to feasibly manually check every page (Appendix B, Additional file 5 *Website search records*). All website searches were conducted on August 21, 2019, and were not updated due to time constraints. All Web of Science and specialized database searches were conducted in February or August 2019 and updated in August 2020 (Appendix B, Additional file 4 *Database search records*).

Web-based Search Engines

We searched Google Scholar using Publish or Perish 6 (Harzing 2017) with the following search strings:

1. All of the words: Avian; Any of the words: Light Spotlight Streetlight Headlight Lamp Beacon Beam Ceilometer
2. All of the words: Avian; Any of the words: Laser Strobe Flash Flare Flaring Reflector
3. All of the words: Bird; Any of the words: Light Spotlight Streetlight Headlight Lamp Beacon Beam Ceilometer
4. All of the words: Beam; Any of the words: Laser Strobe Flash Flare Flaring Reflector

We saved the first 1000 results from each search to .csv files (Appendix B, Additional file 6 *Google Scholar search records*). We combined all search results into a single Microsoft Excel spreadsheet, removed duplicates, and uploaded all search results to Rayyan QCRI (Ouzzani et al.

2016) for further screening (Appendix B, Additional file 6). Rayyan QCRI is a free web and mobile app for screening abstracts and titles for systematic maps and reviews. Using the program Publish or Perish caused a deviation from our protocol, but allowed us to retain a record of the Google Scholar search results and import them into Rayyan QCRI for screening. Using the four search strings, instead of the two written in our protocol, increased the number of unique search results.

Assessing search comprehensiveness

We chose one review for each secondary question for bibliographic checking. To select these reviews, we downloaded a list of all articles we had identified as reviews during screening in Rayyan QCRI and determined their relevance to each secondary question based on their titles. We then scored the articles based on the relevance and date of publication (details in Appendix B, Additional file 7 *Bibliographic checking*), giving higher priority to reviews that specifically focused on birds, artificial light, and one or more of our secondary questions. We randomly selected a review among the top scores for each secondary question and identified all eligible articles referenced in each review. When the first review of bird deterrence yielded only two relevant references, we randomly chose an additional review for this exercise. In total, we used five reviews to assess our search comprehensiveness, and we calculated the proportion of references for each review that were found with our systematic search.

Bibliographic checking confirmed that our search strategy found nearly all available evidence for most secondary questions. We found all four eligible references from the two reviews of deterrents (Gilsdorf et al. 2002; Gorenzel and Salmon 2008), all 17 eligible references from the orientation review (Wiltschko et al. 2010), and eight out of 9 eligible references in the review relevant to habitat selection (Leveau 2018) (Appendix B, Additional file 7 *Bibliographic* *checking*). Our search found 26 of the 44 eligible references in the review of aggregation/mortality (Gauthreaux and Belser 2006).

Finding all articles that documented birds aggregating or colliding around any structure with artificial lights (buildings, windows, towers, oil platforms, etc.) would require substantial additional search effort. Two of the 18 missed articles were theses and were only indexed in Open Access Theses and Dissertations. They did not include the terms "bird," "avian," or "Aves" in their titles (Appendix B, Additional file 7 *Bibliographic checking*). However, the studies in these theses were included in the map because our search found peer-reviewed articles reporting these studies. Eight of the 18 missed articles were not indexed in any of the databases we searched. Searching additional databases would not substantially improve the search comprehensiveness because none of these articles were indexed in Scopus and only one was indexed in JSTOR. The remaining eight articles were indexed in the Web of Science Zoological Record, but were not found because they did not include the term "light" or another intervention/exposure term in their topic fields. The shortest search string that could find all of these articles (*TS = (*bird* OR Avian OR Ave$) AND TS = (tower OR migration OR destruction)*) returned 52,459 results, far more than we could feasibly screen.

Article Screening and Study Eligibility Criteria

We used Rayyan QCRI to screen search records from Web of Science, Google Scholar, and Proquest Dissertations and Theses Global. We first screened articles at the title and (if available) abstract level. Any articles excluded at the full text level are listed in Additional file 9 (*Articles excluded at full text,* Appendix B) with exclusion reasons. The remaining specialised databases did not provide an export to .csv function, so they were screened in Microsoft Word if the text could be easily copied. Otherwise, they were screened on the website with the search results pages saved as PDF files. We initially screened using the information available on the webpage, recorded any articles that were potentially relevant, then made full-text eligibility decisions and recorded reasons for excluding any article (Appendix B, Additional file 9). CAA and AB performed all screening, and neither screener authored any articles considered for inclusion/exclusion.

As we screened articles for study eligibility, we added details to the eligibility criteria published in the protocol to better define the scope of our map and promote consistency in the eligibility determinations (Table 3.1). We included further justifications for these eligibility criteria in Additional file 8 (*Explanation of eligibility criteria,* Appendix B). In accordance with our original criteria, we excluded specific interventions/exposures that did not involve an artificial light source, such as studies of reflected or filtered daylight. This necessarily excluded some studies of bird hazards (e.g. windows), deterrents (e.g. mylar, streamers, mirrors), and orientation (e.g. filters on natural daylight).

For interventions/exposures that are so broadly applied as to make mapping their use prohibitive, we required that they compared bird response under artificial light of different wavelengths or intensities. This criterion excluded laboratory studies using only broad-spectrum (i.e. white) light of a single intensity and a single photoperiod. We included laboratory studies that compared, within the same study, bird responses to light of varying intensities, different spectral compositions, or different photoperiods, providing that they also studied an eligible outcome.

In making eligibility decisions about outcomes, we included outcomes documenting movement through space or behaviours that directly precede movement (e.g. orientation or alert response). We excluded general locomotor activity (e.g. perch-hopping or overall activity levels). We excluded studies testing birds' ability to see specific wavelengths or using light as a visual cue to elicit a trained response. We excluded outcomes involving temporal changes in daily or annual movements (e.g. timing of entering/exiting nest boxes or migration), timing of daily activities (e.g. timing of feeding, sleeping, etc.), or circadian rhythms. We excluded studies of bird foraging behaviour that did not involve movement through space or changes to distribution (e.g. time spent foraging or changes to foraging strategies). We included incidental reports of nocturnal foraging under artificial lights surrounded by dark habitat, while recording the comparator as *None*.

Two members of the map team (CAA and AB) conducted consistency checking by screening the first 200 articles at the title/abstract level in Rayyan QCRI (Appendix B, Additional file 10 *Consistency check records*), resulting in a Kappa score of 0.71. We clarified the eligibility criteria and repeated the consistency checking on an additional 200 articles, achieving 100% agreement. CAA screened the remaining articles. In cases where study eligibility was unclear, CAA consulted with the mapping team and defined additional eligibility criteria. After CAA screened 7000 articles, AB and CAA repeated the consistency checking exercise. To correct for possible bias in the order in which the articles appeared on Rayyan, we screened a random selection of 200 articles from all Web of Science search results. We disagreed on the eligibility of only one article, resulting in a Kappa Score of 0.93. After further discussion, we included this article at the title/abstract stage, but ultimately excluded it at the full text level. In total, we conducted consistency checking on 400 (1.9%) out of 21,150 articles screened on Rayyan QCRI at the Title/Abstract level (including the updated search).

Two members of the map team (CAA and CCSC) conducted consistency checking on 20 randomly selected articles at the full text screening level (Appendix B, Additional file 10

Consistency check records. After disagreeing on 7 articles, we discussed and refined the eligibility criteria until we agreed on all eligibility decisions. We employed an external screener, NL, who had not previously worked on the map to ensure our eligibility criteria were clear to a naive screener. After reading the eligibility criteria, NL made inclusion decisions for the 20 randomly selected articles. NL agreed with CAA and CCSC for 19 out of 20 articles, resulting in Kappa score of 0.77. After further discussion, NL agreed that the article in question should be excluded. In total, we performed consistency checking on 20/819 articles (2.4%) screened at the full text level. CAA screened the remainder of the articles.

Table 3.1 Study Eligibility Criteria

	Eligibility Criteria	Exclusion Criteria
Population	● Any bird species, including domesticated species	
Exposure/Intervention	● Anthropogenic light sources, including, but not limited to, point sources of light, illuminated habitat, and skyglow ● Gas Flares	● Reflected daylight (e.g. mylar tape reflectors, windows) ● Filters on natural daylight
Comparator	● Same site under different lighting conditions ● Nearby site at the same time of day with similar habitat type, anthropogenic activity, migration density (if applicable) and weather as the treatment site ● Documentation of aggregation, mass landing, mortality, foraging, or other relevant outcomes near artificial light sources without comparator were included in the map and coded as “No Control”	● Laboratory experiments that using only one intensity or spectral composition of light within the “light” or “dark” portions of the light cycle ● Laboratory experiments that use an artificial photoperiod but do not vary the photoperiod

Outcome	● Bird density or presence/absence, including (but not limited to) radar observations, visual counts and vocalization counts ● Bird mortality ● Resource consumption (such as crop damage or aquaculture predation) ● Behavioural outcomes directly involving movement through space, including (but not limited to) flight path, flight initiation, diving and flushing ● Behavioural response (flushing or immobilization) to spotlights used for capturing birds ● Behaviours known to precede movement: orientation, overt reaction distance, alert response (e.g. moving head laterally or vertical, crouching) ● Documentation of birds foraging under artificial lights ● Habitat use metrics at foraging sites such as feeders (e.g. arrival/departure times, feeder visit rates)	● Responses that are not conventionally associated with movement (e.g. hormonal responses) ● Behavioural responses that do not include or directly precede movement through space (e.g. preening, dust-bathing, sleep behaviour, vocalizing) ● General locomotor activity (e.g. perch-hopping or time spent walking) ● Temporal changes in daily or annual activity rhythms (e.g. entering/leaving nest box, migration) ● Changes to timing of activities in laboratory experiments (e.g. feeding, drinking) ● Total feed consumption in laboratory experiments ● Trained responses (e.g. trained to perform a task when a light is on) ● Ability to see specific wavelengths (e.g. mate choice or ability to distinguish objects under varying light conditions) ● Changes to timing in chick provisioning in field studies

Study Validity Assessment

We did not conduct a study validity assessment because the diversity of context, discipline, and study design included in the scope of the map did not support consistent criteria for evaluating studies. To facilitate future assessments of study validity, we described the control and coded the type of control design (e.g. none, Before/After, Control/Impact, gradient – spatial, gradient – temporal), the data collection method (systematic or opportunistic), whether the study was observational or experimental (Appendix B, Additional file 11 *Data coding fields*).

Data Coding Strategy

We found a greater quantity of articles than we expected when writing our protocol, so we altered our data coding strategy in order to complete the systematic map. We hired a research assistant (NL) and engaged twenty-five undergraduate student volunteers to code metadata, each contributing on average 60 hours (over 1500 hours total). Undergraduate students were trained by CAA and typically worked in pairs to read articles and extract metadata while CAA supervised on live video calls. CAA proofread all data coding performed by volunteers, reading the abstracts and methods sections of the articles and confirming that metadata were correct. In articles without methods sections (e.g. lighthouse reports), CAA skimmed the articles to find relevant metadata. Any data coding performed solely by CAA or NL were similarly proofread by a volunteer. Any potential mistakes found by the proofreader were discussed by both readers until an agreement was reached. The questions posed by volunteers during data coding were answered and recorded in the coding instructions (Appendix B, Additional file 11 *Data coding fields*), helping to clarify our coding methods. This spreadsheet also lists and justifies all modifications made to the data coding fields outlined in our protocol. We coded any missing data as unavailable (UA). The large number of studies and metadata fields precluded us from obtaining missing data from the authors.

We conducted two data coding consistency checking exercises. In October 2018, three members of the mapping team (AB, CAA, and SS) coded data from 10 articles selected randomly from all of the articles that were known to the authors at that time. Each article was coded by two readers. Minor inconsistencies that occurred in four of these articles were discussed and corrected. The only inconsistencies were between SS, the undergraduate volunteer, and one of the systematic map authors. In March 2020, CAA and NL performed an additional consistency checking exercise on 10 articles. Some inconsistencies occurred in the “Study Design” category, resulting in the addition of “Behavioural Assay - with control” and “Behavioural Assay - no control” to this field’s codes. As part of training, volunteers demonstrated their skills by correctly coding data on two or three sample articles, but we did not complete a full consistency checking exercise with every volunteer. Instead, we used proofreading strategy described above.

Throughout the systematic map process, we identified diverse outcomes (i.e. response variables) that described bird behaviour, distribution, or community, adding outcome codes as necessary during data coding (Appendix B, Additional file 11 *Data coding fields*). As the number of outcomes grew, we categorized them into subcategories to aid our synthesis. The subcategories for distribution outcomes are straightforward (e.g, bird locations, bird counts, mortality), while the behaviour subcategories require more explanation. Any description of flight path (e.g. velocity, altitude, direction) was included in the subcategory titled *flight path characteristics*. In the subcategory titled *approach or flee response*, we included any outcomes showing bird movement towards or away from light when not in flight (e.g. on the ground or in water). There are other logical subcategories for grouping the behaviour outcomes, and we invite users to find studies with outcomes relevant to their specific questions using the search form in our database.

Community outcomes were not originally included in our PE/ICO framework, but we added community as an outcome category because studies reporting community metrics are relevant to our primary question. They measure the distributions (e.g. presence/absence or relative abundance) of groups of birds (e.g. species or functional groups) and summarise these data using various indices (e.g. species richness or functional diversity). The way in which the distribution data were interpreted determined if the study outcome category was coded as Distribution, Community, or both. If the study reported the presence/absence or abundance of individual species, bird groups, or all birds as one group, we coded the outcome category as Distribution. If a study reported metrics that summarized the number or traits of species present, we coded the outcome category as Community. All but one study with a Community outcome also reported a Distribution outcome.

Data Mapping Methods

Our systematic map is a relational database in Microsoft Access (Appendix B, Additional file 13 *Adams et al 2021 Systematic Map*) and in Microsoft Excel (Appendix B, Additional file 15 *Adams et a 2021 Systematic Map Excel*). The search function in the Access version allows the database to be filtered by any of the coded fields, returning a list of studies that meet the criteria chosen in the search form. In our Review Findings, we examine each metadata category (Context, Population, Intervention/Exposure, Comparator, and Outcome) and describe the quantity of evidence for particular populations, interventions/exposures, and outcomes. For each of our secondary questions, we identified the available evidence based on PE/ICO filters that are relevant to these questions, as we have framed them (Table 3.2). Users of the database may refine these criteria to meet their specific management or synthesis objectives. In our Review Findings, we describe evidence clusters and knowledge gaps for each secondary question.

Relevant evidence for our first question (aggregation/mortality of flying birds) included studies that measure flight path characteristics, collision mortality, or the distribution of birds in flight. We filtered the database to include studies where the bird activity during intervention/exposure was coded as *flying* and the outcome measured was in the *distribution* category or in the *flight path characteristics* subcategory.

We also identified the potential evidence for two possible mechanisms of aggregation/mortality: attraction and disorientation. Evidence suggesting attraction included studies of flying birds that measured any of the following behaviour outcome subcategories: *change in flight direction relative to a light source, capture of birds in flight, modeled flight behaviour based on observations of birds in flight,* or *flight altitude.* We did not include outcomes related to bird distributions as evidence of attraction because a different relative abundance of birds in lit than unlit areas could be due to capture (failing to leave illuminated areas once they encounter them) rather than attraction (preferentially flying towards lights). Evidence suggesting disorientation included any study with outcomes in the subcategory of *orientation behaviour*.

To describe the evidence for our third secondary question, we identified the types of light used for the purpose of deterring birds. We included all studies using these types of light and reporting response variables that could demonstrate deterrence. We included studies of flying and non-flying birds because light is used to deter both flying birds (e.g. during aircraft flight) and non-flying birds (e.g. on airport runways and in agricultural fields). Any outcome in the category *distribution* could demonstrate deterrence if the light treatment reduces bird numbers or bird deaths. Behavioural outcomes in the subcategory *approach or flee response* or the subcategory *alert behaviour* could also demonstrate deterrence, as could any of the *flight path characteristics* outcomes that could suggest attraction (listed above).

Using our broad definition of habitat selection as a process rather than a specific study design, evidence relevant to our fourth secondary question included several type outcomes documenting changes to bird presence, abundance, or other measures of distribution. The evidence included, but was not limited to, studies modeling relative selection probability by comparing the light levels at used to available locations (Lele et al. 2013). We included any studies that measured one of the following outcome subcategories: *preferences*, *bird counts*, *bird locations*, or *presence of foraging birds*. We required studies to include a control treatment, control period, or light gradient in order to demonstrate whether the measured outcome was different in lit than unlit times or places. We only included studies involving continuous illumination, excluding lasers and flashing lights because they are not common in the built environment and are typically evaluated in the context of our third secondary question (deterrents). We excluded studies that only observed birds in flight because flying birds have not settled in a particular location that would demonstrate habitat selection.

Table 3.2 Filters applied for each secondary question and quantity of evidence identified

	Aggregation/ Mortality	**Causes of Aggregation**		**Deterrence**	**Habitat Selection**
		Orientation	**Attraction**		
Population Filters	Bird activity during intervention/exposure = *flying*		Bird activity during intervention/exposure = *flying*		Bird activity during intervention/exposure *≠flying*
Exposure/ Intervention Filters					Continuous/Flashing = *Continuous* AND Deterrent Type ≠ *Laser*
Comparator Filters					Control design ≠ *No Control*
Outcome Filters	Outcome category = *Distribution* OR Outcome subcategory = flight path characteristics	Outcome subcategory = *Orientation behaviour*	Outcome subcategory = *preferences* OR Outcome = Change in flight direction relative to a light source, Capture of birds in flight, Modeled flight behaviour based on observations of birds in flight, Distance of flight path from light	Outcome category = *Distribution* OR Outcome subcategory = Approach or Flee Response or Alert behaviour OR Outcome = Change in flight direction relative to a light source, Capture of birds in flight, Modeled flight behaviour based on observations of birds	Outcome subcategory = Preferences, Bird counts, Bird Locations, or Presence of foraging birds

			source, or flight altitude	in flight, Distance of flight path from light source, or flight altitude	
Number of relevant studies	218	38	25	228	88

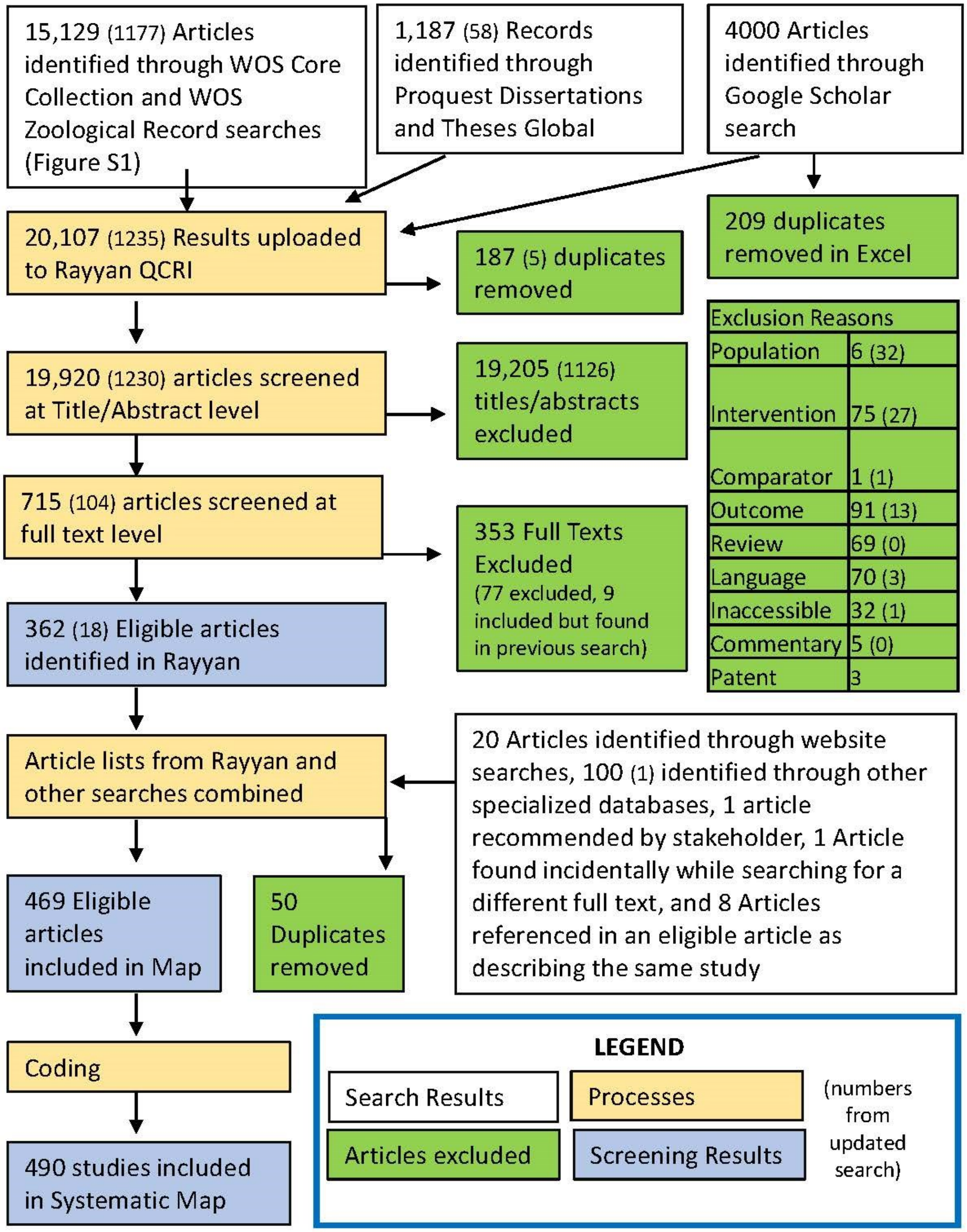
Review Findings

Review descriptive statistics

Our systematic search used multiple steps (Figure 3.1), ultimately resulting in the manual screening of 26,208 records to return 469 eligible articles. The majority of articles (351) came from the comprehensive searches of Web of Science Core Collection and Web of Science Zoological Record (Table 3.3), for which we applied several pre-screening processes (Figure S3.1, Appendix B, Additional file 12 *Supplementary tables and figures*). Specialized databases provided 61 unique articles, with 23 found in the Artificial Light at Night (ALAN) Literature Database, 14 found in Open Access Theses and Dissertations, and 9 found in the Internet Center for Wildlife Damage Management. An additional 10 articles were found on websites and 19 were found incidentally (e.g. recommended by stakeholders or found when searching for the full text of a different article).

We found documentation of bird response to artificial light dating back to 1880 and the number of studies has increased markedly since 1990 (Figure 3.2a). Most studies were conducted in the Northwestern quadrant of the globe (290), and many were also conducted in the Northeastern (129) and Southeastern quadrants (53) (Table S3.2, Appendix B, Additional file 12). We found only 18 studies from the Southwestern quadrant. There were 127 studies involving light that was only turned on at night, 33 during the day only, and 10 at sunset or dusk only (Table S3.3, Appendix B, Additional file 12). Many other studies applied the light treatment at multiple times of day or did not specify when the lights were turned on.

Our interdisciplinary search found studies from many economic sectors with diverse study purposes. The most common sectors were transportation (126 studies) and urban/suburban/rural developments (123) (Table 3.4). Few studies came from the mineral mining or waste management sectors, despite the need to reduce bird numbers at toxic tailings ponds and landfills (Donato et al. 2007; Cook et al. 2008). The majority of studies were conducted to document and/or reduce bird aggregations or mortality (284 studies), while deterring birds (122), monitoring or describing bird migration (66), and documenting birds foraging under artificial light (61) were also common study purposes (Table 3.5).



Exclusion Reasons	
Population	6 (32)
Intervention	75 (27)
Comparator	1 (1)
Outcome	91 (13)
Review	69 (0)
Language	70 (3)
Inaccessible	32 (1)
Commentary	5 (0)
Patent	3

Figure 3.1 Schematic of mapping stages including the search, screening, and coding stages.

Additional information about the number of articles found during each stage of the Web of Sciences searches is provided in Figure S3.1.

Table 3.3 Number of articles found in each search step

Source Type	Captured Articles	Eligible Articles	Unique Articles
Web of Science (Core Collection)	11,331 (1,028)*	136 (14)	136 (14)
Web of Science Zoological Record	6,353 (417)*†	205 (9)	199 (2)
Google Scholar	3,791*	22	19
Proquest Dissertations at Theses Global	1,187 (58)	8 (1)	8 (1)
Specialized Databases	4,734 (132)	100 (1)	60 (1)
Organizational Websites		17	10
Found Incidentally		19	19
	Total: 29,031†		Total: 469

*These represent the number of articles captured after pre-screening with Microsoft Excel Macros (Appendix B, Additional files 2 and 3) and removal of duplicates (Figure S3.1, Appendix B, Additional File 12).

†This is the number of articles captured from the Web of Science Zoological Record before removing articles also found in the Web of Science Core Collection (2555 such articles were removed in the original search, 149 in the updated search). After removing these duplicates, 26,208 articles were screened (21,342 in Rayyan, 4866 on websites or in downloaded documents).

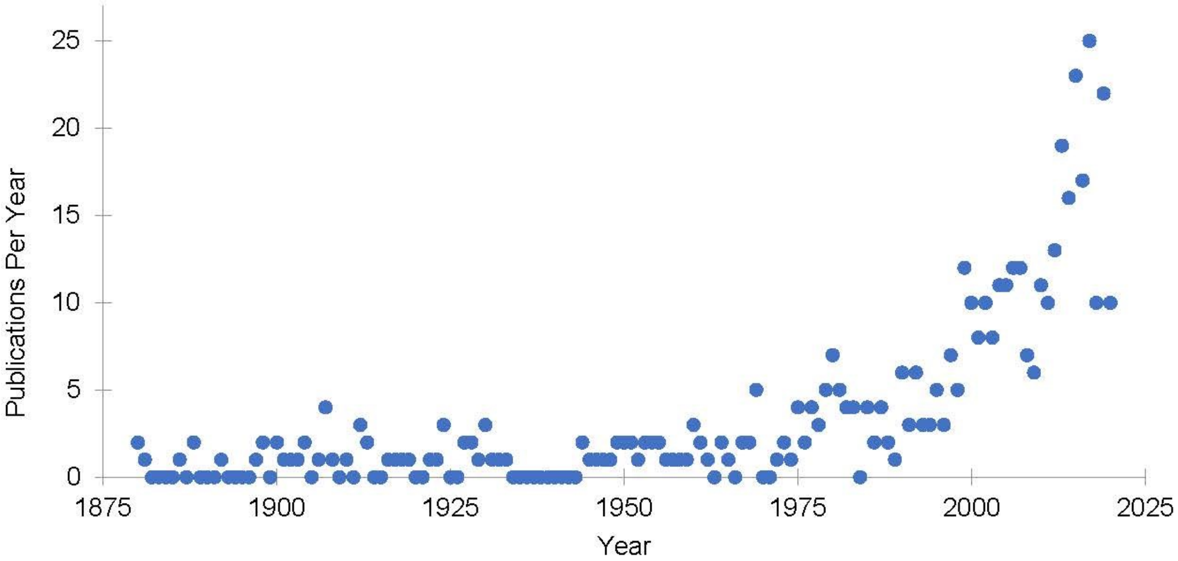
Table 3.4 The number of studies in each economic sector

Sector	Number of Studies
Transportation	126
Urban/Suburban/Rural	123
Laboratory Behavioural Research	56
Wildlife Research	54
Food Production	52
Energy	47
Communication Towers	16
Recreation/Tourism	10
Human-wildlife Conflict - no sector specified	10
Natural Protected Area	8
Military	5
Zoos	4
Forestry	2
Port or Harbour	2
Waste Management	2
Mineral Mining	1

Table 3.5 The number of studies conducted for each study purpose

Purpose of Study	**Number of Studies**
Document and/or reduce bird aggregations or mortality	171
Deter birds	88
Document birds foraging under artificial light at night	47
Test ability to orient under artificial light conditions	40
Study effects of AL on bird distribution or habitat selection	39
Capture or count birds for wildlife research	38
Improve welfare or production of captive birds	36
Monitor or describe bird migration	35
Basic behavioural research	7
Study effects of AL on bird community	4
Document occurrence of a rare species	3
Study weight loss during nocturnal migration	2
Document unusual bird behaviours	2

a) Total number of publications per year



b) Number of publications per decade for the purpose of answering secondary questions

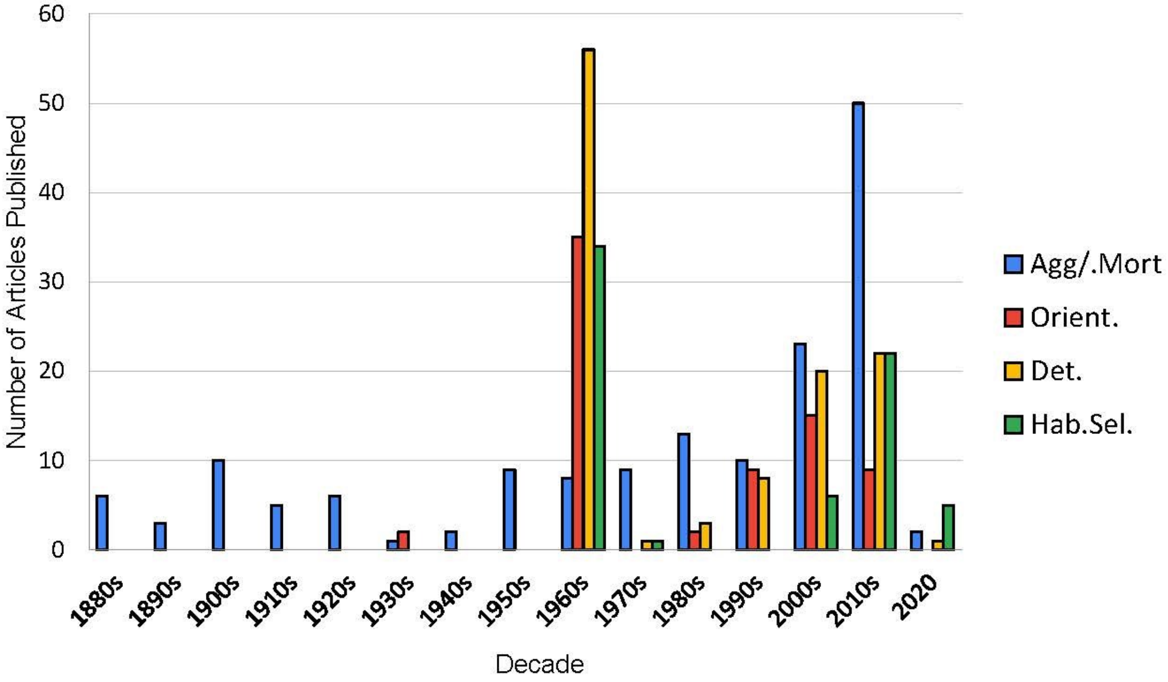


Figure 3.2 Publication count over time

Mapping the quantity of evidence for the primary question

We fulfilled the first objective of our map by providing a database of all available evidence for our primary question regarding the effects of artificial light on bird movement and distribution. In this database (Appendix B, Additional files 13-15), we brought together literature from many research bodies that study relevant populations (birds), interventions/exposures (artificial light), and outcomes (movement and distribution). Others can easily search and filter this database with metadata related to PE/ICO elements to find evidence for specific management questions and future systematic reviews. The metadata and narrative descriptions provided for each study allow the user to quickly evaluate the relevance of each study to their question.

We provide three versions of the systematic map database. The Microsoft Access database (Appendix B, Additional file 13) can be opened and edited using Access, and the Microsoft Access ACCDE Database (Appendix B, Additional file 14) can be opened using the freely available program Microsoft Access Runtime (Microsoft). Both versions of the database can be browsed using the VIEW form or searched using the SEARCH form, which produces a list of studies that meet metadata criteria specified by the user. We also provide a Microsoft Excel version of this database (Appendix B, Additional file 15), but we recommend using the Access version if possible to more easily search for studies and view the metadata fields.

Population

Broad reviews could target the most well-studied taxonomic orders. Of the 40 avian orders in IOC World Birds List (IOC World Bird List), 26 were included in the map at least once (Table 3.6). *Passeriformes* (perching birds) was by far the best studied order, followed by *Charadriiformes* (shorebirds and relatives) and *Procellariiformes* (petrels, shearwaters, and albatrosses). Migrating birds were recorded in 188 studies, with an additional 29 studying fledgling seabirds migrating to sea and 22 studying a mix of migrating and non-migrating birds (Table S3.4, Appendix B, Additional file 12 *Supplementary tables and figures*). Most studies (377/490) involved wild species in the wild, while 81 studied wild species in captivity and 32 studied domesticated species (Table S3.5, Appendix B, Additional file 12).

Knowledge gaps may limit the application of these reviews for particular populations. Fourteen avian orders were never studied (Table S3.6, Appendix B, Additional file 12). Three of these orders are endemic to South America (e.g. *Tinamiformes, Otidiformes,* and *Musophagiformes*). More information on these orders may be available in Spanish or Portuguese, but our map only includes articles written in English. With only 18 studies conducted in the southwest quadrant of the globe (Table S3.2, Appendix B, Additional File 12), there is limited knowledge of how neotropical migrants respond to light during the non-breeding season, an important and understudied part of their life cycle (Calvert et al. 2009) that can be key to increasing our understanding of bird collisions with buildings.

Table 3.6 Orders included in studies relevant to the primary question and each secondary question

Order	**Description**	**Primary Question**	**Aggregation/ Mortality**	**Disorientation**	**Attraction**	**Deterrence**	**Habitat Selection**
Passeriformes	Perching birds	260	143	33	14	120	36
Charadriiformes	Shorebirds and relatives	87	50	0	6	56	9
Procellariiformes	Tube-nosed seabirds	63	54	0	3	22	6
Galliformes	Landfowl	44	7	2	0	18	22
Anseriformes	Waterfowl	43	14	0	3	37	4
Gruiformes	Diverse terrestrial and marshbirds, including rails, cranes, and others	29	20	0	1	23	0

Pelecaniformes	Ibis, herons, pelicans, and others	23	11	0	0	11	2
Columbiformes	Pigeons	18	6	3	0	6	3
Falconiformes	Falcons	16	7	0	1	5	3
Suliformes	Frigatebirds, cormorants, anhingas, and boobies	14	7	0	3	10	1
Caprimulgiformes	Nightjars	14	5	0	0	2	4
Accipitriformes	Raptors including new world vultures	14	7	0	2	6	3
Strigiformes	Owls	12	5	0	0	3	5
Podicipediformes	Grebes	9	6	0	0	6	0
Sphenisciformes	Penguins	8	1	0	0	2	7
Coraciiformes	Kingfishes and allies: rollers, todies, motmots, bee-eaters	6	3	0	0	1	1
Apodiformes	Owlet-nightjars, treeswifts, swifts, hummingbirds	5	0	0	0	0	1
Cuculiformes	Cuckoos	4	3	0	0	1	1
Gaviiformes	Loons	3	1	0	0	3	0
Ciconiiformes	Storks	3	1	0	1	1	0
Piciformes	Woodpeckers and allies	2	1	0	0	0	1
Apterygiformes	Kiwis	2	0	0	0	0	2
Pterocliformes	Sandgrouse	2	0	0	0	1	1
Psittaciformes	Parrots	2	0	0	0	0	2
Rheiformes	Rheas	1	0	0	0	1	0
Bucerotiformes	Hornbills, hoopoes, wood hoopoes	1	1	0	0	0	0

Order descriptions based on the IOC World Bird List (IOC World Bird List).

Exposure/Intervention

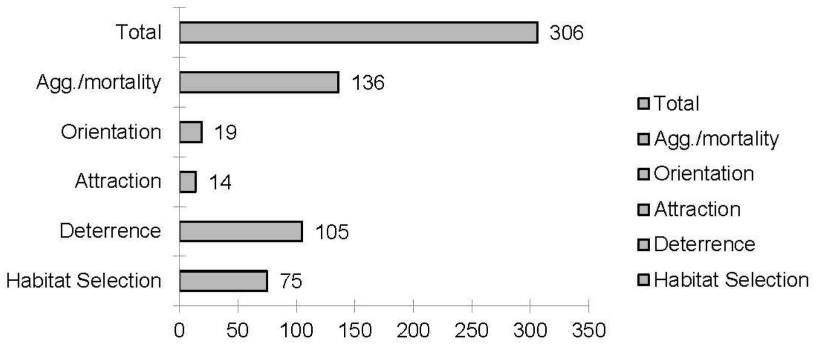
There may be enough evidence to compare interventions/exposures that used well-studied wavelengths and flashing patterns and combinations of these two variables. The majority of studies (272/490) of continuous light were white or presumed white (described by study authors as white or presumed by the mapping team to be white based on context) (Figure 3.3, Table 3.7). Continuous light was well-studied for other wavelengths visible to birds, including red (61), green (55), and blue (29). Only white and red were studied in more than 10 studies using flashing lights, while green, blue/green, and blue had 6, 6, and 8 studies, respectively. Rotating lights (a continuous light whose restricted visual angle rotates on a horizontal plane) were only included in 19 studies, but were likely also present in many of the 36 studies at lighthouses that were coded as UA (unavailable) because the text did not specify that the light rotated.

When identifying which light characteristics are important to study, it is important to consider the avian visual system. Orange, yellow, and ultraviolet (UV) or violet wavelengths were rarely studied (Table 3.7). UV and violet wavelengths are particularly important to consider for birds because some (but not all) bird species have a cone photoreceptor with peak sensitivity in the UV portion of the spectrum (Wiltschko et al. 2010). These wavelengths were only studied 13 times, and flashing UV or violet light was only studied three times. Different lamp types have distinct spectral compositions and flicker rates (Seymoure et al. 2019b). Birds have different spectral sensitivity and temporal visual resolution than humans (Inger et al. 2014; Kelber 2019), so lamp types that all appear white to humans can appear distinct to birds (Inger et al. 2014; Seymoure et al. 2019b). Only two studies using continuous light reported the flicker rate (Briot 2005; Goller et al. 2018). Among the studies reporting lamp type, there were many using LED, incandescent, halogen, or fluorescent bulbs for white lights (Table 3.8), providing an opportunity for review. A review comparing these lamp types could consider only white lights to avoid confounding lamp type with wavelength. Other lamp types that are commonly used for outdoor lighting were rarely recorded in our database, including Metal Halide, Mercury-Vapor, and Sodium Vapor (Elvidge et al. 2010), but were likely common in the 283 studies that did not report lamp type.

Outcome

The fifty-five distinct outcome variables identified in our map demonstrate the diverse ways in which artificial light can change bird movement through space and distribution, with variety far beyond what we anticipated in our own systematic map protocol. We provide the first organized view of this literature, grouping outcomes into three categories (behaviour, distribution, and community) and eleven subcategories. This organization provides an easy way for map users to find evidence that documents particular outcomes or groups of outcomes. Within the behavioural outcome category, there were four subcategories showing distinct types of movement or behaviours preceding movement and each subcategory includes several outcome variables (Table 3.9). Outcomes related to behaviour or distribution were each recorded in well over 200 studies, while only five studies recorded the impact of light on bird communities. In the behaviour category, flight path characteristics, approach or flee response, and orientation were well studied, while studies documenting alert behaviour were relatively rare. All subcategories in the distribution category contained at least 25 studies. While outcomes related to behaviour and distribution were well-studied, there is not enough evidence to inform conservation initiatives targeting avian community outcomes, such as species richness or functional diversity.

a) Number of studies testing broad-spectrum white light



b) Number of studies testing each wavelength

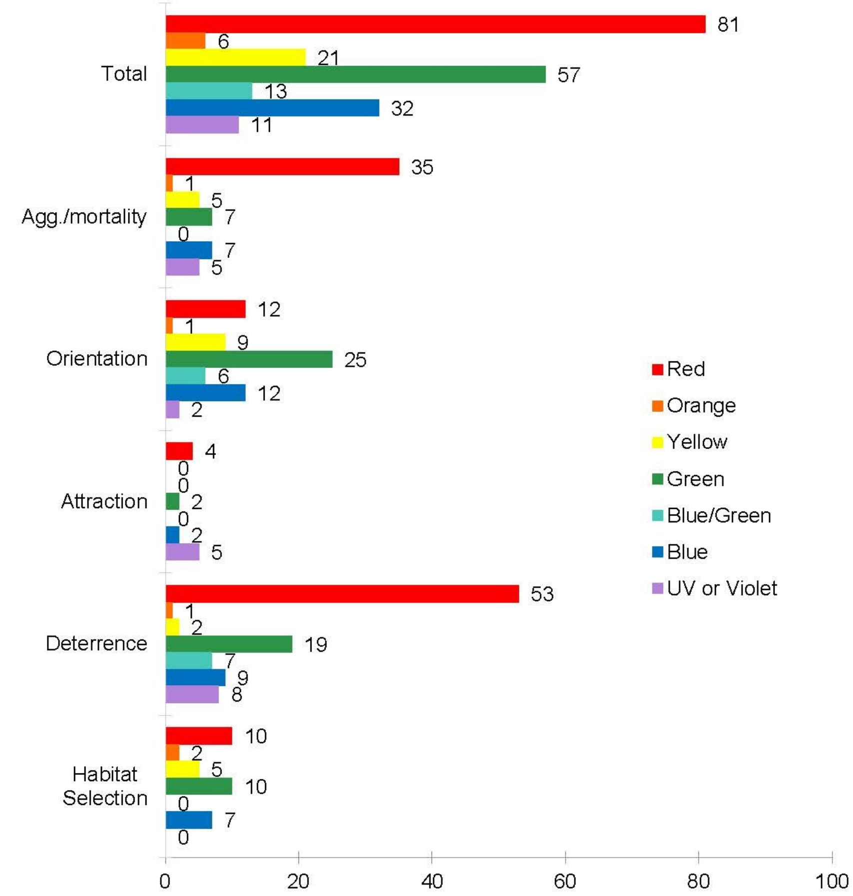


Figure 3.3 Number of studies testing each wavelength of light in the evidence base and for each secondary question

For wavelengths that were used in fewer than 5 studies (green/yellow, yellow/orange, and indigo), we recategorized them as the longer wavelength (yellow, orange, and blue) for this table and for all subsequent tables and figures. Wavelengths described by the article authors as turquoise were counted as Blue/Green.

Table 3.7 Heat map showing the number of studies including interventions/exposures with each light wavelength, flashing pattern, and combinations of wavelengths and flashing patterns.

Wavelength	**Total Number of Studies**	**Continuous**	**Flashing**	**Rotating**	**Simultaneous flashing and continuous lights**	**Unavailable**
White or Presumed White	309	272	32	14	9	11
Infrared	1	1	0	0	0	0
Red	86	61	19	7	15	3
Orange	6	6	1	0	0	0
Yellow	22	20	2	0	0	0
Green	59	55	6	0	0	0
Blue/Green	13	13	6	0	0	0
Blue	33	29	8	0	0	1
UV or Violet	13	9	3	0	2	0
UV+	10	10	0	0	0	0
Flame	10	10	0	0	0	0
Unavailable	92	26	13	6	2	54
	TOTAL	378	57	19	19	67

Blue shading represents the number of studies with each wavelength, from 1(light blue) to 309 (dark blue). Yellow/red shading in columns three through seven represents the number of studies with each wavelength/flashing pattern combination, from 1 (pale yellow) to 61 (red). The *TOTAL* row shows the number of studies with each flashing pattern. The total is less than the sum of the columns because some studies included multiple wavelengths. UV+ treatments added UV wavelengths to broad spectrum white light.

Table 3.8 Number of studies including each lamp type.

Lamp Type	All	White or Presumed White	Aggregation/ Mortality	Causes of Aggregation/Mortality		Deterrence	Habitat Selection
				Attraction	Orientation		
Unavailable	285	202	165	13	8	135	42
LED	72	38	15	5	28	20	18
Laser	45	0	0	0	0	45	1
Incandescent	37	35	8	1	7	11	16
Halogen	27	21	9	2	5	13	4
Fluorescent*	21	20	4	0	1	2	13
Flame	15	3	15	3	0	5	0
Sodium Vapor (Low or High Pressure)*	11	10	7	0	0	1	2
Mercury-Vapor*	9	6	6	0	0	5	0
Metal Halide*	8	8	6	0	0	1	1
Xenon	3	2	1	1	2	0	0
Electric Light (type UA)	3	2	3	0	0	2	0
Neon	1	1	0	0	1	0	0
Multi-metal Vapor	1	1	0	0	0	0	1
Magnesium	1	1	1	1	0	1	0

Table shows the number of studies testing each lamp type in the whole evidence base, for all studies testing white light (or light presumed by the mapping team to be white), and in the evidence base for each secondary question. *Dominant lighting types for older streetlights and other outdoor lighting (Seymoure et al. 2019b).

Table 3.9 Counts of Outcomes, Outcome subcategories, and Outcome Categories

Outcome Category (count)	Outcome Subcategory (count)	Outcome	Study Count
Behaviour (229)	Alert behaviour (9)	Other alert response	6
		Overt reaction distance	2
		Alert reaction time	1
	Approach or flee response (67)	Flying	31
		Capture of birds on the ground or water	28
		Flush (unspecified)	23
		Immobilization	16
		Diving	12

		Running or walking	10
		Unspecified	8
		Distance moved	5
		Other flee response	3
		Swimming	3
		Head movement	2
	Flight path characteristics (123)	Circling, hovering, or other description of "attraction"	77
		Observations of bird collisions	50
		Altitude	19
		Direction	13
		Linear/non-linear flight path	12
		Velocity	7
		Change in flight direction relative to light source	5
		Capture of birds in flight	4
		Distance of flight path from light source	2
		Distance travelled	2
		Modeled flight behaviour based on observations of bird locations or distributions	2
		Other flight behaviour	2
	Orientation behaviour (40)	Ability to orient in migratory direction	32
		Ability to locate reward	3
		Other orientation behaviour	3
		Homing	2
Community (5)	Composition (3)	Abundance of species grouped by type	2
		Stability	1
	Diversity (5)	Species richness	5
		Beta diversity	1
		Evolutionary distinctiveness	1
		Functional diversity	1
Distribution (372)	Bird counts (140)	Abundance or density	101
		Presence/absence	40
	Bird locations (26)	Locations of individual birds	12
		Locations of nests	5
		Locations of roosts or groups of birds	3
		Light exposure of tracked individuals	3
		Mean or median light exposure of a species	2
		Proximity of dead or injured birds to artificial light sources	1
	Mortality (150)	Counts or presence of dead or injured birds	134
		Locations of dead or injured birds	10
		Absence of bird deaths or injuries	5
		Seabird bycatch	5
		Type of mortality observation UA	5
	Preferences	Free choice (time spent in each lighting option)	46

	(61)	Discrete choice (instantaneous choice among lighting options)	15
	Presence of foraging birds (56)	Multiple individuals foraging under artificial lights	38
		One individual foraging under artificial lights	12
		Amount of food consumed	4
		Number of foraging events (individuals not distinguished)	3
		Arrival or departure time of foraging birds	2

Numbers in parentheses show the number of studies in each outcome category and outcome subcategory.

Mapping the quantity of evidence relevant to each secondary question

Our second objective was to provide an evidence base for four secondary questions with conservation and management importance, identifying relevant evidence based on objective PE/ICO criteria rather than the authors' purpose for conducting the study (Table 3.2). Evidence for each question can be found using the *Secondary Questions* tab on the *SEARCH* form in our Access database.

This interdisciplinary approach expanded the quantity and diversity of evidence for each question by including studies that were conducted for many different purposes. For example, evidence relevant to our secondary question about habitat selection came from 30 studies whose purpose was to improve welfare or production of captive birds and five studies conducted to deter birds (Table S3.7, Appendix B, Additional file 12 *Supplementary tables and figures*). Evidence relevant to our secondary question about deterrence included 84 studies whose purpose was to document and/or reduce bird aggregations or mortality and 34 studies that captured or counted birds for wildlife research (Table S3.7, Appendix B, Additional file 12). By considering all studies with relevant populations, interventions/exposures, and outcomes – rather than only considering studies that describe bird responses as attraction, deterrence, or habitat selection – reviews can draw on a broader evidence base with a greater diversity of bird species and light characteristics.

All four of our secondary questions received considerable study constituting evidence clusters, but aggregation/mortality, deterrence, and habitat selection were studied more than disorientation and attraction (Table 3.2). Below, we describe the evidence clusters and knowledge gaps within each secondary questions and explain their importance from perspectives of conservation, management, or basic science.

What information is available documenting that birds in flight aggregate around and collide with artificial lights or structures with artificial lights?

Hundreds of papers documented bird aggregation or collision mortality in association with artificial light. There may be sufficient literature for a review to identify weather or lunar conditions or light characteristics that are associated with high probability or intensity of aggregation and mortality events, helping to target light reduction efforts on nights with those conditions. Such an analysis is likely possible because 75 studies made observations under multiple cloud cover/visibility conditions (Table 3.10) and 36 studies observed bird aggregation/mortality under multiple lunar phases (Table 3.11). The lunar phases in other studies could be calculated based on locations and dates. A more accurate representation of lunar illumination could include illuminated fraction and elevation, in addition to atmospheric conditions (Kyba et al. 2020b).

A review of the evidence in this map could support or amend current recommendations for flashing instead of steady-burning lights (e.g. US Federal Aviation Administration and Bureau of Ocean Energy Management; Patterson 2012 and BOEM 2021) and add details to these recommendations by determining how flashing rate influences bird response. International standards require that communications towers and other obstructions install combinations of red or white and flashing or continuous lights (ICAO 2013), and these towers are a significant source of mortality for birds (Loss et al. 2015). Twenty-five studies included both red and white lights within the same study, and 25 included both continuous and flashing or rotating lights, providing an opportunity to compare the effects of these wavelengths or flashing patterns on bird aggregations and mortality when other conditions were held relatively constant.

Table 3.10 Cloud Cover/Visibility in studies relevant to aggregation/mortality

Cloud Cover/Visibility	**Study Count**
Only clear days/nights	6
Only cloudy days/night	29
Varied – descriptive	31
Varied – events only	17
Varied – events only and descriptive	2
Varied – systematic	25
UA	107

Cloud Cover/Visibility was coded as *Varied – systematic* if it was recorded at regular intervals throughout the study period. It was coded as *Varied – events only* if it was only recorded during aggregation/mortality events and *Varied – descriptive* if authors described in general terms the conditions under which aggregation/mortality were most likely to occur.

Table 3.11 Lunar phase in studies relevant to aggregation/mortality

Lunar Phase	**Study Count**
New	3
Full	0
In between	1
Varied – systematic	26
Varied – descriptive	7
Varied – events only	2
Varied - other	1
UA	176

Lunar phase was coded as *Varied – systematic* if it was recorded at regular intervals throughout the study period. It was coded as *Varied – events only* if it was only recorded during aggregation/mortality events and *Varied – descriptive* if authors described in general terms the conditions under which aggregation/mortality were most likely to occur.

There is insufficient evidence to compare the effects of different types of white light and few studies on wavelengths other than red. Most studies in this evidence base do not describe the spectral compositions of white light, and only 33 describe the type of light bulb used. In circumstances that require steady-burning white light (e.g. office towers, illuminated monuments, and airfield runway lighting), there may be an opportunity to change the spectral properties of white lights to reduce bird aggregation and mortality. Light of wavelengths other than red should also be studied because international standards require yellow and blue lights for mobile obstacles (ICAO 2013) and many other wavelengths are used for decorative lighting on bridges and buildings. In the evidence base for this secondary question, the green and blue each have only 7 studies each, while yellow and UV each have even fewer (Figure 3.3).

There is also a knowledge gap concerning the relative danger of structures with flashing lights compared to unlit structures. Studies in the deterrent literature used flashing lights or UV lights to attempt to prevent collisions by increasing the bird's ability to detect an object in its path (e.g. Dwyer et al. 2019), but there have been no studies comparing collision rates at tall structures with unlit control structures. Most tall structures require aviation safety lights, but new technology may permit unlit structures by using radar detection to turn on obstruction lighting only when an aircraft approaches (Patterson 2018). While structures without lighting may cause less attraction or disorientation, birds will not be alerted to the presence of dark structures in their flight path (May et al. 2015). Before this new technology is adopted, it will be important to compare bird mortality at dark structures to structures with various types of lights, particularly flashing or UV lights that are sometimes used as deterrents.

What evidence exists on aggregation and mortality as a result of attraction and/or disorientation?

While many authors assume that aggregations and mortality result from attraction, we only identified 25 studies with response variables that could suggest attraction (Table 3.2). By definition, these studies can also suggest deterrence if birds fly away from the light source. A review could describe whether birds show opposing responses depending on light characteristics (e.g. moving v. stationary, flashing v. continuous). Identifying where attraction occurs and the mechanism of attraction could help design lighting that is safer for birds. However, the relatively small number of relevant studies limits the potential for review, with only 14 studies including white light, 5 including UV/violet, and even fewer studies including red, green, or blue wavelengths (Figure 3.3).

To conclusively demonstrate attraction to light, birds must be given a simultaneous choice between light treatments when all other conditions are identical (i.e., choice tests; Manly et al. 2007). Only one study used a controlled choice test on birds in flight (Goller et al. 2018) (Table S3.8, Appendix B, Additional file 12 *Supplementary tables and figures*). Two studies modeled flight behaviour based on observations of bird locations or distributions (Troy et al. 2013; Van Doren et al. 2017), but did not directly observe their flight paths. Twenty-three studies recorded a change in altitude, flight direction relative to a light source, or capture of birds in flight, but did not offer simultaneous choice. Further choice tests could determine the light characteristics and ambient conditions under which attraction is most likely to occur, with relevance for both reducing attraction and more effectively deterring birds.

Birds flying around lights (e.g. circling, fluttering, hovering) may be disoriented, but only one orientation mechanism has been extensively tested. Thirty studies tested bird magnetoreception (Table S3.9, Appendix B, Additional file 12), and a review concluded that birds cannot perform magnetoreception in the complete absence of short-wavelength light from UV to green (565 nm) (Wiltschko and Wiltschko 2019). Some conservation biologists have speculated that the long wavelengths in broad-spectrum (i.e. white) light disorient birds by interfering with magnetoreception (Poot et al. 2008), but a review of laboratory research concluded that birds orient appropriately under broad-spectrum light that contains these wavelengths (Wiltschko and Wiltschko 2019). It is unclear whether birds can perform magnetoreception under all types of white light because only incandescent, halogen or xenon white lamps were tested in the twelve magnetoreception studies using white light (Table S3.10, Appendix B, Additional file 12). These lamps have broad emissions spectra, while other lamp types (e.g. metal halide and some LEDs) have distinct spectral peaks (Elvidge et al. 2010). These spectral peaks may interfere with magnetoreception, as is the case for monochromatic and bichromatic light (Wiltschko et al. 2013; Wiltschko and Wiltschko 2019). Two magnetoreception studies did not report the direction of the light, and the remaining 28 used overhead lights to illuminate Emlen funnels (Emlen and Emlen 1966), mazes, or cages. These conditions differ from the built environment that birds experience on migration, where light intensity can vary across a bird's visual field (e.g. when flying in or above cities).

Loss of a single orientation mechanism may not disorient birds because the aviation orientation system includes redundancy (Chernetsov 2016). Only eight studies tested how artificial light interferes with orientation mechanisms other than magnetoreception, including the disorienting effects of horizon glow (3), clock-shifts (3), and photoperiod changes (2) (Table S3.9, Appendix B, Additional file 12 *Supplementary tables and figures*). None tested the impacts of skyglow or satellite clusters on the ability for birds to orient using their stellar compass. Together, conservation biologists and sensory ecologists should collaborate to design studies that fill these knowledge gaps and determine how the many types of artificial light common in the built environment interfere with some or all of birds' orientation mechanisms.

What information describes the effect of light as a means of deterring or dispersing birds?

Lasers formed the most promising evidence cluster for meta-analysis of studies specific to deterrent efficacy, while spotlights and flashing lights could be reviewed while including studies documenting bird aggregation, deterrence, and capture. A review might include red, green, and blue green lasers (studied 21, 10, and 7 times, respectively), while blue and violet were each studied only once (Table S3.11, Appendix B, Additional file 12 *Supplementary tables and figures*). Forty of the 42 studies using lasers measured an approach or flee response, offering a common set of outcomes on which to base a meta-analysis. A meta-analysis of laser efficacy would be particularly useful because they are commonly sold as bird deterrents and were by far the most common type of light-based deterrent in our map (Table 3.12).

For flashing lights and spotlights, including evidence from studies with other purposes increased the size of the evidence base (Table 3.12). A review of bird response to flashing lights and spotlights would have applications for reducing aggregations, improving deterrents, and capturing wildlife. Spotlights were also commonly documented in the aggregation/mortality literature, primarily at lighthouses, and in studies whose purpose was to capture birds for wildlife research (Table 3.12). When capturing birds, many authors recorded whether each species would typically flee or freeze in response to the spotlight. With the 21 taxonomic orders studied at least once in the spotlight studies, there may be an opportunity to investigate which species traits impact the efficacy of spotlights as deterrents or trapping tools. We did not record the characteristics of the spotlight used (e.g. light intensity, beam angle, predictability of movement) in this map, but a review could compare these characteristics to identify important predictors of bird responses. Deterrent efficacy may depend on ambient light levels, which change over the course of the day (Blackwell 2002). The evidence base may support a review of this topic, with

23 studies that applied the intervention/exposure at multiple times of day, 18 studies conducted only during the day, and 72 studies conducted only at night (Table S3.12, Appendix B, Additional file 12).

More research is needed on ultraviolet and violet light as a deterrent and the potential for light-based deterrents to reduce bird collisions or entanglement in wires and lines. UV or violet light was only tested in 8 studies in the deterrence evidence base (Figure 3.3), and only once for lasers (Table S3.11, Appendix B, Additional file 12). Orange and yellow were included in fewer studies, UV/violet could be a particularly important knowledge gap because many bird species have a cone receptor with peak sensitivity in the UV or violet portions of the spectrum (Kelber 2019). For example, a vision model indicated that light peaking in the UV/violet range (380-400 nm) would be most visible to Canada Geese (*Branta canadensis*), which are common targets of laser deterrent efforts, under a specific set of visual conditions (i.e., certain objects with specific types of illumination) (Blackwell et al. 2012). In general, deterrent studies would benefit from more information about the spectral sensitivity of target species (Frid and Dill 2002). In addition to alerting birds to approaching vehicles or dispersing birds from zones of human-wildlife conflict, light-based deterrents were used in a few cases to increase awareness of stationary obstacles like power lines (Dwyer et al. 2019) and fishing lines (Mangel et al. 2018; Field et al. 2019; Bielli et al. 2020). More research is needed to determine what types of lights are effective for warning birds about obstructions without inducing bird aggregations (Martin 2011; May et al. 2015). Like attraction, the strongest evidence for deterrence comes from controlled choice tests, but these were rare. Eighteen studies, coming from only seven unique articles, conducted choice tests using light sources typically used as deterrents (lasers, UV/violet lights, flashing lights, or spotlights) (Table S3.13, Appendix B, Additional file 12). Choice experiments could greatly improve our understanding of the potential for different types of light to attract or deter birds and how the effects depend on species, light characteristics, and context of the intervention/exposure.

Table 3.12 Number of studies documenting bird response to each deterrent type

Deterrent type	**Number of studies using deterrent type to deter birds**	**Total number of studies documenting bird response to deterrent type**
Laser	46	46
Flashing light	23	68
Spotlight	11	158
UV or near-UV light	7	9
Line markers	4	4
Pyrotechnic	1	1

The first column shows the number of studies using each deterrent type to intentionally deter birds. The second column shows the number of studies documenting bird responses to each deterrent type with outcomes that could demonstrate deterrence, regardless of the purpose for which the study was conducted.

What evidence exists on continuous artificial illumination changing bird habitat selection for activities other than flight?

A review of the 88 studies for this secondary question would include 20 different bird orders, providing an opportunity to examine how life history or physiological traits influence selection for or avoidance of artificially illuminated environments. Examples of traits that could influence whether a species prefers or avoids artificially illuminated habitat patches include eye morphology (Ausprey et al. 2021), nocturnality (Sanders et al. 2020), and foraging strategy (Santos et al. 2010). Much of the continuous illumination experienced by birds in the wild comes from outdoor lighting like streetlights and illuminated signs, which are rapidly converting from older technology to LED (Kyba et al. 2017). To study whether LEDs have different effects on habitat selection than other types of white light, a review could compare the results of studies using fluorescent, incandescent, and LED lights (each studied at least 13 times, Table 3.8).

However, such a review may be limited because LEDs can have varying spectral properties and the spectral power distribution of any light is rarely described. A few studies tested blue, green, and red light, providing further opportunity to review how birds respond to different parts of the visual spectrum (Figure 3.3). Because study design varied widely across the evidence base, a review of the impacts of artificial light on bird habitat selection must incorporate multiple study designs to include sufficient evidence for meaningful inference. Seven studies measured relative abundance, while 16 modeled probability of selection or occupancy (Table S3.14, Appendix B, Additional file 12 *Supplementary tables and figures*). Nineteen studies used other types of control/impact, before/after, or gradient designs. The 43 preference tests could form an evidence cluster, but 20 of these tested domestic poultry species, which may have little application to wildlife (Suzuki et al. 2013). While incorporating diverse study designs expands the evidence base, it may limit the comparison of results across studies.

For habitat selection, knowledge gaps remain for non-passerine species, many lamp types commonly used for outdoor lighting, and different spectral properties in LED lamps. Only *Passeriformes* (perching birds), *Galliformes* (landfowl), *Procellariiformes* (tube-nosed seabirds, including petrels, shearwaters, and albatrosses), and *Charadriiformes* (shorebirds and relatives) were studied more than five times, limiting the ability to predict how other taxonomic orders will respond to the global increase in ALAN (Table 3.6). As older street lamps are converted to LED, the choice to convert and the type of LED chosen will alter the night-time environment for decades to come, potentially changing both the sensory experience and prey availability for birds (Longcore et al. 2015, 2018; Plummer et al. 2016; Davies et al. 2017), which may impact their habitat selection. LED lamps vary in their spectral properties and intensities even within comparable costs and energy efficiencies (Longcore et al. 2018), so there may be opportunities to choose lights that are less likely to impact bird habitat selection while keeping costs low. We found that there is little evidence on the impacts of different types of white light on bird habitat selection, with very few studies using lamp types common for older streetlights and outdoor lighting (Table 3.8) and none reporting the spectral power distributions of white light.

Habitat selection is a particularly important domain for understanding the effects of artificial light on birds because it has widespread implications for both management and conservation. Changing or reducing artificial light can discourage birds from settling in areas where they pose a danger or nuisance to humans. For example, three studies in our map showed how artificial light levels can influence roost site selection for nuisance species in urban environments (Gorenzel and Salmon 1995; Jaggard et al. 2015; Daoud-Opit and Jones 2016). Another study changed the colour of runway lighting to reduce insect attraction, thereby reducing the number of birds on the runway (van Tets et al. 1969). From a conservation perspective, understanding the impacts of ALAN on habitat selection can help target light abatement efforts towards species that are most negatively impacted. As ALAN increases, species that avoid using illuminated areas will suffer reduced habitat availability regardless of whether habitat quality is affected. Species that select artificially illuminated habitat despite low reproductive success may face ecological traps and population declines (Gilroy and Sutherland 2007). The evidence in this map can identify loss in habitat availability and potential ecological traps, but does not include evidence of ALAN's effects on bird fitness other than collision mortality. Reviews or further research should also consider additional metrics (e.g. survival or reproduction rates) when evaluating the ecological impacts of artificial light on birds (Johnson 2007).

Mapping the quality of evidence

Further critical appraisal is necessary to determine the number of articles that could be included in systematic reviews. Requiring a comparator would disqualify approximately a third of the evidence in the map, and further critical appraisal may reduce the evidence base. To aid users in assessing how many studies are likely to pass critical appraisal and determining if there is sufficient evidence for a systematic review, we coded each study's control design in the database and wrote a description of the control treatment.

The majority of studies included a comparator, with light characteristics (e.g. presence/absence, intensity, wavelength, polarization, total illuminated area) varying across treatment periods or sites in 290 of 490 studies (Table S3.15, Appendix B, Additional file 12 *Supplementary tables and figures*). The remaining 200 studies had no comparator but offer evidence of bird movement or distribution if certain assumptions are accepted about bird behaviour or distribution in the absence of artificial light (Table 3.S15, Appendix B, Additional file 12). For example, reports of birds aggregating around artificial light sources attribute the aggregations to the presence of light, assuming that aggregations did not occur in unilluminated areas. Fifty-one behavioural assays recorded bird behaviour only when the light treatment (e.g. lasers or spotlights) was applied, assuming that birds did not flee in the absence of a light treatment (Table S3.16, Appendix B, Additional file 12). Other studies did not include a control treatment for light, but included controls with respect to other variables and tested whether the effect of light on bird behaviour or distribution depends on other factors (e.g. recording the number of birds aggregating at the same light source under varying weather conditions; Hüppop and Hilgerloh 2012).

Limitations of Systematic Map

We strove to find all available evidence and our bibliographic checking confirmed successful realization of that goal for the contexts of bird disorientation, deterrence, and habitat selection. However, we missed about one third of articles that documented aggregation/mortality at illuminated structures. Finding all of the eligible articles indexed in the Web of Science Zoological Record that don not reference light in their topic fields would require screening more than 50,000 additional records, which would delay the publication of this map by many months or years. Our systematic search found all references where light was emphasized by the authors as a main contributor to aggregation or mortality in their title, abstract, or keywords. Our search may be biased towards articles that investigated light or assumed light to be a factor contributing to aggregation or mortality, but not articles whose authors considered light irrelevant. Our search may also have a geographic bias towards North America. We only included articles written in English, which may have contributed to the low number of studies found from South America. Most of our stakeholders were located in North America

In our Review Findings, we discuss the limitations of the primary evidence base, which limits the potential for further synthesis or evidence-based management. For example, there were 14 bird orders that were never studied, and most studies using white light did not report lamp type or information on spectral composition. Over forty percent of studies in the systematic map lack a control, with this proportion rising to fifty percent in studies relevant to bird deterrence. Many studies reported changes to bird behaviour and distribution, but distribution data were rarely used to quantify species richness or other community outcomes (Table 3.9).

Where metadata were not possible to code quantitatively or categorically, we described them narratively, and further categorization or unit conversion will be required before conducting a quantitative review or meta-analysis. For example, we categorically coded whether cloud cover/visibility varied within a study, but we narratively reported the cloud cover/visibility values provided by each study's author. These values included proportion cloud cover, visibility distance, clear v. cloudy, and narrative descriptions of how bird behaviour was affected by weather conditions. Lack of detail on weather conditions in many studies limits the potential for reviewing how weather affects bird responses to light. Similarly, we reported light intensity in the units provided by the authors because the variety of units they used (e.g. lux, watts per meter squared, candlepower, candela, nanowatts per square centimetre steradian) are not easily converted to a common unit. The values we reported for light intensity included measurements of brightness, radiance, irradiance, and radiant flux. Further unit conversion and study eligibility screening will be required before comparing bird response across varying light intensities.

Finally, a year has passed between our updated systematic search of the literature and the completion of the map, during which more literature accumulated that we did not assess. The enormous time commitment required of systematic maps and reviews appears to impose a similar limitation on other authors. Creating this database was a substantial effort, involving over 900 hours of work by the authors and an additional 1,500 hours by volunteers. Updating the database would require significant time and funding.

Conclusion

Our systematic map provides a comprehensive database spanning many human applications of artificial light, countries, bird species, and types of light sources. As scientific research grows exponentially (Parolo et al. 2015), the breadth and depth of human knowledge increases, but finding and comprehending all the available evidence on a broad topic becomes more difficult. The number of search results generated by our search string in the Web of

Science Core Collection has nearly doubled over the past 10 years, from approximately 6,500 in 2011 to over 12,500 in 2021. Our inclusive search string and use of specialized databases and websites provided a much more comprehensive evidence base than could be gathered with a basic search of popular databases, such as Google Scholar and Web of Science. Even our own systematic search of these databases found only 75% of the articles that were ultimately included in this map (Table 3.3). Our systematic map provides an evidence base that can be searched based on dozens of metadata fields. We hope others will use our systematic map to find evidence relevant to biological and management questions and write reviews, make policy decisions, and target research towards under-studied topics.

Implications for Syntheses to Inform Policy/Management

Using our database, we identified several key evidence clusters with important conservation and management implications that could be prioritized for review. For aggregation and mortality, a subsequent review could study the effects of cloud cover/visibility and lunar phase on bird aggregation and mortality to predict when mortality events are likely and recommend that lights be turned off or dimmed at these times. Another review in this context could identify obstruction lighting characteristics (specifically contrasting red v. white light and flashing v. continuous light) that reduce bird mortality from collisions with tall structures while meeting international standards for aviation safety (ICAO 2013). For deterrence, the efficacy of red and green lasers could be evaluated in a meta-analysis to provide guidelines for choosing among the most commonly sold lasers. For habitat selection, a review could determine if birds respond differently to white lights produced by halogen, fluorescent, and LED lamps with diverse spectral properties (Elvidge et al. 2010). It may also be possible to review how life history or physiological traits, such as foraging strategy or eye-size (Santos et al. 2010; Ausprey et al. 2021), predict species responses to light.

Implications for Further Laboratory or Field Research

We also identify knowledge gaps with conservation and management implications that require further laboratory or field research. Considering that light may cause birds to aggregate around structures with artificial lights (Gauthreaux and Belser 2006), but can also increase birds' ability to detect and avoid obstacles (Blackwell et al. 2016), field studies should investigate whether turning off all light reduces bird mortality at communication towers and other obstructions. The safest lighting options might maximize detectability while minimizing attraction. Choice tests could determine which combinations of wavelengths and flashing rates attract or deter birds, informing efforts to deter birds from zones of human wildlife conflict and reduce collisions. Further research should test deterrents that use UV lights for those bird species that can see in the UV portion of the spectrum. Orientation research should test magnetoreception under artificial light conditions typically experienced by birds in the wild and determine whether artificial light interferes with other orientation mechanisms, especially the stellar compass. We also recommend comparing the effects of different lamp types on bird aggregation/mortality, habitat selection, and orientation. Testing varying spectral properties of LEDs is particularly important to inform lamp choice as older obstruction lighting and streetlamps are replaced (Kyba et al. 2017).

Declarations

Ethics approval and consent to participate

Not Applicable

Consent for Publication

Not Applicable

Availability of data and materials

All data generated or analysed during this study are included in this published article and its supplementary information files. Where available, article URLs are included in the Systematic Map database.

Competing Interests

The authors declare that we have no competing interests.

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Authors' contributions

CAA, CCSC, EB, and EFJ collectively identified the topic for the systematic map and developed the protocol. CAA conducted the search and data coding processes, with assistance from a research assistant and volunteers (see acknowledgements). CAA and EB designed the relational database in Microsoft Access. CAA conducted the analyses and wrote the manuscript under the advice of CCSC, EB, and EFJ.

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List of Additional Files

- *AF 1 ROSES form.pdf* contains our ROSES form
- *AF 2 WOS search strategy.doc* is a detailed explanation of our Web of Science search and pre-screening strategies

- AF 3 WOS Search Records.zip is a compressed folder containing the results of our Web of Science searches
    - *WOS_CC_Long_String_Search_Results.xlsm* is a record of our search in Web of Science Core Collection using the expanded population search string, before any macros were applied
    - *WOS_CC_Short_Search_Results.xlsm* is a record of our search in Web of Science Core Collection using the shorter population search string, before any macros were applied
    - *Applying_No_A_or_K_Macro.xlsm* contains the macros used to identify articles in our Web of Science Core Collection search results indexed without abstracts or keywords and add those search results to the search results that used the short search string, and shows the results of applying those macros
    - *Applying_Replace_Terms_Macro_CC.xlsm* contains the macros used to identify articles that only used an intervention/exposure search term in an irrelevant context and shows the results after removing those articles.
    - *WOS_CC_for_Rayyan .csv* contains the results of the pre-screened Web of Science Core Collection search, formatted for upload to Rayyan QCRI
    - *WOS_ZR_Search_Results.xlsm* is a record of our search in Web of Science Zoological record, before any macros were applied
    - *Applying_Replace_Terms_ZR.xlsm* contains the macros used to identify articles that only used an intervention/exposure search term in an irrelevant context and shows the results after removing those articles.
    - *Applying_Remove_dups_ZRCC.xlsm* contains the macros used to remove articles that were found in both the Core Collection and the Zoological Record from the Zoological Record search results.
    - *WOS_ZR_for_Rayyan.csv* contains the results of the pre-screened Web of Science Zoological Record search, formatted for upload to Rayyan QCRI
    - Documents in the folder Web of Science Core Collection Updated Search and Web of Sciences Zoological Record Updated Search show the equivalent information for the updated searches
    - Documents in the folder *Blank Macro Workbooks* are blank macro-enabled workbooks that can be used to apply our macros to any Web of Science Core Collection or Zoological Record search results.
- *AF 4 Database_Search_Records.xls* contains several sheets. The first sheet shows the database search records (date of search, screening platform, search string). The other sheets show the articles identified as potentially eligible at the title/abstract screening level, and reasons for exclusion if they were found ineligible at the full text level.A compressed file of PDFs and .doc files containing the raw search records is available upon request

- *AF 5 Website_Search_Records.xls* contains three sheets. The first sheet lists the website searched the search string used in Google or the URL of each page within the website that was searched. The second sheet lists the number of eligible articles found on each website. The third sheet lists the URLs of articles found eligible at the title/abstract level, the exclusion reasons for any articles excluded at the full text level, and the citations for any articles found eligible at the full text level.
- *AF 6 Google_Scholar_Search_Results.xls* contains multiple sheets. The first sheet shows the combined results from the Google Scholar searches after removing duplicates and formatting them for upload to Rayyan QCRI. The other four sheets show the raw Google Scholar search results, before removal of duplicates.
- *AF 7 Bibliographic_Checking.xls* has several sheets. On the *READ ME* sheet, we explained how we selected reviews for bibliographic checking and describes our scoring system. *All_Reviews_From_Rayyan* lists all articles found ineligible at the full text level because they were reviews. This sheet also contains the scores assigned to each review. *Reviews_for_biblio_checking* lists the reviews selected for bibliographic checking. The next 5 sheets list all of the relevant references found in each review and whether or not they were found by our search. The final sheet shows the reasons why some of the references in the review of aggregation/mortality were missed.
- *AF 8 Explanations of Eligibility Criteria.doc* provides a detailed explanation or our eligibility criteria.
- *AF 9 Articles_Excluded_at_Full_Text.xls* has three sheets. The first lists the articles screened on Rayyan QCRI excluded at the full text level, with reasons for exclusion. The second contains the list of articles screen on other platforms excluded at full text, with reasons for exclusion. The third shows a table of the number of studies excluded for each reason. The fourthlists all articles that were excluded from the map because we could not access their full texts.
- *AF 10 Consistency_Check_Records.xls* is the results of the consistency checking exercises for screening at the title/abstract level and the full text level.
- *AF 11 Data_Coding_Fields.xls* lists the metadata fields, the codes used in each field, and a description of how the field or codes changed from the protocol. It also lists instructions and notes given to coders. For fields requiring extensive instructions, we list the codes and their instructions on separate sheets.
- *AF 12 Supplementary tables and figures.docx* contains all supplementary tables and figures
- *AF 13 Adams_et_al_Systematic_Map.accdb* is the systematic map database for viewing and editing in Microsoft Access
- *AF 14 Adams_et_al_Systematic_Map_Runtime.accdr* is the systematic map database for viewing in Microsoft Access or in Microsoft Access Runtime, which can be downloaded for free at https://support.microsoft.com/en-us/office/download-and-install-microsoft-365-access-runtime-185c5a32-8ba9-491e-ac76-91cbe3ea09c9. If opened in Microsoft

Access, the user can edit the database and run queries, but not edits or queries will be saved.

- *AF 15 Adams_et_al Systematic_Map_Excel.xls* contains a version of the systematic map in Microsoft Excel
- *AF 16 How_to_use_the_systematic_map_database.doc* provides instructions on how to search for studies within the Microsoft Access and Microsoft Excel versions of the database.

Chapter 4. Behaviour and landscape contexts determine the effects of artificial light on two crepuscular bird species

Abstract

Artificial light at night (ALAN) is increasing worldwide, with impacts on many biological processes. Aerial insectivores can benefit from foraging on insects congregating at light sources. However, ALAN could negatively impact them by increasing nest visibility and predation risk, especially for ground-nesting species like nightjars (*Caprimulgidae*). We tested predictions based on these two alternative hypotheses, potential foraging benefits vs potential predation costs of ALAN, by assessing the relative abundance patterns of two nightjar species in the Canadian Nightjar Survey in British Columbia: Common Nighthawks (*Chrodeiles minor*) and Common Poorwills (*Phalaenoptilus nuttallii*). Common Nighthawks often forage far from their nesting territories, which can be identified from their performance of wingboom displays. Common Poorwills forage and nest within the same territory. We found some support for the foraging benefit hypothesis from an increase in relative abundance of extra-territorial Common Nighthawks in areas with higher ALAN, but little or no urban land cover. Common Nighthawks' association with ALAN became negative in areas with 25% or more urban land cover. We also found support for the nest predation hypothesis from the strong negative associations with ALAN for both Common Poorwills and territorial Common Nighthawks. We speculate that the positive effects of ALAN on foraging nightjars may be limited to species that can forage outside their nesting territory and to non-urban areas, while the negative effects of ALAN on nesting nightjars may impact many species, particularly those that nest on the ground. Although many species are thought to benefit because they sometimes forage under ALAN, the effects of ALAN on their relative abundance may depend on behavioural and landscape contexts.

Keywords

Light pollution; ALAN; avian ecology; Caprimulgiformes; insectivores

Introduction

Artificial light at night (ALAN) is increasing worldwide (Cox et al. 2022; Falchi et al. 2016; Kyba et al. 2017), as are studies on its biological impacts (Rodrigo-Comino et al. 2021; Adams et al. 2021). While ALAN is typically brightest in urban environments, rural areas are becoming increasingly illuminated as light sources are installed and are experiencing more skyglow when ALAN from distant sources reflects off of particles in the atmosphere back towards the earth (Min and Gaba 2014; Gaston et al. 2015; Falchi et al. 2016). Most species evolved under predictable solar and lunar cycles, which ALAN substantially alters (Gaston et al. 2014). These alterations affect biological systems from the levels of molecules to ecosystems, via such variable effects as gene expression (Chen et al. 2021) and hormone production (Injaian et al. 2021). A growing body of work links ALAN to changes in behaviour, such as vocalizing (Da Silva et al. 2015), sleeping (Aulsebrook et al. 2020), and foraging (Santos et al. 2010), which sometimes combine to alter species abundance and distribution (La Sorte et al. 2017; McLaren et al. 2018). ALAN also impacts predator-prey relationships (Underwood et al. 2017; Ditmer et al. 2020; Nuñez et al. 2021), inter-species competition (Valeria B et al. 2021), and ecosystem services, such as pollination (Knop et al. 2017; Straka et al. 2021) and seed dispersal (Lewanzik and Voigt 2014). Nocturnal and crepuscular species are thought to be more vulnerable to the negative impacts of ALAN than diurnal species (Sanders et al. 2020; Ditmer et al. 2021) because they are exposed to more artificial light than diurnal species when lights turn on after sunset and artificial lights become brighter relative to ambient illumination. While the effects of ALAN are often negative, the costs and benefits can depend on the species under study (Sanders et al.

2020), geographic or landscape features (Barré et al. 2021; Camacho et al. 2021), and the spatial scale at which ALAN is measured (McLaren et al. 2018).

ALAN may provide foraging opportunities for insectivorous birds and bats by aggregating their insect prey under lights (Shields and Bildstein 1979; Bharos 1990; Foley and Wszola 2017). This type of foraging behavior has been documented around the world, but is undoubtedly subject to observation bias because birds foraging away from lights are less likely to be seen by humans (Buij and Gschweng 2017). Evidence from studies on bats suggests they can benefit by foraging on insects aggregating at lights, although not all light-attracted bat species consistently increase their activity near artificial lights and the effects of ALAN on foraging behaviour can depend on landscape context (Mathews et al. 2015). Furthermore, the long-term effects of ALAN on insect abundance have not been adequately studied (Kalinkat et al. 2021), and the benefits for aerial insectivores may diminish over time if mortality and disrupted reproduction at artificial light depletes local insect populations (Eisenbeis 2006; van Grunsven et al. 2019). Finally, the cumulative effects of many light sources over large spatial extents are relatively unknown, but ALAN may reduce insect populations over large extents by creating population sinks (van Grunsven et al. 2020), limiting dispersal (Degen et al. 2016), and creating widespread skyglow that impacts their physiology and behaviour (reviewed by Owens and Lewis 2018 and Owens et al. 2019). Therefore, landscapes with more light pollution may support fewer aerial insectivores, opposite to the prediction based on insect aggregations associated with ALAN (Eisenbeis 2006; Carannante et al. 2021).

In the context of nesting, ALAN may harm aerial insectivores by increasing the visibility of their nests, especially for ground-nesting species. Most previous studies on breeding birds and ALAN have focused on species that nest in cavities, on buildings, or in trees and generally have found no correlation between breeding densities and ALAN (Jong et al. 2015; Russ et al. 2017; Wang et al. 2021). However, cliff-nesting seabirds experienced higher predation in areas of a breeding colony exposed to artificial light (Oro et al. 2005) while a ground-nesting shorebird selected nest sites farther from artificial lights (de Molenaar et al. 2006). Species that nest on the ground and rely heavily on camouflage to avoid nest predation are more likely to be impacted by ALAN than species employing other nesting strategies (Troscianko et al. 2016). Artificial light, especially broad-spectrum light produced by LEDs, has the potential to increase the visibility of camouflaged prey species (McMahon et al. 2022). Increased illumination (from moonlight or ALAN) has been shown to increase detection rates by visually orienting predators (Clarke 1983; Santos et al. 2010). Thus, increases in perceived and/or actual predation risk may cause ground-nesters to select nest sites further away from artificial lights and/or experience nest failure near ALAN.

Nightjars of the *Caprimuligidae* family may experience both the foraging benefits and predation risks of ALAN because they are crepuscular and nocturnal birds that hunt flying insects and nest on the ground. The family includes 89 species found on every continent other than Antarctica (Winkler et al. 2020). Nightjars sometimes forage under artificial lights (Shields and Bildstein 1979; Ingels et al. 1999; Jackson 2003; Foley and Wszola 2017) and species accounts suggest that this behaviour is common (Winkler et al. 2020; Woods et al. 2020; Brigham et al. 2020). However, studies of how artificial light impacts their habitat use have mixed results and are confounded by urbanization. Common Nighthawk (*Chordeiles minor*) occurrence in Wisconsin was positively correlated with streetlights during the breeding season, but showed a stronger correlation with gravel rooftops, which also occur in urban areas and provide an important nesting substrate for nighthawks (Newberry 2018; Viel et al. 2020). The

European Nightjar (*Caprimulgus europaeus*) and Eastern Whip-poor-will (*Antrostomus vociferus*) showed negative responses to urbanization and the associated light pollution during migratory and breeding periods (Sierro and Erhardt 2019; Korpach et al. 2022). Understanding whether foraging under artificial light occurs only in isolated cases or is common enough to influence their occurrence or abundance is important for understanding whether ALAN alters predator-prey relationships between nightjars and insects. Nightjar species that forage away from their nest sites may respond differently to ALAN for territorial behaviors, related to nesting, compared with extra-territorial behaviours, which include foraging. Species that forage and nest within the same area must balance the foraging costs and predation benefits when selecting a territory.

We evaluated the impacts of ALAN on the relative abundance of two nightjar species, Common Nighthawks (*Chordeiles minor*) and Common Poorwills (*Phalaenoptilus nuttallii*), at sites surveyed in British Columbia during the Canadian Nightjar Survey. Breeding Bird Survey trends show both species are declining across much of their range (Sauer et al. 2020). Both have been observed foraging under artificial lights at night (Preston 2015; Foley and Wszola 2017) suggesting a potential benefit of ALAN. Common Nighthawks defend a small nest site with a behaviour called wingbooming (Knight et al. 2021a), but vocalize frequently as they travel up to tens of kilometers to forage, allowing us to separately evaluate how ALAN influences relative abundance of territorial and extra-territorial individuals for this species. Common Poorwills conduct all of their nesting and foraging activities within a relatively small territory (Csada and Brigham 1994), with breeding individuals typically foraging within hundreds of metres from the nest site.

We weighed evidence for two hypotheses by measuring the effects of ALAN on the relative abundance of three types of nightjars (territorial Common Nighthawks, extra-territorial Common Nighthawks, and territorial Common Poorwills) over multiple spatial scales (Table 4.1). The hypothesis that ALAN provides a foraging benefit for nightjars would be supported by an increase in the relative abundance of extra-territorial Common Nighthawks and of territorial Common Poorwills in areas with ALAN, measured at a local scale. The hypothesis that ALAN increases nest predation risk for ground-nesting species would be supported by a decrease in the relative abundance of territorial Common Nighthawks and Common Poorwills at sites with higher ALAN, also at a local scale. Nighthawks may benefit from nesting in a dark area within a landscape where they can travel to forage under a light source. The relative abundance of territorial Common Nighthawks could support both the foraging benefit and nest predation risk hypotheses if it were negatively correlated to ALAN at the local scale, but positively correlated with ALAN at the landscape scale.

Table 4.1 Predictions associated with the foraging benefit and predation risk hypotheses

	Foraging benefit hypothesis: Artificial light provides foraging opportunities for crepuscular aerial insectivores	**Nest predation cost hypothesis: Artificial light increases predation risk for crepuscular, ground-nesting species**
Extra-territorial Common Nighthawks	Increased relative abundance at sites with higher *local-scale ALAN* if they forage under lights	NA
Territorial Common Nighthawks	Increased relative abundance at sites with higher *landscape-scale ALAN* if they travel to forage under artificial lights away from nest site	Decreased relative abundance at sites with *local-scale ALAN* if ALAN increase predation risk at the nest site
Common Poorwill	Increased relative abundance at sites with *local-scale ALAN* if they forage under lights	Decreased relative abundance at sites with higher *local-scale ALAN* if ALAN increases their predation risk for nesting and/or foraging poorwills.

Methods

Study area

Our study area spanned several ecoprovinces in the province of British Columbia, Canada (Demarchi 2011). The Coast and Mountains ecoprovince on the west coast has heavy rain and lush vegetation. The drier, low elevation Georgia Depression includes the heavily populated cities of Vancouver and Victoria. Moving east, the Central Interior has open grasslands and rolling plateaus, while the Southern Interior has Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests as well as urban areas in the Okanagan Valley. In the eastern part of our study area, the Southern Interior Mountains host high peaks and thick forests, with wetlands and rivers in the valleys. For our analysis of Common Poorwills, we only included surveys conducted in the Southern Interior ecoprovince, which encompasses the species' range within British Columbia (Woods et al. 2020), and conducted within the boundary of the Annual Crop Inventory (ACI) (Agriculture and Agri-Food Canada 2020) where the most detailed land use/land cover data were available.

Nightjar surveys

Community scientists conducted roadside point counts for the Canadian Nightjar Survey (CNS) every June and July from 2014 to 2020. Routes were generated using random starting points from all possible roadside locations and random survey directions. Not all routes were surveyed and volunteer preference influenced which routes were taken. Each survey route consisted of six to ten stations spaced approximately 1.6 km apart. Surveys began 30 min before sunset and consisted of 6-min observation periods at each station. Volunteers recorded each individual nightjar, the species, and the detection type (visual, wingboom, or vocalization) for each 1-min interval within observation periods. Additional information on survey protocol is available in the BC Nightjar Survey annual reports (WildResearch 2019).

Male Common Nighthawks establish a territory and defend approximately 400 m around their nest using aerial displays called wingbooms (Rust 1947, Knight et al. 2021a). During their peak activity period, civil twilight (Sidler 2017), wingboom rate is high and we assumed nighthawks heard vocalizing, but not wingbooming, were extra-territorial. We tested this assumption in our detection probability model (described in the Data Analysis section). Studies have found that habitat associations are different for wingbooming and non-wingbooming nighthawks, and they are consistent with habitat requirements for nesting and foraging, respectively (Knight and Bayne 2017; Knight et al. 2021b).

Predictors of nightjar relative abundance

We measured all landscape predictors in three buffer sizes: 400, 1600, and 6400 m, corresponding to the buffer sizes used for another study of Common Nighthawks in Canada (Knight et al. 2022). We only included three of the buffer sizes used by Knight et al. (2022) to allow for model convergence, as explained in the Relative abundance models section. We refer these buffer sizes as scales, which we define as the spatial extent over which we measured landscape features (McGarigal et al. 2016).

We used estimates of artificial light at night derived from the Visible Infrared Imaging Radiometer Suite Day/Night Band sensor on the Suomi Polar-orbiting Partnership Satellite (Cao et al. 2014). The sensor measures light shining upwards from a light source, light reflected off of the ground, and upward-scattered skyglow, which is theoretically similar to the downward scattered skyglow in the same location, especially for light emitted at near-horizontal angles (Sanchez de Miguel et al. 2020). We used the annual composites from the Earth Observation

Group’s VIIRS Nighttime Light Products (VNL) (Elvidge et al. 2017) because they removed natural light in the aurora zone more effectively than the annual composites from NASA’s Black Marble (Román et al. 2018; Appendix C, Figure S4.1). For our analysis, we created an annual composite for each study year by calculating each pixel’s mean of Version (V2) for that survey year and Version 1 (V1) for 2016. V1 is available for only 2015 and 2016, (Elvidge et al. 2017), while V2 is available for all years between 2012 and 2020 (Elvidge et al. 2021), but misses many dim light sources in our study area that were found in V1 (Appendix C, Figure S4.2). We conducted a sensitivity analysis to determine whether different versions of the annual composite (V1 2016 or V2 for the survey year) substantially changed the posterior distributions of our coefficient estimates.

We included land use and land cover types that were positively or negatively associated with Common Nighthawk or Common Poorwill habitat use in previous studies (Appendix C, Table S4.1). For Common Nighthawks, these included burned or harvested forest, water or wetlands, grassland, agriculture, and urban land cover (Ng 2009; Farrell et al. 2017, 2019; Newberry and Swanson 2018; Viel et al. 2020; Knight et al. 2021b). The only study of Common Poorwill habitat associations in the northern part of their range showed positive relationships with native prairie and low-vegetation grassland or rangeland (Macdonald et al. 2003). For both species’ analyses, we used the Annual Crop Inventory (ACI) to classify proportional cover of urban, cropland, pasture, water/wetland (Agriculture and Agri-Food Canada 2020). We classified each pixel based on its most frequent value across all study years (2014-2020). In areas that were not classified as water, wetland, cropland, pasture, or urban by ACI, we used the BC Vegetation Resource Inventory (VRI) from 2020 to measure the proportion cover of sparse forest, shrubland, and grassland (BC Ministry of Forests 2020).

We also included temporal and geographic covariates that potentially influence nightjar activity periods and distribution. As temporal covariates, we included sun angle, day of year, the interaction between lunar presence and illuminated fraction, and their quadratic terms (Brigham and Barclay 1992; Brigham et al. 1999; Jetz et al. 2003; Woods and Brigham 2008; Sidler 2017), measuring all celestial variables using the R package suncalc (Thieurmer and Elmarhraoui 2019). We did not find geographic or topographic predictors in the existing literature, so we evaluated their impact on each species' occurrence before including them in our abundance model. We used the dredge function from the MuMln package (Bartoń 2022) to test for effects of elevation, slope, latitude, longitude, and their quadratic terms and selected the model with the fewest predictors with delta Akaike Information Criteria (AIC) < 2.0. We included these geographic predictors in our relative abundance model. To account for nest site fidelity in the territorial analyses, we included as a predictor the mean number of territorial individuals counted in previous surveys at the same station within the same year or during the previous year.

Relative abundance models

Assuming equal detection probability across surveys, the number of individuals counted in each survey represents a constant, but unknown, proportion of all of the individuals present. The count in each survey thus represents abundance relative to other surveys, which we defined as relative abundance. We tested this assumption by removing surveys in which detection probability was estimated to be < 90%, as we describe below. We conducted the analyses separately for territorial (wingbooming) Common Nighthawks, extra-territorial (vocalizing but not wingbooming) Common Nighthawks, and territorial (vocalizing) Common Poorwills.

We used a multi-step Bayesian modelling process to choose the most appropriate model form, identify the most predictive scale for each landscape covariate, and then estimate the effect of each covariate. First, we used DIC comparison to identify which model form best fit our data (Appendix C, Table S4.2). Second, we used Bayesian latent indicator scale selection (BLISS) to select the buffer size at which each covariate best explained relative abundance (Stuber et al. 2017). BLISS is scale-selection procedure that evaluates all combinations of covariates and scales within a single model run, rather than using separate models to select the optimal scale for each covariate independently or to select a single optimal scale for all covariates. BLISS generated a joint posterior distribution for two coefficients for each landscape covariate: (a) the effect estimate, which represented the log of the expected change in nightjar count per unit change in the covariate; and (b) the scale of effect, which represented the buffer size at which the covariate best explained the observed nightjar counts. We identified the spatial scale of the effect of each covariate as the buffer size selected in the largest proportion of the posterior distribution. In cases where a landscape covariate had a positive effect when one scale was selected, but a negative effect when another was selected, we included both scales as separate covariates in our final model. To identify these cases, we compared the effect estimates for each covariate from samples of the joint posterior distribution from the BLISS model that selected each scale. To ensure that we identified the most explanatory spatial scale of effect for our covariates of interest, we refit the BLISS model for ALAN, urban land cover, and their interaction with all other landscape covariates measured at their selected scales. We then fit the relative abundance model with all covariates measured at their selected scale or scales to finalize the estimates for the effect of each covariate. All predictors were included in the final model. All Bayesian models were fit using JAGS (Plummer 2003) and the *R2Jags* package (Su and Yajima 2021), using three chains with 12,000 iterations each and 3,000 burn-in iterations, for a total for 27,000 samples of the joint posterior distribution. After burn-in, we retained all samples in the chains because thinning would likely reduce the precision of our parameter estimates (Link and Eaton 2011). We validated our models by testing their ability to correctly estimated coefficient values from simulated data. We also plotted the correlation among the three correlated covariates (urban land cover, ALAN and the interaction between the two) across samples of the posterior distribution to determine if the presence of multicollinearity masked an important effect of one of our covariates (McElreath 2019).

We originally fit the BLISS models with six buffer sizes (400, 800, 1600, 3200, 6400, and 12800 m), but they did not converge after 24 hours, likely because of spatial autocorrelation across the six buffer sizes. We thinned our analysis to use three representative scales to approximate the scale of effect as local (400 m), intermediate (1600 m), or landscape (6400 m), recognizing that the specific scale at which nighthawks perceive and respond to each predictor was not precisely identified by our model and likely varies across our study area and over time.

We included post-hoc analyses to further investigate unexpected results and test our predictions. These included modelling the effects of ALAN on the relative abundance of extra-territorial Common Nighthawks separately for surveys conducted before and after sunset. We also modeled the effects of local and landscape-scale ALAN when both were included as separate covariates in the same relative abundance model for territorial nighthawks. We removed four stations that were surveyed many times across the study period from our model for territorial nighthawks. We provide further justification and explanation of these post-hoc analyses in our results section.

To describe how ALAN influenced the relative abundance of nighthawks in our model, we calculated the mean and 95% credible intervals (CIs) of the posterior predictions for the expected nightjar count as the covariate value increased from 0 to the 95th percentile ALAN value recorded in our dataset at the selected scale. We described the relationship between ALAN and relative abundance at varying proportions of urban land cover, including median, mean, and high (95th percentile) of urban land cover within the selected buffer size. To avoid interpreting model outputs beyond the range of ALAN values that exist in our data at each urban land cover level, we limited these descriptions to the 99th percentile ALAN values that occurred at surveys with urban land cover equal to or less than the urban land cover proportion we observed. When we calculated the expected number of nighthawks, we set all other covariates to their mean values, unless otherwise specified.

Detection probability models

We modeled individual detection rate to determine whether the influence of ALAN on detection probability could bias our estimate of ALAN on relative abundance. Using the minute-by-minute detection data for each individual nightjar, we modeled the effect of artificial light and temporal covariates on the number of minutes (out of six) in which each individual was detected using a binomial GLM. We used this model to predict the probability that an individual, if present, would be detected in each survey. We modeled this detection probability separately for extra-territorial Common Nighthawks, territorial Common Nighthawks, and Common Poorwills. In a sensitivity analysis, we removed surveys with < 90% detection probability and refit the relative abundance models. We compared the resulting coefficient estimates for ALAN, urban, and their interaction with those from the full model to determine if they influenced the scale or direction of the estimated effects.

Results

Survey results

We included 6,577 surveys conducted at 1,806 unique survey stations in British Columbia between 2014 and 2020. Volunteers recorded wingbooming Common Nighthawks in 973 of these surveys (15%) and non-wingbooming Common Nighthawks in 1,569 surveys (24%). In surveys where wingbooming nighthawk were observed, their mean count was 1.71 (SD = 1.16). In surveys with non-wingbooming nighthawks, their mean count was 1.67 (SD = 1.11). Common Poorwills were recorded during 236 (8%) of the 2,737 surveys within the Southern Interior ecoprovince, with a mean count of 1.5 (SD = 0.79) individuals in surveys where they were observed. Common Poorwills were also observed in 11 surveys outside of their traditional species range, in the south-eastern corner of the province along the Kootenay River in the Rocky Mountains. We did not include these 11 surveys in our relative abundance model for Common Poorwills.

ALAN and urban land cover estimates

Artificial light estimates were low in most surveys, with median values of 0, 0.04, and 0.17 $nWcm^{-2}sr^{-1}$ for the 400, 1600, and 6400-m buffer sizes, respectively. The 95th percentile values were 6.18, 6.30, and 6.13 $nWcm^{-2}sr^{-1}$. For reference, 1600-m buffers with less than 1 $nWcm^{-2}sr^{-1}$ showed an isolated light source or overlapped a small, dimly lit settlement (Figure 4.1). A 1600-m buffer with 6 $nWcm^{-2}sr^{-1}$ typically included a small settlement or the edge of a town. Median percent urban land cover was 7.23%, 3.75%, and 3.37% for the three buffer sizes, and the 95th percentile values were 56%, 42%, and 35%. Buffers of 1600 m that had 40-50% urban land cover typically overlapped a small settlement or town.

ALAN and proportion of urban land cover had Pearson's correlation coefficients of 0.56, 0.63, and 0.85 for the 400, 1600, and 6400-m buffer sizes, respectively, across all surveys. For the subset of surveys in the Common Poorwill range, the correlation coefficients were 0.68, 0.78, and 0.86, respectively. For Common Nighthawks, our model identified the correct spatial scales and coefficient values when we fit it using relative abundance values simulated from our coefficient estimates, suggesting that our model adequately estimated the marginal effects of ALAN and urban land cover despite their correlation (Appendix C, Figure S4.3). The coefficient estimates were less reliable for the analysis of Common Poorwills, which had only a quarter the sample size of the Common Nighthawk analyses, but the model still identified the correct scales and effect directions for both ALAN and urban land cover.

ALAN estimates likely included direct illumination and skyglow. Where positive ALAN values occurred in pixels near urban land cover but with no plausible light sources, ALAN estimates may have included light scattered through the atmosphere and upwards towards the satellite. This upward scatter theoretically and empirically correlates with skyglow, artificial light scattered towards the ground, within a pixel of the VIRRS night-time light products (Sanchez de Miguel et al. 2020).

Relative abundance models

In the preliminary modeling stages, we identified elevation, elevation squared, slope squared, and latitude as the combination of predictors with the lowest AIC in the preliminary count model for both territorial and extra-territorial Common Nighthawks. For Common Poorwills, the lowest AIC model included longitude, longitude squared, slope, and slope squared. We included these covariates in their respective relative abundance models. Among the candidate model forms for the Bayesian relative abundance model (zero-inflated Poisson, negative binomial, and Poisson), we selected the negative binomial because it had the lowest DIC for all three nightjar groups (Appendix C, Table S4.2). For all three analyses, our results were insensitive to the version of the EOG annual composite (V1, V2, or the mean of V1 and V2) used to measure ALAN (Appendix C, Figure S4.4).

Extra-territorial Common Nighthawks

The BLISS models revealed that the relative abundance of extra-territorial Common Nighthawks was best explained by ALAN measured at the landscape scale (6400 m), but with differing effects in combination with land cover. This landscape scale was selected both for the main effect of ALAN (96% of the posterior) and for ALAN in interaction with urban land cover (98% of the posterior) (Figure 4.2a; Appendix C, Figure S4.5 and Table S4.3). The BLISS model also selected the landscape scale for the main effect of urban land cover, and the intermediate scale (1600 m) for its interaction with ALAN.

The relationship between the relative abundance of extra-territorial Common Nighthawks and ALAN switched from positive to negative when urban land cover at the intermediate scale exceeded 25% (95% CI: 10%, 38%) (Figure 4.3a). Percent of urban land cover at the intermediate scale in our survey sites had a median value of 3%, a mean of 10%, and a 95th percentile of 42%. The 99th percentile ALAN values occurring at surveys with urban land cover equal to or less than these values were 3.98, 5.2, and 10.3 nWcm^{-2}sr^{-1}, respectively. For a survey with median urban land cover, the expected number of extra-territorial nighthawks increased by 35% (3%, 72%) when ALAN values increased from 0 to 3.98 nWcm^{-2}sr^{-1} (Figure 4.3a; Appendix C, Table S4.4). A similar increase occurred where ALAN increased to 5.2 nWcm^{-2}sr^{-1} in areas with mean urban land cover. At the 95th percentile urban land cover, an increase to 10.3 nWcm^{-2}sr^{-1} corresponded to a 43% (5%, 70%) decrease in the number of extra-territorial nighthawks. The 95% CI for the main effect of urban land cover alone overlapped zero (Appendix C, Figure S4.6).

Territorial Common Nighthawks

The BLISS procedure selected the intermediate spatial scale for the main effect of ALAN and the landscape scale for its interaction with urban land cover (Figure 4.2b). In the final model, the 95% CI for this interaction overlapped zero (Appendix C, Figure S4.6). Two scales were selected for urban land cover, with a negative effect at the local scale and a positive effect at the landscape scale in both the BLISS model and the final model (Appendix C, Figures S4.5 and S4.6). In the final model the 95% CI for the landscape scale overlapped zero when we removed surveys conducted in one highly sampled region, described below.

The relative abundance of territorial Common Nighthawks was negatively associated with ALAN. In areas with median urban land cover (7%) at the local scale, an increase in ALAN from 0 to 1.44 $nWcm^{-2}sr^{-1}$ corresponded to a decline in the expected number of territorial nighthawks of by 27% (17%, 35%) (Figure 4.3b; Appendix C, Table S4.4). Where urban land cover was at its mean (14%), the expected number of territorial nighthawks decreased by 55% (39%, 69%) when ALAN increased to 3.76 $nWcm^{-2}sr^{-1}$. In areas with high urban land cover (56%), the 99th percentile ALAN value reached 9.97 $nWcm^{-2}sr^{-1}$, and at this ALAN value the expected number of territorial nighthawks was 87% (73%, 95%) lower than in surveys with high urban land cover but no detectable ALAN. The 95% CI for the interaction term between ALAN and urban land cover overlapped zero (Appendix C, Figure S4.6).

Urban land cover was selected at both the local scale (with a negative coefficient) and the landscape scale (with a positive coefficient), but the positive effect at the landscape scale arose from the high relative abundance of territorial nighthawks in one small, highly sampled area.

Fifty-six surveys at four stations, clustered < 2 km of each other on the outskirts of Victoria, accounted for 70% of the surveys where landscape-scale urban land cover was > 30%. After removing these surveys, the coefficient for landscape-scale urban land cover decreased substantially and the 95% CI overlapped zero. No other model coefficients changed substantially after removing these stations (Appendix C, Figure S4.7).

For territorial nighthawks, landscape-scale ALAN was not selected in any sample of the posterior distribution in the BLISS model (Figure 4.2b). We modified our relative abundance model in two ways to determine if ALAN at the landscape scale could have a positive marginal effect, after accounting for the negative effect at the intermediate scale, which was missed by our scale selection procedure. When we included both scales as separate covariates in our model, both had negative coefficient estimates (Appendix C, Table S4.5). When we fit a version of the model only including surveys at stations with no artificial light within 1600 m, the coefficient estimate for ALAN at the landscape scale was slightly negative, but with a very wide 95% CI that overlapped zero.

Common Poorwills

In the BLISS model, the spatial scale of ALAN that best explained the relative abundance of Common Poorwills was the intermediate scale (Figure 4.2c). We removed the interaction term between ALAN and urban in our final model for Common Poorwills because the sign of the coefficient for ALAN in the posterior samples depended on the coefficient of the interaction term, indicating that these two highly correlated variables were likely masking each others' effects (Appendix C, Figure S4.8). Nearly all samples of the posterior distribution included a negative coefficient for ALAN or for the interaction term, but the uncertainty about which covariate had a negative coefficient resulted in credible intervals for each covariate that included zero. To better estimate the main effect of ALAN, we removed the interaction term from the model and repeated the BLISS procedure, which selected the intermediate scale for ALAN. For urban land cover, the intermediate and landscape scales received equal support. We selected the intermediate scale because this scale was selected in our sensitivity analyses (Appendix C, Figures S4.4 and S4.10).

Relative abundance of Common Poorwills was negatively associated with ALAN. This relationship was less apparent at median and mean levels of urban land cover, where the range of ALAN values was small. For surveys with median (2%) or mean (5%) urban land cover at the intermediate scale, the expected number of poorwills declined by 20% (1%, 39%) and 21% (0%, 40%) as ALAN increased to 0.81 $nWcm^{-2}sr^{-1}$ and 0.88 $nWcm^{-2}sr^{-1}$, respectively (Figure 4.3c; Appendix C, Table S4.4). Where urban land cover was high (26%), ALAN reached up to 6.06 $nWcm^{-2}sr^{-1}$, which corresponded to a 32% (2%, 97%) decrease in the expected number of Common Poorwills. The 95% CI of the coefficient for urban land cover overlapped zero (Appendix C, Figure S4.6).

Detection probability models

We found some evidence that detection probability for individual nightjars was lower in sites with light pollution, but it did not influence the outcomes of our relative abundance analyses. When we modeled the effects of ALAN on the vocalization rates for each species and the wingboom rate for Common Nighthawks, the coefficients for ALAN and the CIs overlapped zero only for Common Poorwills. However, the probability that an individual, if present, would be detected within a 6-minute survey (i.e. detection probability) was above 75% even at the highest ALAN values (Appendix C, Figure S4.9). When ALAN increased from 0 $nWcm^{-2}sr^{-1}$ to the 99th percentile ALAN value (14.42 $nWcm^{-2}sr^{-1}$), detection probability decreased from 99% to

94% for extra-territorial Common Nighthawks, from 95% to 75% for territorial Common Nighthawks, and 98% to 78% for Common Poorwills. Although these decreases are notable, detection probability estimates may be unreliable at high ALAN values because data were sparse: only 10 territorial Common Nighthawks and 3 Common Poorwills were detected during surveys with ALAN radiance > 3 $nWcm^{-2}sr^{-1}$. Excluding surveys with < 90% detection probability from our relative abundance model did not substantially change the coefficient estimates for any nightjar group (Appendix C, Figure S4.10), indicating the effect of ALAN on nightjar counts was not confounded by the slightly lower detection probability during surveys with higher ALAN. For extra-territorial Common Nighthawks, excluding these surveys changed the selected scale for ALAN from the landscape scale to the local scale, and the coefficient values for ALAN and its interaction with urban land cover increased. These changes may have resulted from the removal of surveys that occurred before sunset. We saw the same changes when, instead of removing surveys based on detection probability, we removed surveys conducted before sunset (Appendix C, Figure S4.11).

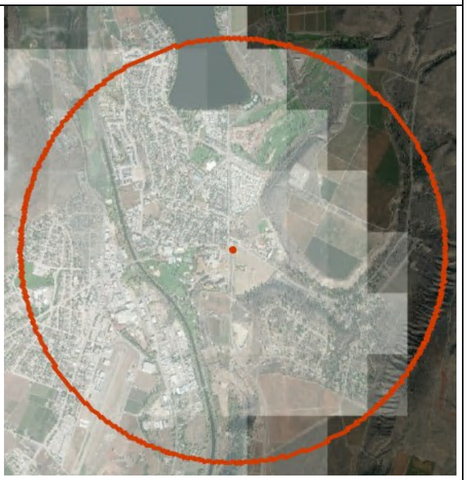
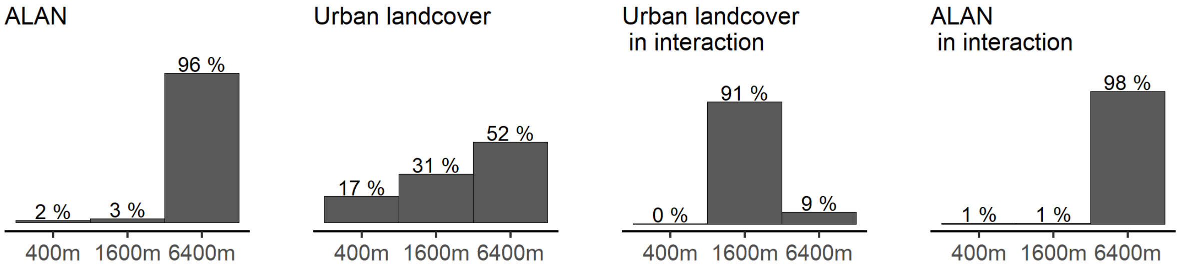
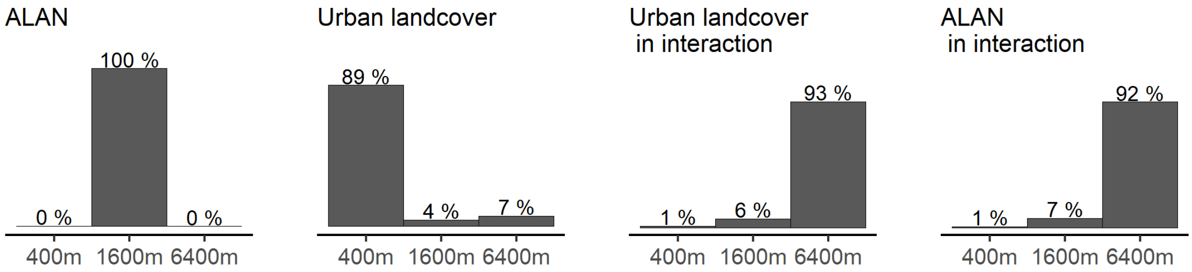
	Urban land cover	
	0-10 %	40-50%
Artificial light radiance:		
0 – 1 nWcm^{-2}sr^{-1}		
5-6 nWcm^{-2}sr^{-1}		
Legend: 0.0 – 0.5 0.5 – 1.0 1.0 – 3.0 3.0 – 5.0 5.0 – 10.0 10.0 – 20.0 20.0 – 200.0 (nWcm^{-2}sr^{-1})		

Figure 4.1 Examples of artificial light radiance values and urban land cover in a 1600-meter buffer

We calculated mean radiance within a 1600-meter buffer using the average of the Earth Observations Groups V1 annual composite for 2016 and V2 annual composite for the survey year. The red points represent survey points and red circles represent a 1600-meter radius. Pixels within these buffers with artificial light but no anthropogenic structures likely show skyglow, the reflection of the light off of particles in the atmosphere.


(a) Extra-territorial Common Nighthawks


(b) Territorial Common Nighthawks

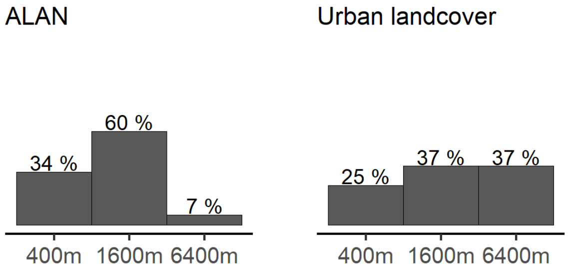

(c) Common Poorwills

Figure 4.2 Proportions of the posterior selecting each spatial scale for ALAN, urban, and their interactions in the BLISS models.

The BLISS model generates a posterior distribution for each covariate for the buffer size that best explains the relative abundance of nightjars. We tested three buffer sizes: 400, 1600, and 6400 meters. Bars show the percent of the 27,000 samples of the posterior distribution that selected each buffer size.

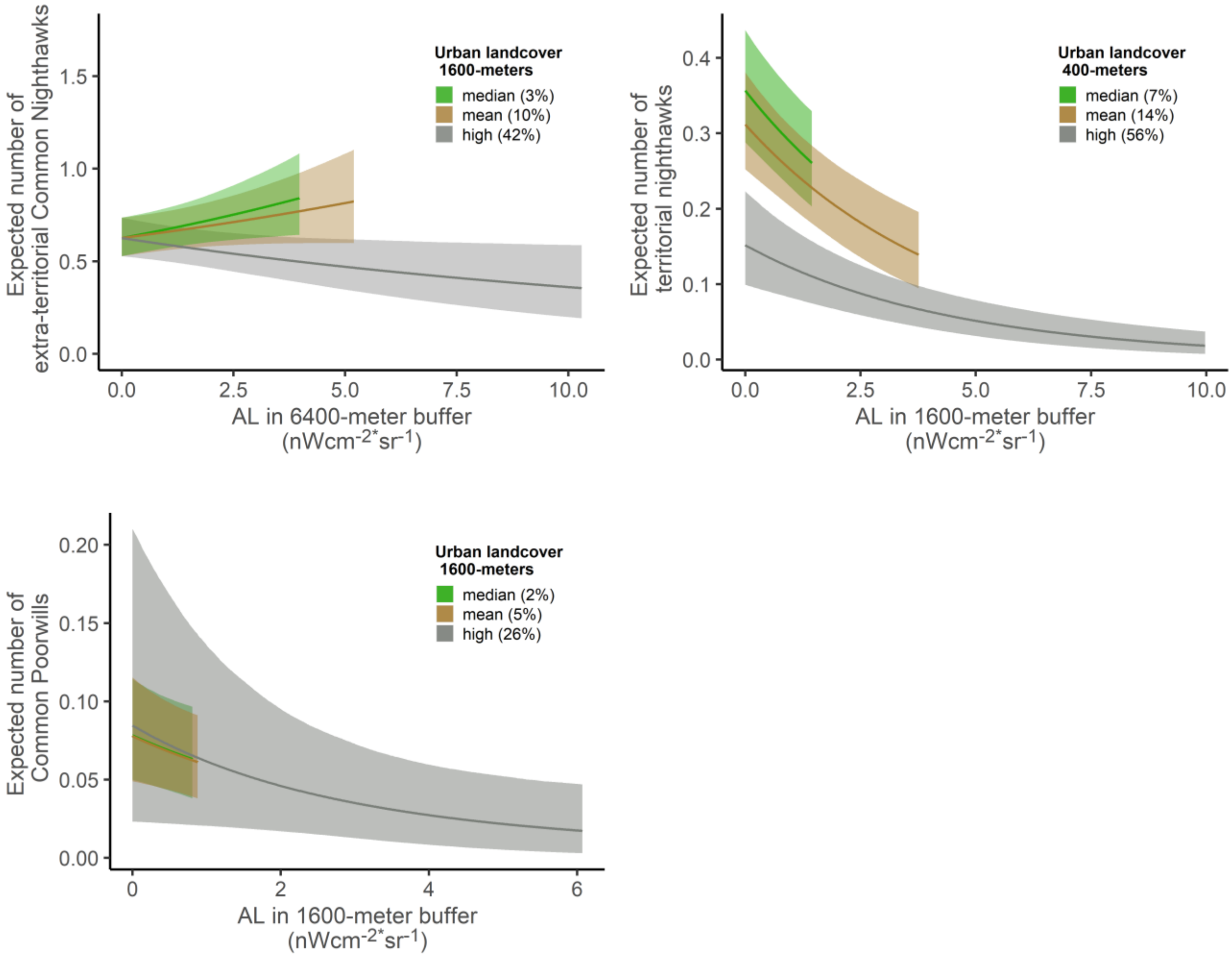


Figure 4.3 Model predications of relative abundance across ALAN levels at varying levels of urban land cover.

Results for (A) Extra-territorial Common Nighthawks, (B) Territorial Common Nighthawks, and (C) Common Poorwills. The high value of urban land cover shown is the 95th percentile within the selected buffer sizes. For each proportion urban land cover shown, we included model outputs up to the 99th percentile of ALAN values in surveys with up to and including that proportion of urban land cover. We set all other covariates to their mean values, unless otherwise specified.

Discussion

As ALAN increases in both urban and remote areas, it potentially benefits species that hunt flying insects by aggregating their prey, but could also increase predation risk, especially for species that nest on the ground. We used data from the Canadian Nightjar Survey in British Columbia to test the foraging benefit and predation risk hypotheses by investigating whether the relative abundance of Common Nighthawks and Common Poorwills increased or decreased in areas with ALAN. For Common Nighthawks, we found that the association with ALAN depended on whether nighthawks were exhibiting territorial or extra-territorial behaviour, and on the level of urbanization. The increased relative abundance of extra-territorial Common Nighthawks in sites with ALAN supported the foraging benefit hypothesis, but only in areas with low proportions of urban land cover. The predation risk hypothesis was supported by the decreased relative abundance of territorial Common Nighthawks and of Common Poorwills, which forage and nest within the same territory. Altogether, this work demonstrates that the effects of ALAN can shift depending on behavioural context, level of urbanization, and whether a species forages outside of its nesting territory.

Foraging benefit hypothesis

Although many aerial insectivores have been observed foraging under artificial lights, our results suggest that these foraging benefits of ALAN may be limited to less urbanized areas and to species that can spatially separate their foraging from their nesting sites. We found a negative effect of artificial light on the relative abundance of Common Poorwills, suggesting that this species was not foraging under artificial lights. In contrast, the relative abundance of extra-territorial Common Nighthawks showed a positive association with artificial light in areas with low proportions of urban land cover, suggesting that ALAN was attracting them to areas with light, presumably to forage. However, the wide 95% credible intervals show a high degree of uncertainty about this relationship.

The interaction between ALAN and urban land cover for extra-territorial Common Nighthawks resulted in a negative association in areas where urban land cover was > 25%, suggesting that they do not forage under artificial lights in these areas. This level of urban land cover characterizes low-density neighborhoods and areas on the edges of towns and cities (Appendix C, Figure S4.12), so this negative relationship occurs even at low levels of urbanization. There are several possible explanations for why extra-territorial Common Nighthawks showed a negative relationship with ALAN in urban areas. The cumulative effects of urban stressors may reduce insect populations (Langevelde et al. 2018; Boyes et al. 2020, 2021) could result in in fewer insects attracted to streetlights (Camacho et al. 2021). Aerial-hawking bats have also been found to benefit more from artificial light in natural areas than in cities (Barré et al. 2021). Difficulty foraging in areas with urban clutter (e.g. fences and buildings), which prevented large-sized bats from foraging under ALAN (Li and Wilkins 2022), could also explain this pattern for nighthawks. We only measured urban land cover, which is based on impervious surfaces, but other metrics of urbanization may reveal which aspects of human development interact with ALAN to affect the relative abundance of aerial insectivores.

The change in the spatial scale at which ALAN best explained the relative abundance of extra-territorial nighthawks from landscape scale before sunset to local scale after sunset further supports the hypothesis that Common Nighthawks may forage under artificial lights in non-urban areas at night. Nighthawks may not begin foraging under light sources until after sunset, when lights turn on and the number of insects attracted to light increases as ambient light levels decline (Eisenbeis 2006). Individuals that forage under light sources at night may travel through the surrounding landscape throughout the day, resulting in the positive association between extra-territorial Common Nighthawks and ALAN at the landscape scale before sunset. This increase in abundance at the landscape scale at certain times may have important implications for their prey species and their competitors. Such movements by Common Nighthawks and other species with large home ranges would be one mechanism by which local impacts of ALAN can extend beyond the directly illuminated area.

Our final prediction for this hypothesis was not supported; the relative abundance of territorial nighthawks did not show a positive relationship with ALAN at the landscape scale as we expected if they traveled from their nest sites to forage under artificial lights. Despite fitting additional versions of our model to test for the marginal effects of landscape scale ALAN on the relative abundance of foraging nighthawks, we consistently found a negative effect. The discrepancy between the relative abundance of nesting and foraging nighthawks in light-polluted landscapes has several possible explanations.

Predation cost hypothesis

Both territorial Common Nighthawks and Common Poorwills were negatively associated with ALAN, supporting the hypothesis that artificial light increases nest predation risk. Predation was the most common cause of nest failure in several studies of nightjars (Langston et al. 2007; Allen and Peters 2012). Nightjar eggs, nestlings, and incubating adults are particularly vulnerable to predators because they have limited mobility for three weeks after hatching (Brigham et al. 2020). Foraging adults have a lower predation risk because they can move away from predators, and artificial light may actually improve their ability to detect predators and take evasive action (Prugh and Golden 2014). The decrease in relative abundance of Common Nighthawks only when on their territories, where they are most vulnerable to predation, supports the hypothesis that increased predation risk drives this pattern of relative abundance. However, other stressors specific to nesting, such as ALAN's impacts on sleep and nestling development (Raap et al. 2016c; Grunst et al. 2020) or correlations between predator abundance and ALAN, could also explain territorial nighthawks' lower relative abundance near ALAN. The overall negative effect of ALAN on the relative abundance of Common Poorwills suggests that the costs of nesting near ALAN outweigh the foraging benefits for species that conduct both activities in the same territory.

The response of Common Nighthawks and Common Poorwills to intermediate scale ALAN demonstrates how the impacts of ALAN extend far beyond directly illuminated areas, but our ability to identify the most predictive scale was limited. A spatial scale between 1.6 km and the next buffer size we tested (6.4 km) may have been selected if we could have included more scales in the BLISS model. The ALAN measured in the 1.6 km buffer included light that originated outside of that buffer because the EOG radiance estimates are influence by skyglow (Sanchez de Miguel et al. 2020). Furthermore, the radiance value for each pixel in the composite is influenced by light sources outside of the pixel boundary because the composites use area-weighted-averages of multiple images with different pixel positions and orientations (Kyba et al. 2020a). While the spatial scale of ALAN's impacts on the relative abundance of territorial nightjars is uncertain, it is likely larger than 1.6 km.

Artificial light may have affected nest predation risk directly by increasing skyglow or indirectly by affecting trophic relationships. Skyglow can increase ambient illumination levels tens of kilometers from a light source, especially on cloudy nights (Kyba et al. 2011; Jechow et al. 2017), which may have increased the actual or perceived nest predation risk for nightjars in our study area. Some nest predators like American Crows (*Corvus brachyrhynchos*) prefer to roost in illuminated areas at night (Gorenzel and Salmon 1995), which may also increase their abundance in artificially illuminated landscapes during the day. Our results contrast with studies that found no correlation between breeding bird densities and ALAN when studying non-ground nesting species and only measuring ALAN at a local scale (Jong et al. 2015; Russ et al. 2017;

Wang et al. 2021). This contrast suggests that ALAN affects ground-nesting nocturnal birds more than other species, or that the effects of ALAN occur at larger spatial scales than measured in other studies.

Common Nighthawks can forage far from their nest sites, possibly allowing them to reap the benefits of foraging on insects that aggregate under ALAN while avoiding any negative impacts of lighting on nest success. However, the negative effects of ALAN on territorial Common Nighthawks across multiple spatial scales casts doubt on whether individuals with territories are actually foraging under ALAN. There are several possible explanations for the lower relative abundance of territorial nighthawks in light polluted landscapes despite the higher relative abundance of extra-territorial individuals. Nesting nighthawks may have traveled farther than 6.4 km to forage under artificial lights, which would require a high energetic benefit from this foraging behaviour to sustain the travel cost (Evens et al. 2018). Another explanation is that there were more nighthawks nesting in artificially lit landscapes than we counted, but they spent less time wingbooming because nestlings with increased nocturnal activity under ALAN required the adults to spend more time foraging to meet their energetic demand (Titulaer et al. 2012, but see Welbers et al. 2017 and Injaian et al. 2021). Alternatively, most individuals foraging under artificial lights may not have been able to establish a nest or they made breeding attempts that failed (Van Horne 1983). Because the Canadian Nightjar Survey does not track individuals over time or conduct repeat visits, we cannot evaluate these potential explanations. Our analysis shows that the impacts of ALAN on patterns of nightjar relative abundance are widespread, and the processes that drive these patterns occurs throughout the species' ranges in British Columbia.

Implications

Reports of species foraging under artificial lights in particular locations should not be interpreted to mean that this behaviour is ubiquitous and that ALAN has net benefits for them. Our results contrast with reports of nightjars sometimes foraging under artificial light in cities (Shields and Bildstein 1979; Foley and Wszola 2017). Occasional observations of foraging under ALAN do not necessarily mean that this behaviour is common in a population or species relative to individuals of the same population foraging in less illuminated areas. Due to these observation biases, this behaviour may be overrepresented in the literature. Research that covers large spatial scales and includes both illuminated and unilluminated areas is important for understanding whether this behaviour is widespread enough to impact species abundance patterns. Community science programs should continue to target dusk and nighttime surveys, documenting all bird species seen or heard, to better understand the impacts of ALAN over broad spatial scales.

Behaviour research over smaller spatial scales is also necessary to reveal the mechanisms that drive the patterns we observed in our study. Experimental illumination over several breeding seasons could reveal whether the introduction of ALAN alters relative abundance of ground-nesting species and foraging aerial insectivores, and how it affects their survival and reproductive success. Foraging under artificial lights may result in lower survival and/or reproductive success if it exposes nightjars and other birds to road mortality, especially if they roost on gravel roads between foraging bouts (Jackson and Slotow 2002; Jackson 2003; Fortney 2010). Birds preying on insects could themselves become prey to raptors whose hunting activity extends into the night in artificially lit areas (Rutz 2006; Canário et al. 2012; Buij and Gschweng 2017). Ultimately, experimental and mechanistic studies are needed to understand how ALAN's influence on behaviour and habitat use influences population trajectories for aerial insectivores and/or ground-nesting birds.

Our results suggest that limiting light pollution in the ranges where nightjars occur would have positive effects on these species. Efforts to reduce the impacts of ALAN for nightjars could target nest sites identified by the Canadian Nightjar Survey and eBird, as well as likely nest sites, which include gravel, sand, bare rock, recently disturbed forest, and open pine forest (Brigham et al. 2020; Knight et al. 2021b). Because the impacts of ALAN extend beyond the directly illuminated area, nightjars could benefit from reduced artificial light within several kilometers of ecologically sensitive areas.

Highlighting ALAN's impacts on breeding birds of sensitive and declining species could increase public support for reducing light pollution during the breeding season, just as bird collisions with illuminated structures have inspired efforts to turn off city lights during migration (National Audubon Society). Surveys have found that the negative effects of ALAN on wildlife motivate people to support light pollution regulation (Lyytimäki and Rinne 2013; Beaudet et al. 2022). Reducing light pollution during the avian breeding season would benefit other taxa, including insects, bats, and even humans (Svechkina et al. 2020).

There are many strategies for reducing light pollution, including removing unnecessary light sources and preventing new light sources from being installed (Gaston et al. 2012). When lights cannot be eliminated, motion sensors can turn them on only when light is needed and dimming lights can reduce their ecological impacts (Rowse et al. 2018). Shading light sources can limit the directly illuminated area and reduce skyglow, limiting the spatial extent of ALAN's impacts. As humans extend our activities into the night over a growing portion of the globe, year-round reductions in light pollution will promote both human and ecological health.

Statements & Declarations

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Competing interests

The authors have no financial or non-financial interests to disclose.

Author Contributions

All authors contributed to developing the study objectives and design. Data processing and analysis were conducted by Carrie Ann Adams, who also wrote the first draft of the manuscript. All authors commented on subsequent versions of the manuscript and read and approved the final manuscript.

Data Availability

Data from the Canadian Nightjar Survey are available through the NatureCounts platform (https://naturecounts.ca/nc/default/main.jsp). To request a copy of the data organized into number of individuals counted per survey for Common Nighthawks and Common Poorwills, please contact caadams1@ualberta.ca.

Chapter 5. Artificial light sometimes alters spatial but not temporal habitat use by a crepuscular aerial insectivore

Abstract

As artificial light increases worldwide, it has biological effects from the molecular to ecosystem level, which may be particularly severe for crepuscular and nocturnal animals. We investigated how artificial light affected spatial and temporal patterns of habitat use by Common Nighthawks (*Chordeiles minor*) in the southern Grassland region and northern Boreal region of Alberta. Nighthawks potentially benefit when foraging from aggregations of insects near light sources, but may suffer increased predation risk at their cryptic ground nests if light increases their visibility. We predicted a negative association with artificial light for territorial habitat use where nighthawks are likely nesting and a positive association for extra-territorial habitat use where they are likely foraging. We recorded the different sounds made by nighthawks that reveal when they are defending a breeding territory and then measured intensity of territorial and extra-territorial habitat use at 259 acoustic recording stations in the Grassland region and 255 in the Boreal region. Where nighthawks were more abundant, we also determined whether vocal activity patterns across sun angle and twilight periods differed between stations with and without artificial light at different latitudes. We found a negative association with artificial light for both territorial and extra-territorial habitat use in the Grassland region, but no effect of light on use of either type of habitat in the Boreal region. Similarly, we found no effect of artificial light on overall vocal activity patterns, sun angles of peak activity, or activity during nautical and astronomical twilight. Artificial light may be more likely to affect spatial habitat use by crepuscular birds in southern Canada, where natural illumination is lower during twilight than in

northern areas. Artificial light does not appear to affect circadian rhythms or extend foraging activity for Common Nighthawks in Alberta.

Introduction

Artificial light is growing worldwide, creating a very different nocturnal environment from that under which most life evolved (Falchi et al. 2016; Kyba et al. 2017; Seymoure et al. 2019a). The negative effects of artificial light have been documented across many taxa and levels of biological organization, from changes in gene expression to altered community composition (Davies et al. 2012; Sanders et al. 2020; Chen et al. 2021; Rodrigo-Comino et al. 2021). Both direct illumination and skyglow, the reflection of artificial light off of particles in the atmosphere and back towards earth, are changing the nocturnal environment within cities, rural areas, and natural protected areas (Gaston et al. 2015; Falchi et al. 2016). Between sunset and sunrise, artificial light increases spatial variation in illumination levels where artificially illuminated areas are much brighter than the surrounding landscape. Furthermore, areas that are illuminated throughout the night necessarily have less temporal variation in illumination levels than areas experiencing natural darkness.

Artificial light may affect habitat use patterns by altering individual movement and habitat selection. Some species show an innate attraction to or avoidance of artificial light, including sea turtles (*Chelonioidea*) drawn towards lights on their first journey to sea (Thums et al. 2016) and nocturnally migrating birds aggregating around illuminated structures (Gauthreaux and Belser 2006). Other species respond behaviourally to changes in the environment caused indirectly by artificial light, such as increased prey densities or predation pressures (Rodríguez et al. 2020; Nuñez et al. 2021), by selecting or avoiding illuminated areas (Quiñones-Llópiz et al. 2021). Over time, the effects of artificial light on individual mortality and/or reproductive success can also alter spatial habitat use (Owens and Lewis 2018; van Grunsven et al. 2020), even leading to local extinctions in extreme cases (Yoon et al. 2010). Increases or decreases in spatial habitat use patterns are used to infer whether artificial light benefits or harms a species (Simons et al. 2021; Korpach et al. 2022), while recognizing the potential of artificial light as an ecological trap for species that increase habitat use in illuminated areas (Gilroy and Sutherland 2007; Firebaugh and Haynes 2019).

Artificial light can also alter temporal patterns of habitat use, especially the periods of activity and inactivity in occupied sites across the daily light cycle. Most organisms have circadian clocks that are entrained, or synchronized, to the 24-hour light cycle and maintained through complex physiological feedback loops involving gene expression (reviewed by Rusak and Zucker 1979; Cymborowski 2010). Illumination also governs daily activity patterns by directly inhibiting or stimulating physiological changes without involving circadian gene expression in a process called masking, named as such because it masks the expression of circadian rhythms (Hut et al. 2012; Kronfeld-Schor et al. 2013; Russart and Nelson 2018). Artificial light can also alter temporal habitat use by inducing behavioural responses to new environmental pressures and opportunities, allowing individuals to alter their daily activity patterns even when circadian rhythms remain unchanged (Kronfeld-Schor et al. 2001) . For mobile species, behavioural responses can include moving between illuminated and dark sites, resulting in changes in the number of individuals present in each type of site throughout the day (Santos et al. 2010). Many diurnal and crepuscular species have been documented foraging under artificial light at night, representing a major shift from their typical patterns of temporal habitat use (King 1967; DeCandido and Allen 2006; Buij and Gschweng 2017; Maurer et al. 2018).

The spatial and temporal aspects of habitat use can be intertwined, with spatial habitat use sometimes changing over time and temporal habitat use changing over space. When measuring patterns of spatial habitat use, one must define the temporal extent of these patterns or assume that temporal habitat use patterns remain constant across sites. The probability of detecting a species at an occupied site can shift over the course of the day. To maximize detection probability, researchers often schedule data collection to correspond to the peak activity times of the species of interest (e.g. Pérez-Granados et al. 2021, Tozer et al. 2016) or the time when detection rates are most stable (Ralph et al. 1995). However, this could cause errors in estimates of habitat use if artificial light affects temporal patterns of habitat use. For example, diurnal birds are known to begin singing earlier in the presence of artificial light (Miller 2006; Da Silva et al. 2014, 2015; Da Silva and Kempenaers 2017; Wilkinson et al. 2022; Marín Gómez 2022). Little is known about how crepuscular and nocturnal birds shift their vocal activity in sites with artificial light, although they can change their daily activity patterns across the lunar cycle (Aldridge and Brigham 1991; Brigham and Barclay 1992; Jetz et al. 2003; Woods and Brigham 2008). Spatial factors can also influence temporal patterns of habitat use, and the influence of artificial light on vocal activity timing can change across latitudes (Da Silva and Kempenaers 2017).

We investigated the relationship between artificial light and the spatiotemporal habitat use for a crepuscular species, the Common Nighthawk (*Chordeiles minor*). We defined habitat use as the vocalizations and territorial displays of our study species, which indicate that they are actively using the site for breeding and/or other behaviours at the time of the detection. We used acoustic recordings to measure habitat use in two regions of Alberta and included recordings from sun angles ranging from before sunset to after sunrise. If artificial light exhibits consistent effects on birds regardless of natural light levels, we predicted that the association between their spatial habitat use and artificial light would remain consistent across their range. We expected to find patterns similar to those we observed in our previous study in British Columbia, where we found that territorial habitat use was negatively associated with artificial light, possibly due to increased nest predation risk. In British Columbia, there was a positive association with artificial light for extra-territorial habitat use in areas where there was little urban development, possibly because it enhances foraging on light-attracted insects. We expected to find a similar positive association in Alberta if nighthawks gained an energetic advantage from foraging under artificial light during late twilight.

At recording stations where Common Nighthawks occurred, we also studied their temporal patterns from before sunset to after sunrise to determine whether artificial light changed their vocal activity patterns in relation to sun angle. If artificial light shifted their vocal activity pattern through circadian entrainment or masking effects, we predicted a shift in the peak activity periods towards lower sun angles, meaning later in the evening and earlier in the morning. If nighthawks foraged on insects aggregating under artificial lights, we expected activity during nautical and astronomical twilight to be higher at stations with artificial light than stations without. We compared the relationship between artificial light and their spatial and temporal habitat use in the two regions that experience different natural illumination levels during the breeding season, one in the forested areas of Northern Alberta and one in the open grassland/agricultural areas of Southern Alberta.

Methods

Study Area

Our study area included the Grassland and Boreal natural regions of Alberta, Canada. The Grassland region is mostly flat with gently rolling plains and includes badlands, native prairie, rangelands, and areas of intensive agriculture. Our study stations in the Grassland region ranged in latitude from 49.0°N to 51.5 °N. The Boreal region consists of upland and lowland forests, as well as low-lying wetlands. Our study stations were between 54.4°N to 57.8°N. We collected acoustic recordings between June 1st and July 15th. In the Grassland region on these dates, true night, defined by a sun angle lower than -18°, only occurs at the lowest latitudes and astronomical twilight (-12° to -18° sun angle) occurs for a minimum of 2.76 hrs and a maximum of 4.5 hours (Figure 5.1). Total twilight is shorter in the Boreal region than in the Grassland region, but civil (0° to -6°) and nautical (-6° to -12° sun angle) twilights are longer (Figure 5.1). In the Boreal region, astronomical twilight only occurs during our study period at the lower latitudes and true night does not occur.

Measuring artificial light

We created annual composites to estimate artificial light based on the monthly composites from the Earth Observation Group (EOG) (Elvidge et al. 2017). The annual composites provided by the EOG (Annual VNL V2) did not detect dim lights in our study area which were visible in the monthly composites, possible due to the aurora correction procedure applied to annual composite. In our annual composites, we included the monthly composites from August, September, and October. Summer months had little or no coverage in many pixels, while winter months had high variability year-to-year. This variability is likely due to changes in snow cover, which strongly affects radiance estimates (Levin 2017). We applied a natural light correction adapted from the Ceosfeld et al.'s (2020) airglow correction. This procedure divided the study area into grid cells and found a point unlikely to have artificial light in each grid cell based on the 2015 Annual VNL V1 composite from EOG (Elvidge et al. 2017) and the Global Human Settlement Layer from 2014 (Schiavina et al. 2022). We then subtracted the radiance value at that point from the other pixels within the grid cell. We use a grid cell size of 0.25° latitude by 0.5° longitude. Radiance values below 0.2 $nWcm^{-2}sr^{-1}$ were set to 0 to reduce the residual influence of the aurora. Finally, we used the median value of the three monthly composites for each year to create annual composites. We compare these composites to Annual VNL V2 in Figure S5.1.

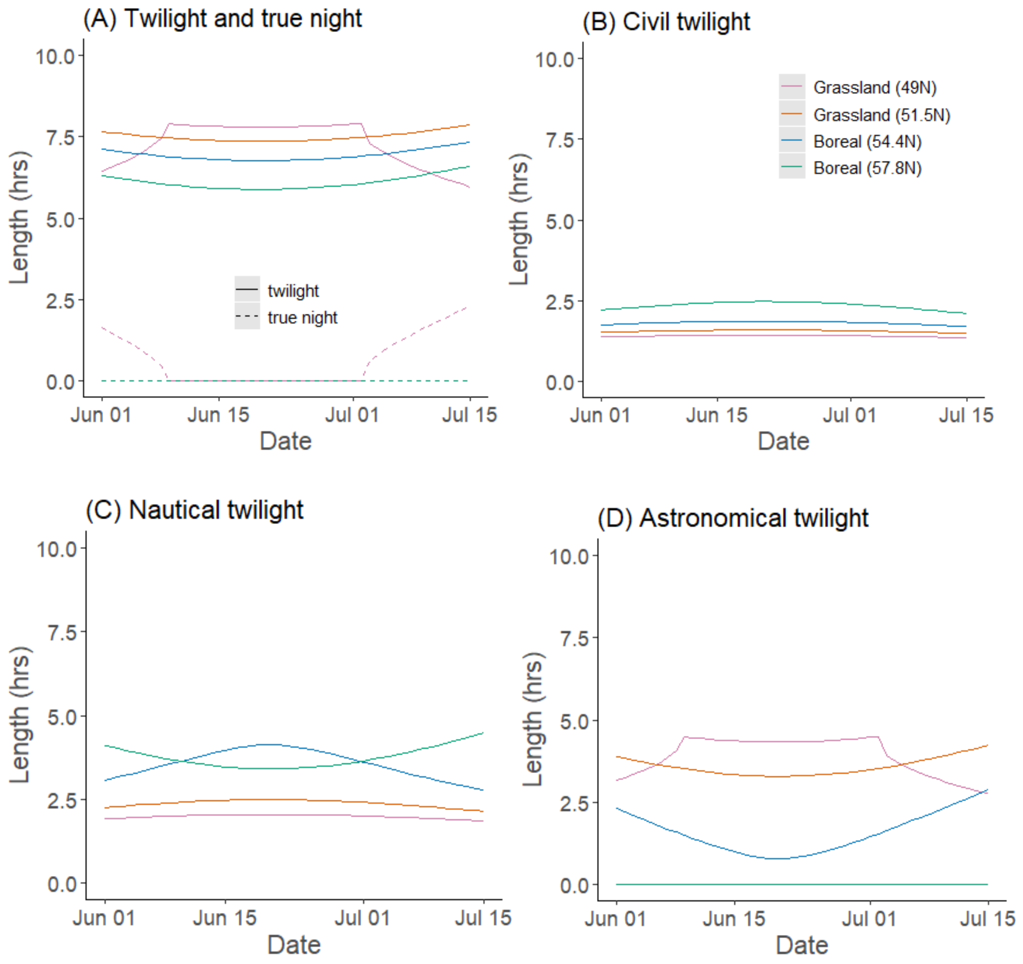

Figure 5.1 Length of twilight periods and true night at the minimum and maximum latitudes for survey stations in each region during the study period

Twilight is divided into civil (0° to -6° sun angle), nautical (-6° to -12° sun angle) and astronomical twilight (-12° to -18° sun angle). Twilight lengths include both morning and evening twilight periods. True night occurs below -18° sun angle. The twilight curves in panels (A) and (D) show a different shape for 49ºN than for the other latitudes at the beginning and end of the study period because some of the time between sunrise and sunset is taken up by true night (<-18º sun angle), which doesn't occur at higher latitudes. The maximum latitude in the Boreal region (57.8ºN) shows a different curve in panel (C) than the other latitudes because astronomical twilight does not occur at this latitude on these dates, so the entire time between -6º in the evening and -6º in the morning is classified as nautical twilight. This period is shortest on June 21st, the summer solstice. At the other latitudes, the transition to/from astronomical twilight marks the end of nautical twilight in the evening and the beginning of nautical twilight in the morning. Nautical twilight is longest on June 21st, when this transition occurs latest in the evening and earliest in the morning.

Spatial patterns of habitat use

In the Grassland region, we placed 259 acoustic recording units at least two kilometers apart from each other on wooden telephone poles on dirt roads for at least 5 days (Figure 5.2). They were placed in areas with little to no urban development, sometimes near rural residences, farms, livestock operations, or oil and gas infrastructure. The 241 units recording in 2021 recorded for three minutes every twenty minutes, while the 18 units recording in 2020 recorded for 3 or 10 minutes at various times throughout the day. In the Boreal region, we used the acoustic recordings that were collected for other projects in the Lower Athabasca Planning Region (Knight et al. 2020, 2021b, 2022), which had varying recording schedules. We selected locations that had twilight and nighttime recordings and spatially thinned the locations by selecting one in each 3.55 km^2 grid cell using the *dggridr* package in *R 4.2.1* (Barnes and Sahr 2017). We preferentially retained stations with artificial light, which were less common, to maximize the number of these stations in our sample.

Common Nighthawks defend a small territory (~10 ha) around their nest using a mechanical wingboom, and vocalize across their home range (Knight et al. 2021a). We used visual scanning of spectrograms to identify Common Nighthawk vocalizations and wingbooms in one-minute recordings. We used stratified random sampling across the activity period in each region, which included sun angles < 12° in the Boreal region and < 24° in the Grassland region, where we found that nighthawk activity began earlier in the evening. We measured all solar and lunar variables using the *suncalc* package in *R* (Thieurmer and Elmarhraoui 2019). We divided this range into 6° sun angle increments and selected three recordings from each increment, using separate increments for evening (before the zenith) and morning (after the zenith) sun angles. The lowest sun angle increment included all sun angles < -6° in the Boreal region and <-12° in the Grassland region. We divided the recordings into ten-second clips and created spectrograms in *SoX* using a sample rate of 13k, showing frequencies between 0 and 6.5 kHz (Bagwell). The first author visually identified vocalizations and wingbooms, listening to the recordings when necessary.

We defined the intensity of territorial use at each station as the proportion of recordings in which we detected wingbooms and the intensity of extra-territorial use as the proportion in which we detected peent vocalizations. We used quasi-binomial generalised linear models (GLM), with the intensity of territorial or extra-territorial habitat use as the response variables. We included occurrence predictions from previous studies as covariate in our GLMs. In the Grassland region, we used the probability of occurrence map created by Knight *et al.* (Knight et al. 2021c) for both our territorial and extra-territorial model. These predictions were based on point count data from the Breeding Bird Survey and the Canadian Nightjar Survey and included urban landcover from the 2010 Land Cover of Canada dataset (Natural Resources Canada). In the Boreal region, we used the probability of occurrence for the Lower Athabasca Planning Region published by Knight *et al.* (Knight et al. 2022), using the territorial occurrence probability predictions for our territorial model and the home range occurrence probability predictions for our extra-territorial model. Industry footprint, based on the Alberta Biodiversity

Monitoring Institute human footprint layer (Alberta Biodiversity Monitoring Institute 2022), was included in these occupancy predictions, but had low relative influence (Knight et al. 2022). These predictions were based on nighthawk detections in acoustic recordings, some of which were recorded in the same locations where we measured intensity of habitat use. For the extra-territorial analysis, we removed stations where nighthawks were detected wingbooming. Because we could not distinguish individuals, we did not know whether extra-territorial individuals, in addition to the territorial individuals, were present at these stations.

We estimated the mean and standard errors for model coefficients using bootstrap sampling. We spatially thinned the stations included in each bootstrap sample, selecting one recording from each 10.66 km^2 hexagonal grid cell created using *dggridr* and then resampling with replacement (Barnes and Sahr 2017; Robinson et al. 2018; Ploton et al. 2020). We fit five versions of the model in each bootstrap sample, each with a different buffer size for artificial light. We tested 400, 800, 1600, 3200, and 6400 m, the same as were used in previous studies of our species (Knight et al. 2021b, 2022). We used any stations that were not selected in each bootstrap sample as test data and calculated the prediction error as the mean of the squared residuals in each buffer size. We selected the buffer size that had the lowest mean prediction error across bootstrap samples.

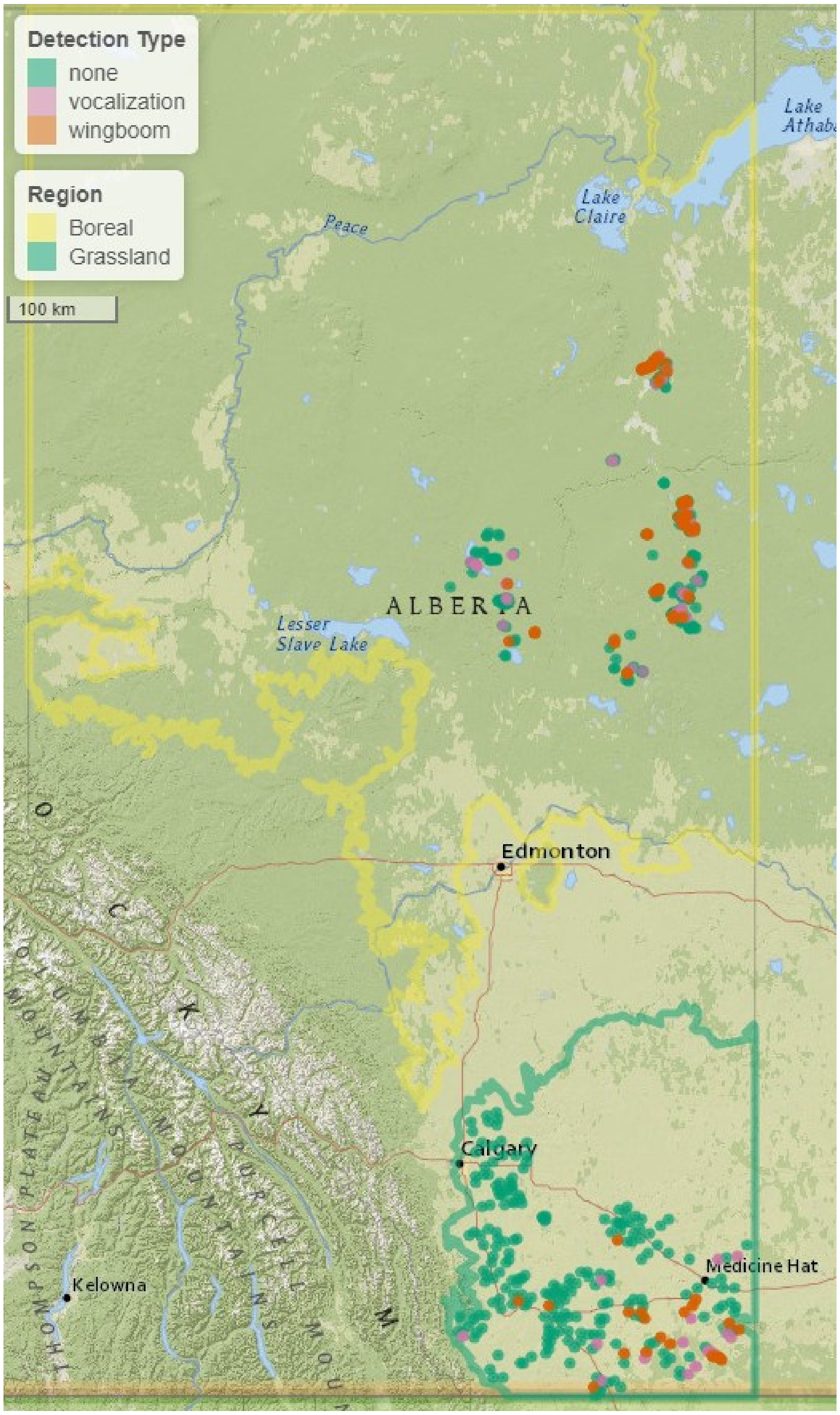

Figure 5.2 Map of study area and recordings stations for spatial habitat use analysis

We used recordings from 259 autonomous recordings units (ARUs) in the Grassland region of Alberta and 255 ARUs in the Boreal region to study intensity of spatial habitat use by Common Nighthawks.

Temporal patterns of habitat use

We defined vocal activity as the probability of detecting a nighthawk at least once in a one-minute recording. We compared vocal activity in relation to sun angle at stations with and without artificial light where nighthawks have been detected (Figure 5.3). We included stations where nighthawks were found when visual scanning for our spatial habitat use analysis, as well as stations with nighthawks identified through visual scanning in *Wildtrax* (Alberta Biodiversity Monitoring Institute and Bioacoustic Unit) or by a Song Scope recognizer for other analyses (Knight et al. 2020, 2021b, 2022). We only included stations where we detected nighthawk vocalizations in at least 5% of recordings with < 6° sun angle. We spatially thinned these stations to be ≥ 2 km apart by randomly selecting stations with artificial light that were at > 2 km apart from each other, then randomly selecting dark stations ≥ 2 km from the selected light stations and from each other. The spacing ensured that the same nighthawk vocalization would not be counted at two stations. The maximum detection radius for nighthawks using ARUs and viewing spectrograms in Raven Pro is estimated at 500-meters (Bioacoustics Research Program 2014; Yip et al.), and our detection radius using *SoX* spectrograms may have been larger.

At the selected stations, we visually scanned six one-minute recordings that we randomly selected within each 6° sun angle increment lower than 18°. We extended our analysis to sun angles < 30° in the evening at stations where astronomical twilight occurred (i.e. sun angle reached < -12°) after we found that nighthawks sometimes remained active at 18° sun angle. In the Boreal region, we conducted separate analyses on the days when sun angle did or did not reach as low as -12°, the upper boundary of astronomical twilight. We did this to avoid fitting our models to sun angles far below those which occurred at a particular station/day combination. If a station had recordings from days with and from days without astronomical twilight, we selected up to six recordings in each sun angle increment during each type of day. If fewer than six recordings were available in a sun angle increment, we selected all of the available recordings. For the analysis of days with astronomical twilight, we removed stations that had fewer than 20 recordings from days in this category.

We classified stations with greater than 0.5 nWcm-^{2}sr^{-1} radiance within a 500-meter buffer as light stations and stations with 0 nWcm-^{2}sr^{-1} as dark stations. We excluded from the analysis any sites with artificial light estimates between 0 and 0.5 nWcm-^{2}sr^{-1} to ensure an adequate difference between the light and dark groups.

Separately for the Boreal and Grassland regions, we used Hierarchical Generalised Additive Models (HGAMS) to model the non-linear relationships between sun angle and vocal activity (Pedersen et al. 2019). With vocal activity as the response variable, we used a random effect spline for station and a parametric model term for light to account for differences in mean vocal activity at different stations or at light versus dark stations. We used a thin-plate regression spline (TPRS) smoother for the effect of ordinal day on vocal activity. We modeled the interactive effect of lunar fraction and sun angle on vocal activity using a tensor product interaction, which estimates the interaction and the main effects for each variable. When the moon was below the horizon, we set lunar fraction to zero.

To model the effect of artificial light on the overall relationship between vocal activity and sun angle, we compared four versions of each HGAM with different smoothers for sun angle. The first version modeled an interaction between sun angle and artificial light by using separate TPRS sun angle smoothers for stations with and without artificial light and separate smoothing penalties. We compared the Akaike's Information Criteria (AIC) of this model to one with a common global smoother for all stations (Pedersen et al. 2019), modeling no interaction effect of sun angle and artificial light on vocal activity. We also compared each of these models to versions with individual sun angle smoothers for each station that shared a smoothing penalty, allowing each station to have its own response curve but penalizing curves that were too far from the average. This comparison tested for variation in the relationship between sun angle and vocal activity across stations, unrelated to artificial light. In any model iterations where the number of basis function for a smoother was not at least two greater than the effective degrees of freedom for that smoother, we increased the number of basis functions by five (Pedersen et al. 2019).

Using the HGAM with separate global smoothers for light and dark stations, we estimated the difference in sun angle of vocal activity peaks between light and dark stations in the morning and evening. For 1,000 bootstrapped samples from our recording data, we fit the HGAM and then subtracted the predicted sun angles of peak vocal activity for dark stations station from the predictions for light stations. Computational constraints prevented us from estimating these peaks for versions of the HGAM with station-level sun angle smoothers.

Using the same recordings that we used for the HGAM, we used binomial generalised linear mixed effects models to compare the probability of detecting a vocalization in a one-minute recording in light and dark stations during civil twilight (0° to -6° sun angle), nautical twilight (-6° to -12°) and astronomical twilight (-12° to -18°), separating the morning and evening twilight periods. We used the *lme4 R* package (Bates et al. 2015) and included a random effect for station. We used separate analyses for the Grassland region and for the Boreal region for days with and without astronomical twilight. We used the Likelihood Ratio Test to compare the goodness-of-fit for nested models with only twilight period as a predictor, with main effects for twilight and artificial light, and an additional interaction between twilight and artificial light. Using the model with the interaction term, we made *post hoc* pairwise comparisons for the differences in mean vocal activity between light and dark stations during each twilight period using the *emmeans R* package (Lenth et al. 2022), calculating p-values using both a Bonferroni and a Sidak correction for multiple tests.

We did not include occupancy predictions in our analyses of temporal habitat use because all stations included in these analyses were occupied and because it would reduce our sample size in the Boreal region, where the predictions only covered the Lower Athabasca Planning Region (Knight et al. 2022). We also had no *a priori* reason to believe that occupancy probability should affect the timing of activities within stations, though it could correlate with overall vocal activity via higher nighthawk abundance. For any of the GLMMs of vocal activity showed a significant main effect of artificial light on vocal activity, we fit a version of the model with occupancy predictions as a covariate, removing any stations for which the predictions were unavailable.

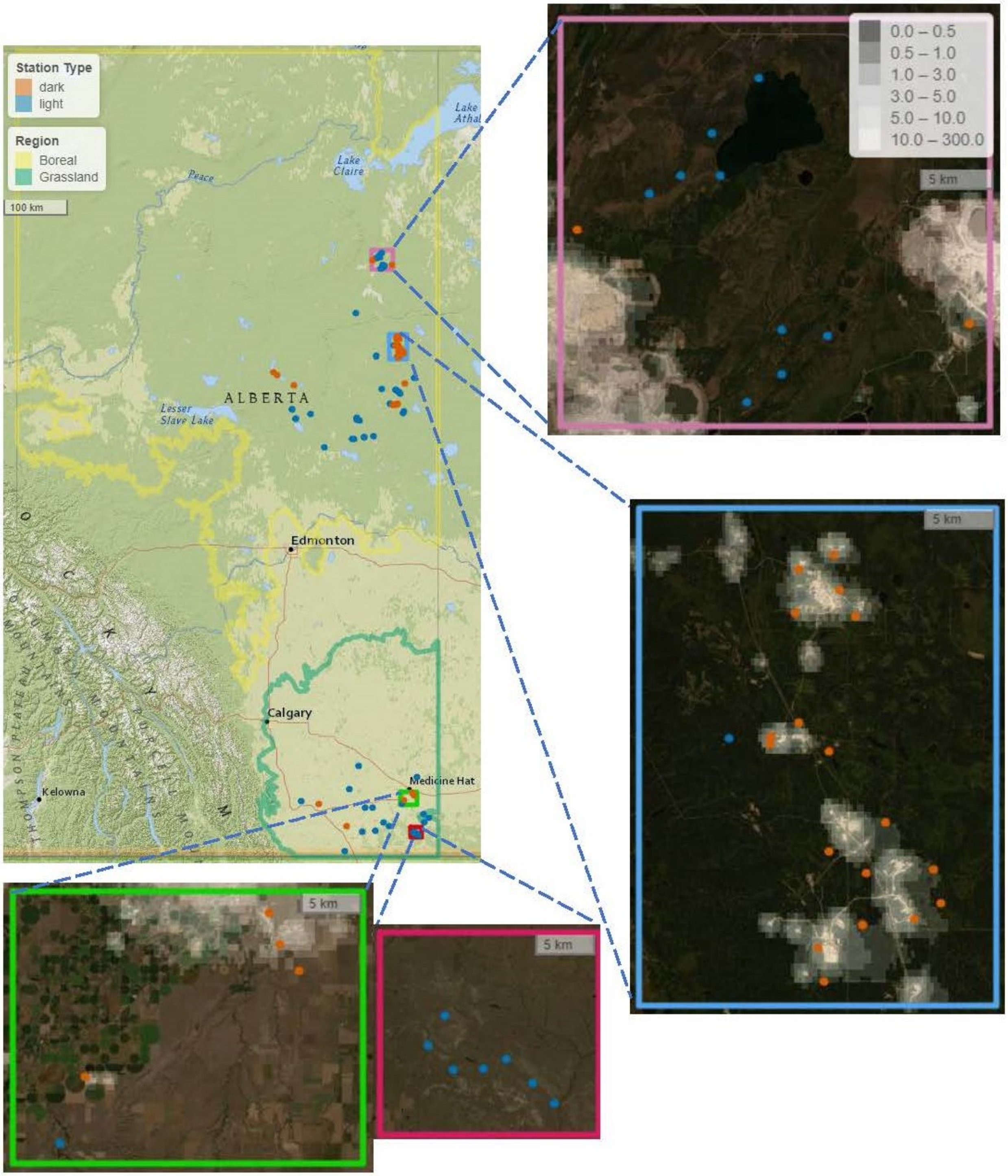

Figure 5.3 Map of recordings stations for temporal habitat use analysis.

Zoomed-in views show areas with a high density of recordings stations, with colored boxes corresponding to boxes on the main map. Shading on the zoomed-in views corresponds to artificial lights estimates in nWcm^{-2}sr^{-1}

Results

Spatial patterns of habitat use

In the Grassland region, we detected wingbooms signalling territorial habitat use at 21 (8.1%) of the 259 stations. We detected vocalizations at an additional 19 stations (7.3%). In the Boreal region, we detected wingbooms at 64 (25.1%) of the 255 stations and vocalizations at an additional 38 stations (14.9%).

In the Grassland region, the intensity of both territorial habitat use and extra-territorial habitat use was negatively associated with artificial light (Figure 5.4a). The buffer size with the lowest mean prediction error was 800-meters for territorial and 6400-meters for extra-territorial nighthawks. The mean coefficient for artificial light was -3.08 (-7.23, -0.97) for territorial use and -11.58 (-45.00, -1.19) for extra-territorial use.

In the Boreal region, we found no association between artificial light and intensity of habitat use (Figure 5.4b). The buffer size with the lowest mean prediction error was 1600-meters for territorial and extra-territorial habitat use. The mean coefficient estimate for artificial light was -0.11 (-0.42, 0.16) for territorial and 0.10 (-0.07, 0.25) for extra-territorial habitat use.

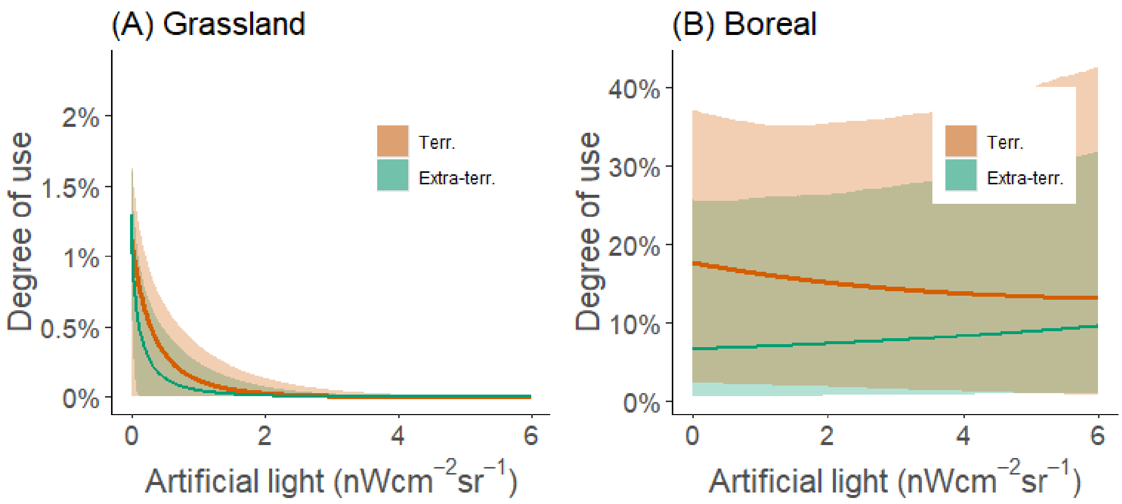

Figure 5.4 Proportion of recordings in which territorial and extra-territorial Common Nighthawks are detected in the (A) Grasslands and (B) Boreal based on quasibinomial GLMs

Lines and the shaded areas represent the mean, fifth, and 95th percentile predictions across 10,000 bootstrap samples. Occurrence probability predictions from previous studies were also included in the GLM and set to their 90th percentile values for predictions in this figure

Temporal patterns of habitat use

In the Grassland region, we found 28 stations with Common Nighthawks in at least 5% of recordings with < 6° sun angle, six light stations and 22 dark stations. In the Boreal region, we detected Common Nighthawks in ≥ 5% of recordings below a 6° sun angle at 27 light stations and 31 dark stations that were ≥ 2 km apart. When we divided the analysis into days with and without astronomical twilight, there were 5 light stations and 8 dark stations in the Boreal region that had at least 20 recordings on days with astronomical twilight. All but one station, a dark station, had at least 20 recordings on days without astronomical twilight.

In both regions, overall relationship between vocal activity and sun angle remained consistent between stations with and without artificial light. The Hierarchical Generalised Additive Models (HGAMs) with common global sun angle smoothers applied to light and dark stations had a lower AIC than the HGAM with separate sun angle smoothers for light and dark stations, both in the Grassland region and the Boreal region on days with and without astronomical twilight (Table 5.1). The model predictions for the HGAM with separate sun angle smoothers for light and dark stations show similar curve shapes for stations with and without artificial light in the Grassland and in the Boreal on days without astronomical twilight (Figure 5.4). In the Boreal on days with astronomical twilight, there was an additional peak in vocal activity in evening between 18° and 12° sun angle (Figure 5.4b). Only nine recordings were available on these days in this sun angle increment, and only two of these recordings had nighthawk vocalizations, both of which occurred at a dark station (Table S5.1). The model may have overfit to these two data points. There was support for variation across stations in the relationship between vocal activity and sun angle, unrelated to their status as light or dark stations. In all three analyses, the HGAM with the lowest AIC included individual sun angle smoothers for each station. In the Boreal region on dates with astronomical twilight, the best model included an additional separate sun angle smoothers for light and dark stations. This result may again reflect overfitting to recordings at dark stations with nighthawk detections between 18° and 12° sun angles in the evening.

Activity peaks were not significantly different between light and dark stations in the Grassland nor in either analysis in the Boreal (Table 5.2). The bootstrapped 95% confidence intervals for evening peak activity shifts included sun angles up to 3.71° higher or 5.61° lower in stations with artificial light. In the Boreal region on days when astronomical twilight occurred, there was even more uncertainty about the shift in evening activity peak, with confidence intervals spanning 5.45° degrees higher to 6.34° lower at light stations than dark stations. These samples only included four and five light stations, respectively, likely contributing to this uncertainty. Our sample size was higher for the Boreal region on days without astronomical twilight (27 light stations and 30 dark stations). The 95% confidence intervals for the difference in sun angle of peak activity between light and dark stations in this analysis were narrower, showing shifts no greater than 1.6° in either direction.

We did not find evidence that nighthawks increase their activity during the darkest parts of the daily light cycle at stations with artificial light relative to stations without. Vocal activity was nearly zero during astronomical twilight in both light and dark stations (Figure 5.5). Vocal activity was not significantly different between light and dark stations during nautical twilight in either region (Table S5.2). The only twilight period during which we found significantly increased vocal activity at light compared to dark stations was in the Boreal region on days without astronomical twilight (LRT $p < 0.05$), when vocal activity as estimated at 43.9% (30.3% - 58.5%) at light stations and 22.8% (14.2% - 34.5%) at dark stations (Figure 5.5; Appendix D, Table S5.1). In this model, vocal activity was also higher at light stations than dark stations in other twilight periods, but not significantly (Appendix D, Table S5.2), and the model with the interaction term did not perform better than the model with only a main effect for light (Appendix D, Table S5.3). When we removed stations for which occupancy predictions were not available and added the predictions as a covariate in the model, we found that vocal activity was not significantly different between light and dark stations during any twilight period (Appendix D, Table S5.2) and the model with artificial light as a covariate was not significantly better than the model without (Appendix D, Table S5.3).

Table 5.1 AIC from Hierarchical Generalised Additive Models with different model structures.

	Separate global smoother for light and dark stations	**Common global smoother for light and dark stations**	**Separate global smoother for light and dark stations, individual smoothers for each station**	**Common global smoother for light and dark sites, individuals smoothers for each station**
Grassland	1441.44	1434.98	1377.80	1364.61
Boreal with astronomical twilight	346.95	341.85	336.22	344.73
Boreal without astronomical twilight	1625.40	1617.44	1617.53	1611.94

The HGAMs with separate global smoothers for light and dark stations allow the relationship between sun angle and vocal activity (the probability of vocalizing in a one-minute survey) to be different for light and dark stations, while the common global smoother assumes that the relationship remains consistent across light and dark stations. The models with individual smoothers for each station allow variation in the relationship between sun angle and vocal activity across stations, while shrinking the relationship at each station towards the global smoother.

Table 5.2 Mean and 95% confidence intervals from the 10,000 bootstrapped estimates for the difference in the sun angles of peak vocal activity between light and dark stations.

	Evening	**Morning**
Grassland	-1.18° (-5.61°, 3.71°)	0.87° (-1.20°, 3.21°)
Boreal with astronomical twilight	-0.02° (-6.34°, 5.45°)	-0.34° (-2.22°, 1.41°)
Boreal without astronomical twilight	-0.35° (-1.4°, 0.6°)	0.6° (-0.40°, 1.6°)

Bootstrap estimates were generated using an HGAM with a separate sun angle smoother for light and dark stations. Negative values in the evening indicate that that the peak occurred later at light stations than dark stations, while negative values in the morning indicate that the peak occurred earlier at light stations.

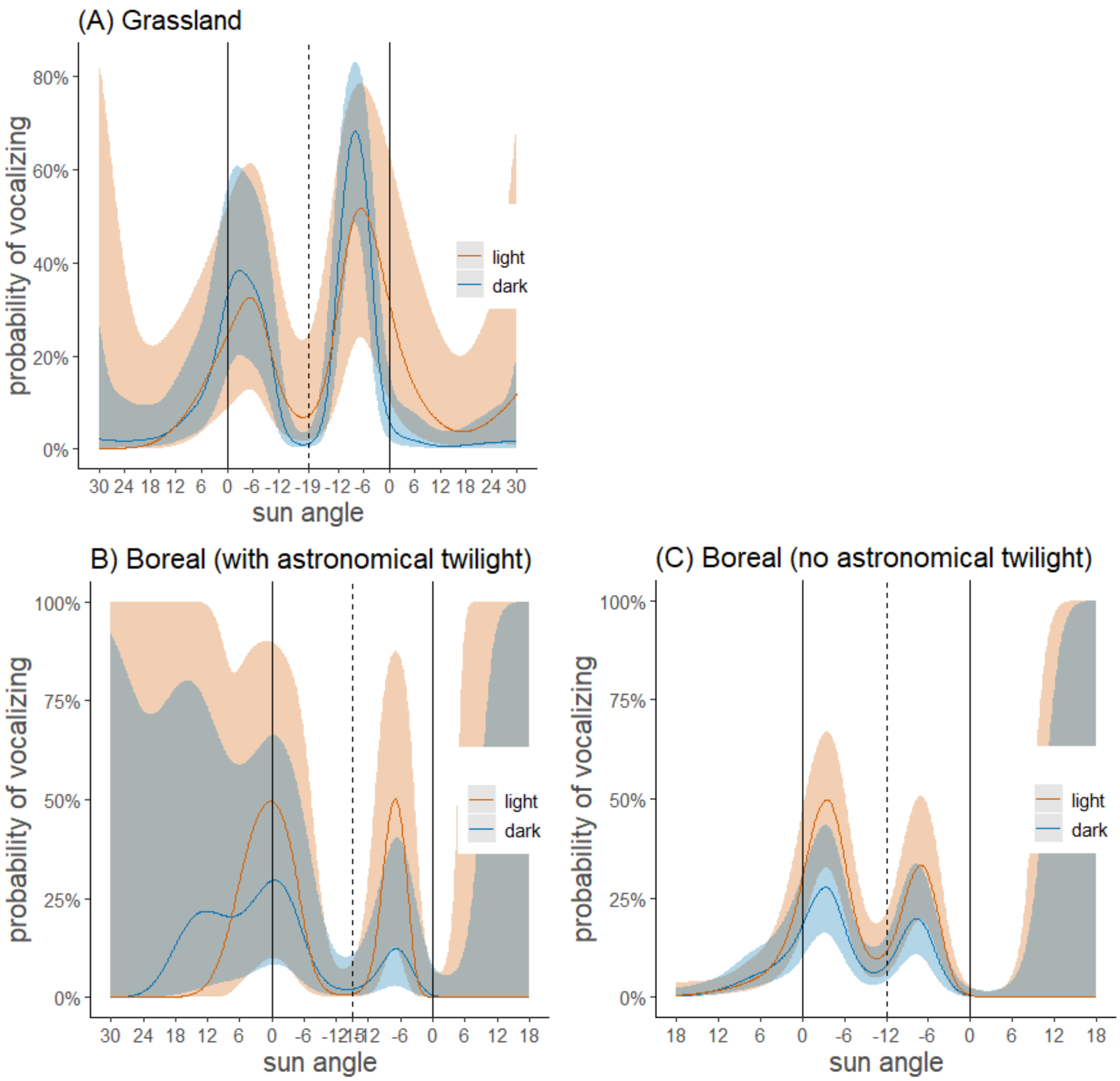

Figure 5.1 Hierarchical Generalised Additive Model (HGAM) estimates of the relationship between sun angle and vocal activity

We defined vocal activity as the probability of detecting a Common Nighthawk vocalization in a one-minute survey in the (A) Grassland region, (B) Boreal region on nights where astronomical twilight occurred (sun angle reached lower than -12°) and (C) Boreal region on nights when astronomical twilight did not occur. Light stations had artificial light estimates >= 0.5 nWcm^{-2}sr^{-1}. The HGAM shown used separate sun angle smoothers for light and dark sites. Curves represent the mean estimate and shaded areas represent the 95% confidence interval. Solid vertical lines show sunrise and sunset and the dashed vertical line represent the lowest sun angle included in each analysis. Day of year was set to 190 and moon was set to present and at an illuminated fraction of 0.5.

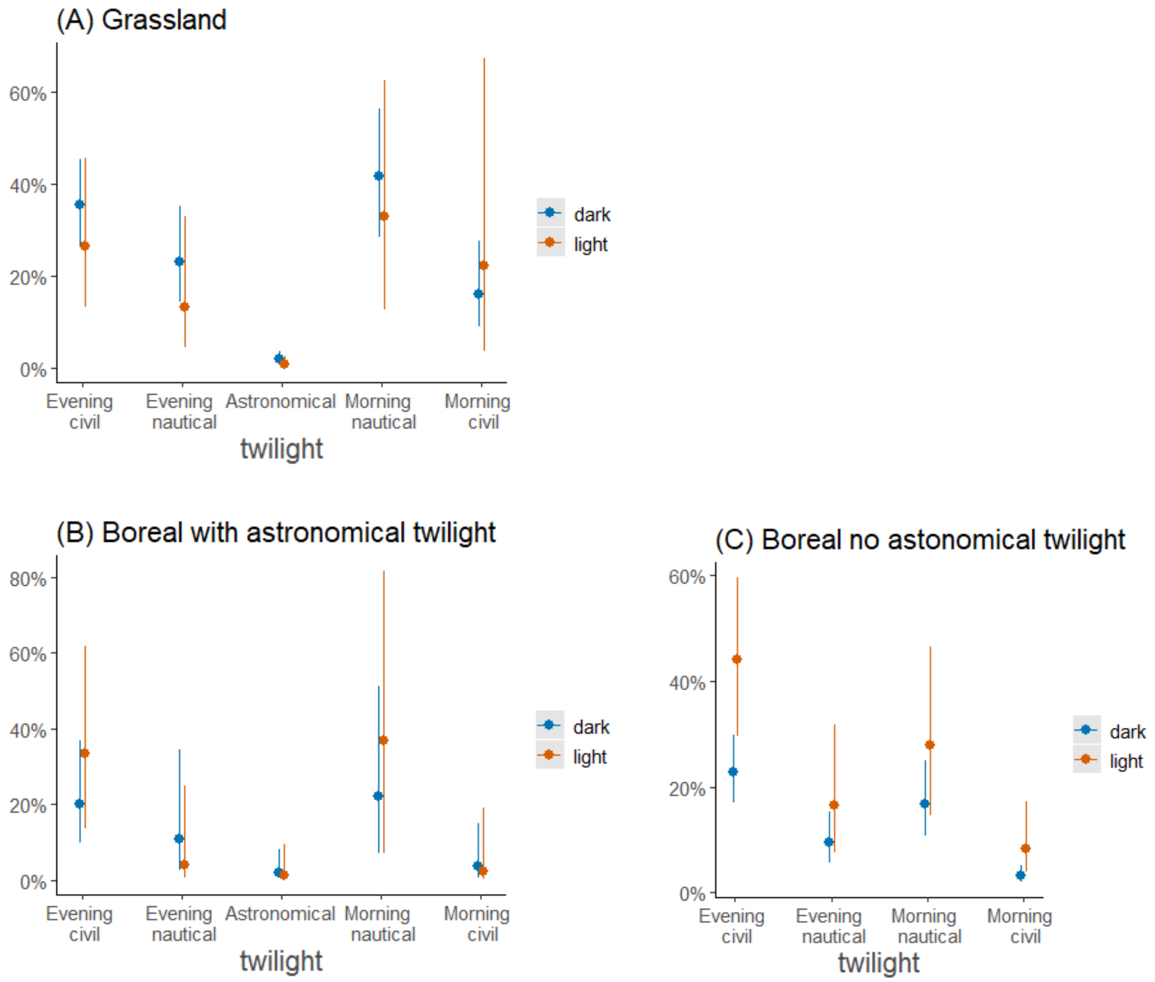

Figure 5.2 Probability of vocalizing for Common Nighthawks during a one-minute recording in light and dark stations.

We modeled the probability of detection in a generalised linear mixed effects model with station as a random effect and an interaction between light and twilight period.

Discussion

Crepuscular bird species like Common Nighthawks may alter their habitat use patterns in response to artificial light to take advantage of the opportunity to forage on insects aggregating at light sources (Shields and Bildstein 1979; Bharos 1990), avoid increased nest predation risk in light polluted areas (Oro et al. 2005), or match their peak activity times with illumination levels (Kronfeld-Schor et al. 2013). We use acoustic recordings units at northern and southern latitudes in Alberta to investigate how artificial light affected the intensity of their spatial habitat use. At stations where nighthawks were frequently observed, we also studied whether artificial light affected their temporal habitat use, including overall vocal activity patterns, sun angle of peak activity, and activity during the darkest portions of twilight. In the southern Grassland region, Common Nighthawks used stations with artificial light less intensely than dark stations, both for their territorial habitat use associated with nesting and for their extra-territorial habitat use associated with foraging. At higher latitudes in the Boreal region, we found no association between intensity of habitat use and artificial light, suggesting that the effects of artificial light during the breeding season diminished with latitude. We did not find evidence that artificial light affected their temporal habitat use by altering their circadian rhythms or allowing them to extend their foraging activities later into the night. Together, the spatial and temporal habitat use patterns suggest that nighthawks do not consistently forage at artificial lights, and that they avoid artificial light for territorial activities at Canada's southern latitudes.

We predicted that habitat use by Common Nighthawks would have a similar association with artificial light across regions and latitudes, but we only found an association in the Grassland region, suggesting that artificial light does not affect their habitat use at higher latitudes where natural illumination is higher. The negative association between territorial habitat use and artificial light in the Grassland region aligned with our study of this species in the neighboring province of British Columbia (Chapter 4 of this thesis), which included surveys from latitudes similar to the Grassland region of Alberta. Nighthawks may avoid establishing nesting territories in light polluted areas if doing so increases their nest visibility to predators during late twilight and night (Troscianko et al. 2016, McMahon et al. 2022). The lack of association between artificial light and territorial habitat use in the northern Boreal region may have occurred because natural illumination was relatively high. Astronomical twilight was always longer in the Grassland region than the Boreal region during our study, and astronomical twilight did not occur between June 1st and July 15th at the highest latitudes in the Boreal region (Figure 5.1). The length of astronomical twilight always exceeded 3.25 hours in the Grassland region, and the lengths of astronomical twilight and true night combined exceeded five hours at the lowest latitude (49ºN) on July 15th. Artificial light may increase nest predation risk primarily during astronomical twilight and true night, when natural illumination is lowest. Other factors, like differences in nest predator populations, could also explain the different territorial habitat use patterns in the Grassland and Boreal regions.

Extra-territorial habitat use also only showed an association with artificial light in the southern Grassland region and not the northern Boreal region, and the negative direction of the association in the Grassland region suggested that nighthawks did not benefit from foraging on insects aggregating at artificial lights. This pattern contrasted with the positive association that we observed in British Columbia outside of urban areas (Chapter 4 of this thesis), despite all ARUs in the Grassland being placed in areas with low urban land cover. Further analysis of the interactions between artificial light and other landcover features could reveal the landscape contexts in which extra-territorial habitat use by Common Nighthawks is positively or negatively associated with artificial light. For example, in some bat species, response to light depends on forest cover or proportion of farmland (Barré et al. 2021). In the Boreal region, the prevalence of natural illumination could explain the lack of any association between artificial light and extra-territorial habitat use. With longer twilights, the foraging window is naturally longer and fewer insects are attracted to lights when background illumination is higher (Eisenbeis and Hänel 2009).

We did not find support for the hypothesis that artificial light alters temporal habitat use patterns through physiological or behavioural changes. In both regions, the HGAM with a common smoother for light and dark stations had more support than the HGAM with separate smoothers, indicating that artificial light did not affect the overall relationship between vocal activity and sun angle. The best models in both regions included individual sun angle smoothers for each station, indicating that the relationship between sun angle and vocal activity varied across stations. Features specific to each station or to the individual nighthawks at those stations could account for this variation. Temperature can interact with sun angle to influence nighthawk activity levels, but we did not collect temperature data for our study (Sidler 2017). Nightjar activity also corresponds with peak prey availability, and the sun angles of peak prey availability may have differed across our study stations depending on habitat type and insect community composition (Jetz et al. 2003; Woods and Brigham 2008).

Our results indicate that artificial light did not alter nighthawk perception of daylength or threshold illumination levels enough to affect the sun angle at which their vocal activity peaked. Other studies have found that artificial light alters bird perception of daylength, resulting in earlier onset of daily activities and of seasonal reproductive development for diurnal species (Dominoni 2013; Russ et al. 2015, 2017). Artificial light can also lower the sun angle at which illumination thresholds governing the timing of many activities occur, including the dawn chorus in birds (Da Silva and Kempenaers 2017, Da Silva et al. 2015, Wilkinson et al. 2022) and roost emergence in bats (Boldogh et. al. 2007, Luo et al. 2021). In the Boreal region on days without astronomical twilight, the sun angle of peak vocal activity differed by no more than 1.6° in either direction in either the morning or evening. In the Grassland region, the confidence intervals were especially wide for the evening activity peak, including up to 5.6° lower or 3.6° higher sun angle of peak vocal activity in the evening at stations with artificial light, preventing us from making inferences about the effects of artificial light on peak activity patterns at lower latitudes.

We also did not find support for the hypothesis that artificial light alters activity timing by causing nighthawks to extend their foraging behaviour into nautical and astronomical twilight. There was virtually no vocal activity during astronomical twilight in either region, and no significant differences in vocal activity between light and dark stations during the nautical twilight periods. This finding contrasts to documented cases of nighthawks foraging under artificial lights after the end of nautical twilight (Shields and Bildstein 1979; Foley and Wszola 2017). Nighthawks may only display this behaviour in areas with bright artificial lights and low natural illumination. Astronomical twilight and artificial light estimates brighter than 2 $nWcm^{-2}sr^{-1}$ only occurred together at one station in our temporal habitat use analysis, and we did not detect any nighthawk vocalizations at this station during astronomical twilight. It is also possible that nighthawks foraged during astronomical twilight without vocalizing, remaining undetected in our recordings.

The higher vocal activity at stations with artificial light in the Boreal region on days without astronomical twilight, which was statistically significant during civil twilight ($p < 0.5$), may simply reflect the higher habitat quality at stations with artificial light for our sample of stations. When we added occupancy predictions from Knight *et. al.* (2022) as a measure of habitat quality, excluding the nine stations for which these predictions were unavailable, we found that the differences in vocal activity between light and dark stations were not significant during any twilight period.

Our analyses were limited both by our ability to measure artificial light and by the spatial distribution of nighthawks in our study area. Our satellite-based measurements of artificial light were positive in pixels with no probable light sources, but near human developments, indicating that our artificial light estimates included skyglow (Sanchez de Miguel et al. 2020). If nighthawks only respond to direct illumination, the inclusion of skyglow in our estimates of artificial light could explain why we did not see different vocal activity at stations with and without artificial light. Although we compared Common Nighthawk habitat use in a northern region to a southern region, we could not study how the relationship between Common Nighthawk habitat use and artificial light changes across the full latitude range of Alberta because nighthawks are rare between 51°N and 54°N (Knight et al. 2021c). Within the Grassland region, we only found nighthawks between 49.08°N and 50.38°N. The Boreal region had a larger latitudinal gradient, but when we fit a version of the spatial habitat use model that included an interaction term between latitude and artificial light, the coefficients for artificial light and its interaction with latitude were highly correlated with each other and both had confidence intervals overlapping zero (Table S5.4). Further studies including data from across Canada at a wider range of latitudes could identify the latitude at which artificial light begins to influence habitat use patterns.

Our results suggest that the Canadian Nightjar Survey (CNS) is not under or overestimating habitat use at stations with artificial light by surveying primarily during civil twilight because vocal activity did not differ in occupied light v. dark stations in our analysis. However, this analysis was particularly limited by the absence of nighthawks at all but six light stations in the Grasslands region. The CNS, which surveys more than 2000 stations across Canada, may extend to regions where nighthawks use sites with artificial light more often and the larger number of stations improves the chance that nighthawks will be found at stations with artificial light. Extending the CNS later into the evening and early morning is likely impractical for volunteers. However, conducting some of these surveys throughout nautical and astronomical twilight would allow researchers statistically account for any shifts in habitat use over different twilight periods and improve our understanding of how artificial light affects temporal habitat use patterns for nightjar species.

The negative relationship between artificial light and both territorial and extra-territorial habitat use in the Grassland region suggest that Common Nighthawks could benefit from efforts to reduce light pollution this area. Although population trends for Common Nighthawks in Alberta are uncertain, sources agree that this species' population has declined in recent decades (Haché et al. 2014; Sauer et al. 2017). Conservation efforts in the Grassland region are particularly important for Common Nighthawks because populations are lower in the Grassland than the Boreal region of Alberta (Haché et al. 2014). Plans to protect habitat for Common Nighthawks in Alberta should include protection from light pollution, especially in the south east corner of the province where occupancy predictions for this species are highest (Knight et al. 2021c) and where most habitat use in our study in the Grassland region occurred (Figure 5.1). Negative associations with artificial light have also been found for European Nightjars (*Caprimulgus europaeus*) and Eastern Whip-poor-wills (*Antrostomus vociferus*) (Sierro and Erhardt 2019; Korpach et al. 2022), and the effect of artificial light on spatial habitat use should be further investigated for other crepuscular and nocturnal species. Although we did not find differences in temporal habitat use patterns between stations with and without artificial light, nighthawks may respond more at lower latitudes where natural illumination is lower or in areas with brighter artificial light. In these areas, artificial light may attract more insects or have a stronger influence on circadian rhythms. Other crepuscular species may be more affected by artificial light, especially species like bats or other nightjars whose onset of activity occurs at lower sun angles (Preston 2015; Mariton et al. 2022). As the research on the biological effects of artificial light continues to grow (Rodrigo-Comino et al. 2021), comparisons across species, space, and time can show where and when these effects are likely to be most disruptive.

Chapter 6. Discussion

Both artificial light and the research on its environmental impacts are growing each year, with many of these studies focusing on birds (Sánchez de Miguel et al. 2021; Rodrigo-Comino et al. 2021). Research targeting bird response to artificial light has been published in the scientific literature since the 19th century (Allen 1880), and knowledge of these responses has been used for centuries to capture birds by disorienting (MacPherson 1897) or attracting them (Hiroa and Buck 1950). Artificial light extends far beyond urban centers through rural development, other isolated light sources, and skyglow (Gaston et al. 2021). To study how bird response varies across behavioural, spatial, and temporal contexts, I used a broad and comprehensive literature search and field studies that covered large spatial extents. In my systematic map, I searched for evidence in 11 bibliographic databases, 18 organizational websites, and four Google Scholar searches. The resulting evidence base for the effects of artificial light on bird movement and distribution spanned three centuries, many types of artificial light, 15 economic sectors, and 75 countries. In my studies of nightjar habitat use in Western Canada, community science data and acoustic recordings units allowed me to measure bird responses to light in three large study areas, one in British Columbia and two in Alberta. I studied the effects of artificial light for both Common Nighthawks and Common Poorwills, over varying proportions of urban land cover, latitudes, and sun angles. In Nighthawks, I also studied variation in responses to light for territorial vs. extra-territorial contexts and across the daily light cycle.

Fulfillment of thesis objectives

Objective 1. Document the diverse effects of artificial light on bird movement and distribution

Using a comprehensive, pre-published search strategy, I found 469 articles, containing 490 studies, that documented the effects of artificial light on bird movement or distribution. I increased the number of articles for my evidence base by searching Web of Science for articles indexed without abstracts and keywords with a more comprehensive search string than I used to search for other articles. Checking the reference lists of other, more targeted reviews revealed that our search strategy found nearly all articles relevant to most of our secondary questions, but missed some articles related to bird aggregations and collisions at illuminated structures where the authors did not refer to artificial light in the title or abstract. Nevertheless, the search produced a comprehensive and unbiased body of evidence for the effects of artificial light on bird movement and distribution.

To create the systematic map of the evidence, I organized and extracted a broad set of metadata related to context, population, intervention/exposure, and outcome variables. I used these metadata to organize the articles into a database that can be searched for a variety of research and management objectives. By defining 55 outcome variables and organizing them into three categories (behaviour, distribution, and community) and 11 subcategories, I showed the diversity in both research strategies and bird responses to light. I identified evidence for each secondary question of conservation or management importance based on characteristics of the population, intervention/exposure, comparator, or outcome, regardless of the purpose for which the study was conducted. This strategy both increased the amount of evidence available for each secondary question and provided a useful framework for future systematic reviews, which must also define objective eligibility criteria for relevant evidence.

Of the hundreds of possible evidence clusters and knowledge gaps that could be identified based on our eligibility criteria, I focused on those I considered to be of particular conservation or management importance. For example, there appears to be enough evidence to review effects of weather and lunar conditions on the likelihood of bird aggregation and mortality. Another evidence cluster is available in the comparison of bird response to red or white and flashing or continuous lights. The number of birds aggregating around lights at night indicates that they are likely attracted to light sources, though explicit choice tests are needed to demonstrate this attraction and identify the conditions under which it occurs. Such choice tests would also improve the evidence base for bird deterrents. The effectiveness of lasers has enough evidence for review, but other deterrent types need further laboratory and field tests. For orientation, laboratory testing of birds under the artificial light types that are common in the built environment could reveal which types of light disorient birds in the wild. The habitat selection literature would also benefit from studies comparing bird responses to different types of broad-spectrum white light. A review of the habitat selection literature could identity species characteristics that predict responses to light, and would also include several studies that have been published since the conclusion of our systematic map search (Rodríguez et al. 2020; Wang et al. 2021; Simons et al. 2021; Korpach et al. 2022; La Sorte et al. 2022). The systematic map provides a comprehensive body of evidence through August 2020 and a replicable strategy for updating this search.

Objective 2. Document how artificial light affects habitat use by nightjars across landscape, behavioural, and temporal contexts

Within the systematic map, there are 25 records of birds foraging on flying insects under lights at night, yet it is unclear whether this behaviour is common or beneficial enough to alter their association with artificial light over large spatial extents. Aerial insectivores hunt exclusively on flying insects and include birds in the swift (*Apodidae*), swallow (*Hirundinidae*), flycatcher (*Tyrannidae*), and nightjar (*Caprimulgidae*) families. Crepuscular aerial insectivores may be particularly likely to hunt flying insects under light sources, but may also have fewer prey available if light pollution drives insect declines over large spatial scales (Owens and Lewis 2018; Kalinkat et al. 2021). Within the evidence base for habitat selection in the systematic map, no study included an aerial insectivore species and also controlled for other anthropogenic disturbances. Among the families of aerial insectivores, nightjars are particularly likely to respond to artificial light because they are most active after sunset, when lights turn on and become brighter than background illumination, and nest on the ground, where they may be more vulnerable to nest predation (Wilcove 1985).

The results of the spatial habitat use patterns in Chapters 4 and 5 suggest that the negative effects of artificial light on nightjar habitat use are more widespread than potential benefits from foraging. Common Poorwills (*Phalaenoptilus nuttallii*) and Common Nighthawks (*Chordeiles minor*) in British Columbia, as well as Common Nighthawks in the Grassland region of Alberta, showed a strong negative association with artificial light for territorial habitat use. We did not observe any association between artificial light and nighthawk habitat use in the northern Boreal region of Alberta, where the sun angle stays above -12° (denoting the limit of nautical twilight) for most of the breeding season, causing natural illumination to be higher than in the Grassland region. The negative effects of artificial light on habitat use for breeding nightjars may diminish with increasing latitude, but artificial light may affect territorial habitat use in northern regions for other bird species that nest earlier in the spring, such as owls.

Results from both the spatial and temporal habitat use models indicate that foraging under artificial light is not driving habitat use by nightjars in our study areas. We observed a positive association with artificial light for extra-territorial Common Nighthawks, which are likely to be foraging, only in British Columbia and only in areas with very low levels of urban land cover. This pattern was not apparent in either region of Alberta. Habitat use for Common

Poorwills, which forage near their nest sites, showed a negative association with artificial light in British Columbia. Because the Canadian Nightjar Survey was conducted primarily during civil twilight, this survey design may have failed to count nightjars that foraged at artificial lights later in the evening. Our temporal habitat use analysis in Alberta indicated that this was not the case for Common Nighthawks, which showed no difference in vocal activity between stations with and without artificial light during nautical or astronomical twilight, and almost never vocalized during astronomical twilight at any stations. The relationships between vocal activity and sun angles were not different between stations with and without artificial light. Reports in the literature confirm that nightjars sometimes forage under artificial lights at night (Shields and Bildstein 1979; Bharos 1992; Ingels et al. 1999; Foley and Wszola 2017), but our research on British Columbia and Alberta suggests that this behaviour is not common enough in Western Canada to be an important driver of spatial or temporal habitat use by nightjars.

Summary and final conclusions

In the systematic map and the study of nightjars in Western Canada, I found that artificial light can both benefit and harm birds. Both sources of information indicate that the harmful effects are more prevalent. Of the 218 articles that formed the evidence base for bird aggregation/mortality, most reported both aggregation and mortalities at illuminated structures. Although some bird species may benefit from foraging under artificial lights, and 66 of these reports were included in the systematic map, our study of two nightjar species showed that this behaviour may not be widespread and may depend on life history traits and landscape features. The findings in this thesis agree with the dominant message in the literature, that artificial light is a pollutant that should be managed to reduce its harmful effects on wildlife and biodiversity, which likely outweigh the benefits experienced in some contexts by some species (Gaston et al. 2021; Rodrigo-Comino et al. 2021; Gaston and Sánchez de Miguel 2022).

There are many strategies for reducing light pollution, including removing lights, using motion sensors to turn them on only when needed, and shading light sources to reduce skyglow (Gaston et al. 2012). Knowledge of the negative effects of artificial light on wildlife can motivate public support for policies and individual actions that reduce light pollution (Lyytimäki and Rinne 2013; Silver and Hickey 2020; Beaudet et al. 2022). For example, the well-documented harms for birds migrating at night have motivated two nation-wide programs to reduce light pollution during the spring and fall migration seasons; the Fatal Light Awareness Program in Canada and Lights Out in both Canada and the United States (Ogden 1996; National Audubon Society). Bringing attention to the harmful effects of artificial light during the breeding and wintering seasons on charismatic birds like nightjars could further support efforts to reduce light pollution during the summer breeding season.

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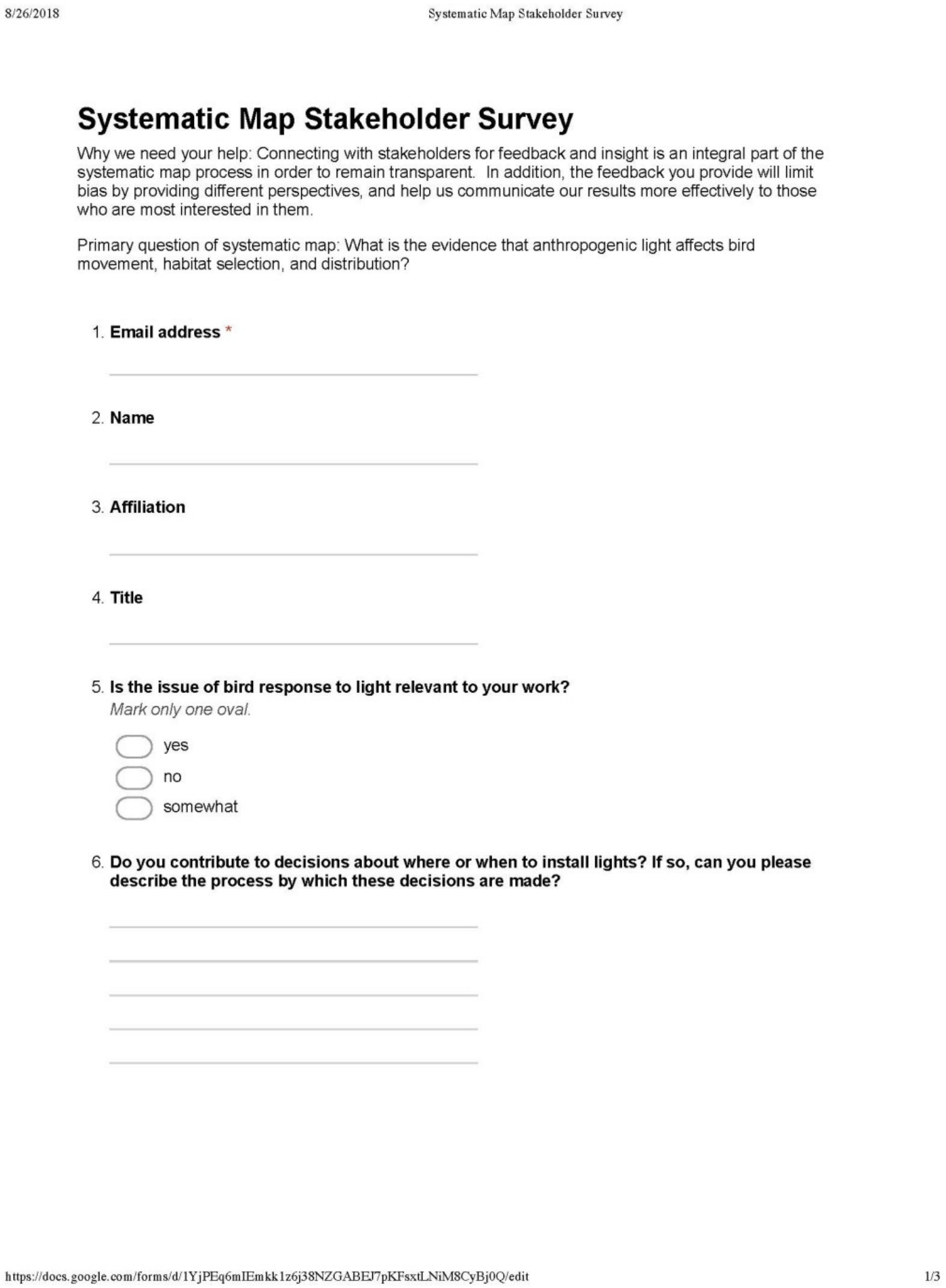
Appendix A. Additional files for Chapter 2

Additional File 1. Stakeholder Survey



8/26/2018 Systematic Map Stakeholder Survey

Systematic Map Stakeholder Survey

Why we need your help: Connecting with stakeholders for feedback and insight is an integral part of the systematic map process in order to remain transparent. In addition, the feedback you provide will limit bias by providing different perspectives, and help us communicate our results more effectively to those who are most interested in them.

Primary question of systematic map: What is the evidence that anthropogenic light affects bird movement, habitat selection, and distribution?

1. **Email address** *

2. **Name**

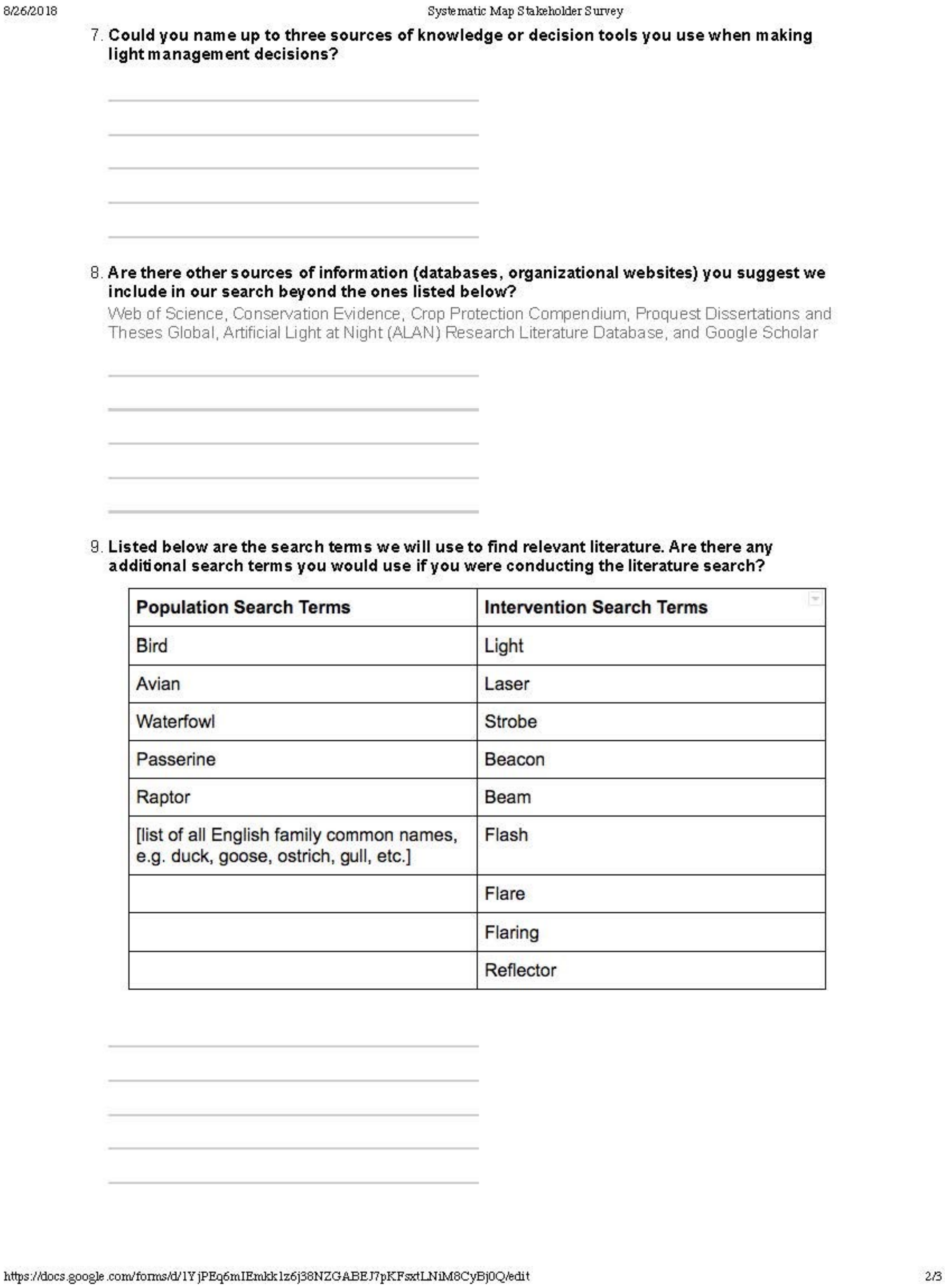
3. **Affiliation**

4. **Title**

5. **Is the issue of bird response to light relevant to your work?**
   Mark only one oval.
   ○ yes
   ○ no
   ○ somewhat

6. **Do you contribute to decisions about where or when to install lights? If so, can you please describe the process by which these decisions are made?**

https://docs.google.com/forms/d/1YjPEq6mIEmkk1z6j38NZGABEJ7pKFsxtLNiM8CyBj0Q/edit 1/3



7. **Could you name up to three sources of knowledge or decision tools you use when making light management decisions?**

8. **Are there other sources of information (databases, organizational websites) you suggest we include in our search beyond the ones listed below?**
   Web of Science, Conservation Evidence, Crop Protection Compendium, Proquest Dissertations and Theses Global, Artificial Light at Night (ALAN) Research Literature Database, and Google Scholar

9. **Listed below are the search terms we will use to find relevant literature. Are there any additional search terms you would use if you were conducting the literature search?**

Population Search Terms	Intervention Search Terms
Bird	Light
Avian	Laser
Waterfowl	Strobe
Passerine	Beacon
Raptor	Beam
[list of all English family common names, e.g. duck, goose, ostrich, gull, etc.]	Flash
	Flare
	Flaring
	Reflector

10. **Are there research questions or subtopics regarding bird behavioral response to light that you believe urgently require more primary research (as opposed to review)? For example...**
Check all that apply.

☐ Does anthropogenic light increase bird collisions at human-made structures?
☐ Which light-based interventions are effective bird deterrents?
☐ Are birds' behavioral responses to light affected by light characteristics (e.g. color, intensity, direction)?
☐ How do habitat variables (e.g. vegetation type, human disturbance, resource availability) affect birds' behavioral responses to light?
☐ How does weather affect birds' behavioral response to light?
☐ What are the physiological mechanism by which anthropogenic light at night disorients birds?

11. **List other research topics or questions that you believe require more primary research here:**

____
____
____
____
____

12. **Do we have permission to identify you as a stakeholder in the published systematic map?**
Mark only one oval.

○ Yes
○ No

13. **May we share your responses in the published systematic map?**
Mark only one oval.

○ Yes
○ No
○ Please contact me first

14.
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☐ Send me a copy of my responses.

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Google Forms

Additional File 2. Benchmark Articles

Content:

A. Benchmark articles indexed in the Web of Science Core Collection

B. Benchmark articles not indexed in the Web of Science Core Collection

A. Benchmark articles indexed in the Web of Science Core Collection

Articles in bold faced type were not found by the proposed search string. See "Population" section of manuscript for details

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Additional File 3. Expanded Population Search String

English common family names listed in the IOC World Bird List (Gill and Donsker 2014b) were used during scoping to develop a Web of Science population search string. We determined that the population search string TS=(*bird* OR Avian OR Ave$) will find all relevant studies in Web of Science that are indexed with titles and abstracts. We will conduct an additional search in Web of Science using this expanded population search string, which includes all English common family names. Results from this additional search will only be included in screening if they do not contain an abstract and keywords and do not contain “*bird*,” “avian,” or “ave$” in their title.

TS = (*bird* OR Avian OR Ave$ OR Ostrich* OR Rhea$ OR Kiwi$ OR Cassowar* OR Tinamous* OR Screamer$ OR Magpie$ OR Duck$ OR Megapode* OR Chachalaca$ OR Guineafowl OR Quail OR Pheasant$ OR Loon$ OR Penguin$ OR Petrel$ OR Albatross* OR Shearwater$ OR Grebe$ OR Flamingo$ OR Tropicbird$ OR Stork$ OR Ibis* OR Heron$ OR Hamerkop$ OR Shoebill$ OR Pelican$ OR Frigatebird$ OR Gannet$ OR Cormorant$ OR Anhinga$ OR Vulture$ OR Secretarybird$ OR Osprey$ OR Kite$ OR Bustard$ OR Mesite$ OR Seriema$ OR Kagu$ OR Sunbittern$ OR Flufftail$ OR Finfoot$ OR Rail$ OR Trumpeter$ OR Crane$ OR Limpkin$ OR Buttonquail$ OR Curlew$ OR Sheathbill$ OR Plover$ OR Oystercatcher$ OR Ibisbill$ OR Stilt$ OR Snipe$ OR Jacana$ OR Plains-wanderer$ OR Seedsnipe$ OR Sandpiper$ OR Courser$ OR Gull$ OR Skua$ OR Auk$ OR Sandgrouse OR Grouse OR Pigeons$ OR Hoatzin$ OR Turaco$ OR Cuckoo$ OR Owl$ OR Frogmouth$ OR Oilbird$ OR Potoo$ OR Nightjar$ OR Treeswift$ OR Swift$ OR Hummingbird$ OR Mousebird$ OR Trogon$ OR Roller$ OR Kingfisher$ OR Tody OR Todies OR Motmot$ OR Bee-eater$ OR Hoopoe$ OR Hornbill$ OR Jacamar$ OR Puffbird$ OR Barbet$ OR Toucan$ OR Honeyguide$ OR Woodpecker$ OR Caracara$ OR Parrot$ OR Cockatoo$ OR Wren$ OR Sapayoa$ OR Broadbill$ OR Pitta$ OR Ovenbird$ OR Antbird$ OR Antthrush* OR Antpitta$ OR Gnateater$ OR Tapaculo$ OR Crescentchest* OR Flycatcher$ OR Cotinga$ OR Manakin$ OR Tityra$ OR Lyrebird$ OR Scrubbird$ OR Bowerbird$ OR Treecreeper$ OR Honeyeater$ OR Bristlebird$ OR Pardalote$ OR Warbler$ OR Babbler$ OR Logrunner$ OR Satinbird$ OR Berrypecker$ OR Wattlebird$ OR Stitchbird$ OR Whipbird$ OR Wattle-eye$ OR Woodshrike$ OR Helmetshrike$ OR Bushshrike$ OR Boatbill$ OR Vanga$ OR Bristlehead$ OR Woodswallow$ OR Berryhunter$ OR Iora$ OR Cuckooshrike$ OR Whitehead$ OR Sittella$ OR Ploughbill$ OR Bellbird$ OR Whistler$ OR Shrike$ OR Vireo$ OR Figbird$ OR Drongo$

OR Fantail$ OR Monarch$ OR Crow OR Crows OR Mudnester$ OR Melampitta$ OR Ifrit$ OR Bird*-of-paradise OR Robin$ OR Rockfowl OR Rockjumper$ OR Waxwing$ OR Hypocolius OR Palmchat$ OR Oo OR Oos OR Hylocitrea$ OR Flycatcher$ OR Tit$ OR Nicator$ OR Reedling$ OR Lark$ OR Bulbul$ OR Swallow$ OR Wren-babbler$ OR Crombec$ OR Bushtit$ OR Grassbird$ OR Donacobius* OR Cisticola$ OR Fulvetta$ OR Laughingthrush* OR White-eye$ OR Dapple-throat$ OR Sugarbird$ OR Bluebird$ OR Goldcrest$ OR Elachura$ OR Hyliota$ OR Gnatcatcher$ OR Nuthatch* OR Wallcreeper$ OR Mockingbird$ OR Starling$ OR Oxpecker$ OR Thrush* OR Chat$ OR Dipper$ OR Leafbird$ OR Flowerpecker$ OR Sunbird$ OR Sparrow$ OR Weaver$ OR Waxbill$ OR Indigobird$ OR Accentor$ OR Wagtail$ OR Finch* OR Euphonia$ OR Longspur$ OR Tanager$ OR Spindalis* OR Wrenthrush* OR Oropendola$ OR Cardinal$ OR Emu$ OR Goose OR Geese OR Swan$ OR Guan$ OR Curassow$ OR Spoonbill$ OR Bittern$ OR Boobies OR Booby OR Shag$ OR Darter$ OR Hawk$ OR Eagle$ OR Crake$ OR Coot$ OR Tick-knee$ OR Avocet$ OR Pratincole$ OR Tern$ OR Skimmer$ OR Dove$ OR Falcon$ OR Calyptura$ OR Sharpbill$ OR Becard$ OR Longbill$ OR Butcherbird$ OR Greenlet$ OR Oriole$ OR Turnagra$ OR Jay$ OR Chickadee$ OR Martin$ OR Kinglet$ OR Thrasher$ OR Rhabdornis* OR Snowfinch* OR Widowbird$ OR Munia* OR Whydah$ OR Pipit$ OR Bunting$ OR Blackbird$ OR Grosbeak$)

Additional File 4. Data Extraction Categories and Values

Table S2.1 Articles data extraction categories and values

Data Extraction Category	**Description**	**Drop-down Options (additional options may be generated during data extraction)**
ID	Unique number assigned to each paper	
Citation	CSE Style in text citation	
Title		
Year of Publication		
Publication Venue	Journal name, conference, etc.	
Publication Type		Academic Journal;Book Chapter;Conference Proceedings;Government Agency Publication;Industry Publication;Non-profit Publication;Magazine Article;Thesis
Peer-reviewed		Yes/No
Full Text Available to Authors		Yes/No
Language		
Contains Excluded Studies		Yes/No
PICO/PECO Reasons for Exclusion		Population; Intervention/Exposure; Outcome
Reasons for Exclusion Notes	Briefly describe the reasons any studies within the article were exlcuded from the Studies table	

Table S2.1 Studies table data extraction categories and values

Data Extraction Category	**Description**	**Drop-down Options**	**PICO/PECO Component**
Article Citation	Citation of article in which the study is reported		
Study Name	Unique name assigned to each study		
Also Reported In	Citations for other papers that also describe this study		
Study Summary	Brief summary of study purpose and methods, not results		
First Study Year			Context
Sector		Agriculture;Aquaculture;Communications;Land-based Oil Extraction;Livestock;Mining;Offshore Oil;Land-based oil extraction;Transportation;Urban;NA	Context
Land/Water		Coastal;Pelagic;Freshwater; Terrestrial	Context
Latitude			Context
Longitude			Context
Country			Context
State/Province			Context
Site/Area	Site name (e.g. Edmonton Airport, name of a city)		Context
Setting		Field; lab; pen	Context
Study Duration (years)	Code as "0" if study duration < 1 year		Context

Study Duration	Description of the duration of the study		Context
Time of Day Categorical		Night;Sunrise;Day;Sunset;Multiple	Context
Moon Phase	"UA" if not reported. "Varied" if reported and varied within study period.	New; full; in between; varied; UA	Context
Ambient Light Quantitative	In units reported in article		Context
Cloud Cover (categorical)		Only clear days/nights;Only cloudy days/nights;Both clear and cloudy days/nights;UA	Context
Cloud Cover (qualitative)			Context
Cloud Height			Context
Precipitation			Context
Wind Speed			Context
Wind Direction			Context
Qualitative Weather Description			Context
Population Description	If multiple species, list all common names. List all that apply: songbirds, nocturnal migrants, raptors, waterfowl, seabirds, poultry.		Population
Species Common Name			Population
Species Latin Name			Population
IUCN Status			Population
Domestication Status		Wild; captive wild; domesticated	Population
Migrating	Are the birds actively migrating during the treatments?		Population
Bird Activity During Intervention/Exposure		Foraging/hunting;Loafing;Roosting;Nesting;Flying;Other	Population

Study Design		BACI;BA;CI;CI-Rotating;Behavioural Assay;Incidental Report;Habitat/Resource Selection	Comparator
Control	Description of control		Comparator
Intent of Intervention		Attraction; deterrence; other	Intervention/Exposure
Allocation of Treatments		Random; systematic non-random; by availability	Intervention/Exposure
Wavelengths tested	All wavelengths tested in the study, reported in nanometers		Intervention/Exposure
Colors Tested	All wavelengths tested in the study, categorized by color	White;Red;Orange;Yellow; Green;Blue; Turquoise;Purple;UV;Infrared;UA;UA (presumed white)	Intervention/Exposure
Flashing Patterns Tested	All flashing patterns tested in the study	Flashing;Continuous;Both	Intervention/Exposure
Light Source		Beam;Gas Flare;Illuminated Structure;Laser;Obstruction Lighting;Road Lights;Urban/suburban Sources (unspecified);Other	Intervention/Exposure
Light Direction		Up;Down;Horizontal;Non-directional;Directed at birds	Intervention/Exposure
Light Source Movement	check all that apply	Stationary;Moving;Rotating	Intervention/Exposure
Light Bulb Type			Intervention/Exposure
Brand/Model			Intervention/Exposure
Light power (milliwatts)			Intervention/Exposure
Light Intensity Range in units reported			Intervention/Exposre
Light Intensity Range in lumen			Intervention/Exposure
Notes on Light Source			Intervention/Exposure
Other Simultaneous Interventions		Acoustic;Human presence;Live predator presence;Other visual;Object approach;None	Intervention/Exposure
Notes on Other Interventions			Intervention/Exposure

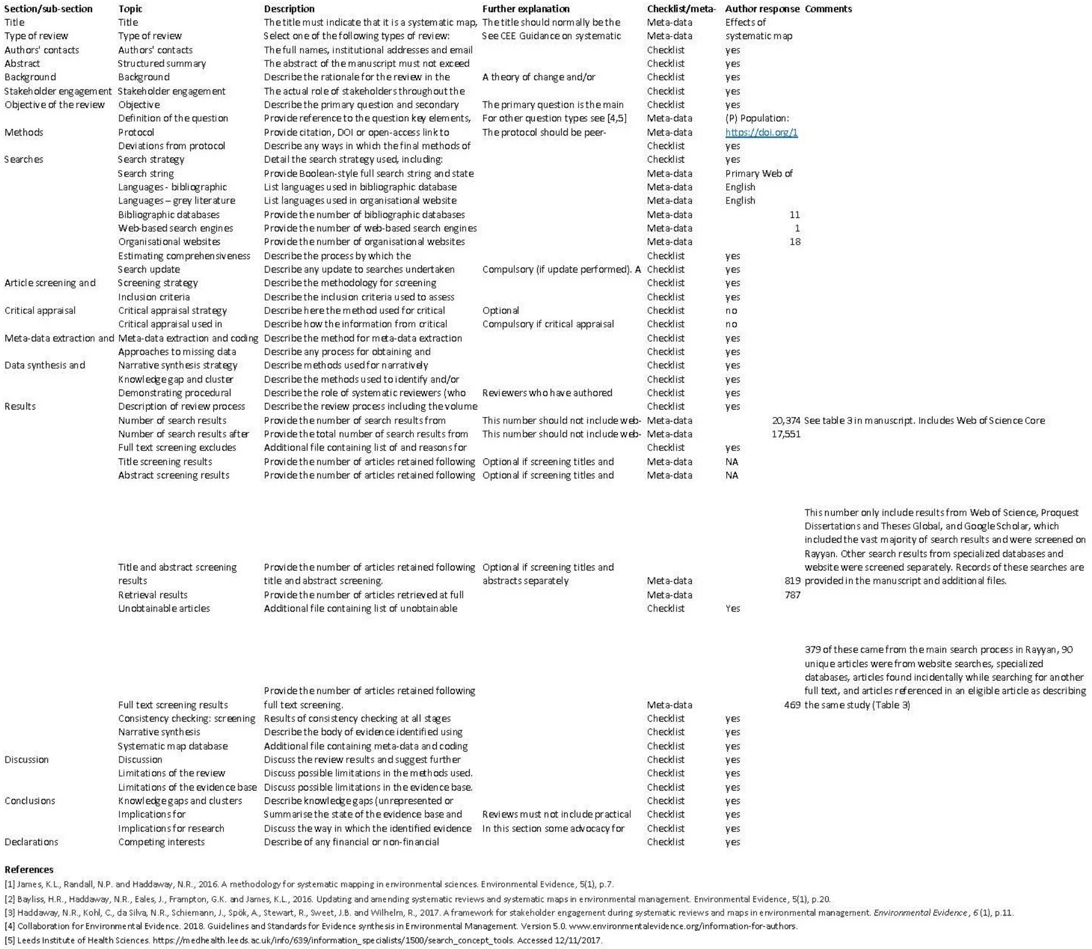
Outcome Studied	What is the outcome the authors were trying to understand?	Density/abundance;Mortality;Resource consumption;Behaviour	Outcome
Outcome Measurement	What did the authors actually measure?	Bird count;Vocalization count;Other vocalization measure;Carcass survey;Flight initiaion;Diving;Other avoidance response;Overt reaction distance;Other alert response;Flight velocity;Flight altitude;Qualitative flight path;Absolute flight direction;Changes in flight direction;Hunting/foraging behaviour;Habitat use;Orientation;Timing of activities	Outcome
Measurement Method	How did they measure the outcome?	Visual survey - unassisted;Visual survey - magnification;Visual survey - thermal imaging;Visual survey - light amplifier;Visual survey - ceilometer;Photography;Video;Radar;Radio telemetry;Acoustic recording;Vocalization count - not recorded;GPS tracking;Radio transmitters;eBird data;Emlen funnel;Recovery of Banded Birds	Outcome
Outcome Measurement Latency		During treatment; immediately after treatment; more than 1 minute after treatment	Outcome
Outcome Measurement Scale		Site (<1 km radius);Local (>= 1 km, <= 5 km radius);Regional (>5 km radius);Multiple	Outcome
Notes on Effect	Brief summary of results		Outcome

Appendix B. Additional files for Chapter 3

All additional files are available to download at https://environmentalevidencejournal.biomedcentral.com/articles/10.1186/s13750-021-00246-8#Sec32.

Where possible, I have included copies of the additional files in this Appendix

Additional File 1. Roses form



Section/sub-section	**Topic**	**Description**	**Further explanation**	**Checklist/meta-**	**Author response**	**Comments**
Title	Title	The title must indicate that it is a systematic map,	The title should normally be the	Meta-data	Effects of	
Type of review	Type of review	Select one of the following types of review:	See CEE Guidance on systematic	Meta-data	systematic map	
Authors' contacts	Authors' contacts	The full names, institutional addresses and email		Checklist	yes	
Abstract	Structured summary	The abstract of the manuscript must not exceed		Checklist	yes	
Background	Background	Describe the rationale for the review in the	A theory of change and/or	Checklist	yes	
Stakeholder engagement	Stakeholder engagement	The actual role of stakeholders throughout the		Checklist	yes	
Objective of the review	Objective	Describe the primary question and secondary	The primary question is the main	Checklist	yes	
	Definition of the question	Provide reference to the question key elements,	For other question types see [4,5]	Meta-data	(P) Population:	
Methods	Protocol	Provide citation, DOI or open-access link to	The protocol should be peer-	Meta-data	https://doi.org/1	
	Deviations from protocol	Describe any ways in which the final methods of		Checklist	yes	
Searches	Search strategy	Detail the search strategy used, including:		Checklist	yes	
	Search string	Provide Boolean-style full search string and state		Meta-data	Primary Web of	
	Languages - bibliographic	List languages used in bibliographic database		Meta-data	English	
	Languages – grey literature	List languages used in organisational website		Meta-data	English	
	Bibliographic databases	Provide the number of bibliographic databases		Meta-data	11	
	Web-based search engines	Provide the number of web-based search engines		Meta-data	1	
	Organisational websites	Provide the number of organisational websites		Meta-data	18	
	Estimating comprehensiveness	Describe the process by which the		Checklist	yes	
	Search update	Describe any update to searches undertaken	Compulsory (if update performed). A	Checklist	yes	
Article screening and	Screening strategy	Describe the methodology for screening		Checklist	yes	
	Inclusion criteria	Describe the inclusion criteria used to assess		Checklist	yes	
Critical appraisal	Critical appraisal strategy	Describe here the method used for critical	Optional	Checklist	no	
	Critical appraisal used in	Describe how the information from critical	Compulsory if critical appraisal	Checklist	no	
Meta-data extraction and	Meta-data extraction and coding	Describe the method for meta-data extraction		Checklist	yes	
	Approaches to missing data	Describe any process for obtaining and		Checklist	yes	
Data synthesis and	Narrative synthesis strategy	Describe methods used for narratively		Checklist	yes	
	Knowledge gap and cluster	Describe the methods used to identify and/or		Checklist	yes	
	Demonstrating procedural	Describe the role of systematic reviewers (who	Reviewers who have authored	Checklist	yes	
Results	Description of review process	Describe the review process including the volume		Checklist	yes	
	Number of search results	Provide the number of search results from	This number should not include web-	Meta-data	20,374	See table 3 in manuscript. Includes Web of Science Core
	Number of search results after	Provide the total number of search results from	This number should not include web-	Meta-data	17,551	
	Full text screening excludes	Additional file containing list of and reasons for		Checklist	yes	
	Title screening results	Provide the number of articles retained following	Optional if screening titles and	Meta-data	NA	
	Abstract screening results	Provide the number of articles retained following	Optional if screening titles and	Meta-data	NA	
	Title and abstract screening results	Provide the number of articles retained following title and abstract screening.	Optional if screening titles and abstracts separately	Meta-data	819	This number only include results from Web of Science, Proquest Dissertations and Theses Global, and Google Scholar, which included the vast majority of search results and were screened on Rayyan. Other search results from specialized databases and website were screened separately. Records of these searches are provided in the manuscript and additional files.
	Retrieval results	Provide the number of articles retrieved at full		Meta-data	787	
	Unobtainable articles	Additional file containing list of unobtainable		Checklist	Yes	
	Full text screening results	Provide the number of articles retained following full text screening.		Meta-data	469	379 of these came from the main search process in Rayyan, 90 unique articles were from website searches, specialized databases, articles found incidentally while searching for another full text, and articles referenced in an eligible article as describing the same study (Table 3)
	Consistency checking: screening	Results of consistency checking at all stages		Checklist	yes	
	Narrative synthesis	Describe the body of evidence identified using		Checklist	yes	
	Systematic map database	Additional file containing meta-data and coding		Checklist	yes	
Discussion	Discussion	Discuss the review results and suggest further		Checklist	yes	
	Limitations of the review	Discuss possible limitations in the methods used.		Checklist	yes	
	Limitations of the evidence base	Discuss possible limitations in the evidence base.		Checklist	yes	
Conclusions	Knowledge gaps and clusters	Describe knowledge gaps (unrepresented or		Checklist	yes	
	Implications for	Summarise the state of the evidence base and	Reviews must not include practical	Checklist	yes	
	Implications for research	Discuss the way in which the identified evidence	In this section some advocacy for	Checklist	yes	
Declarations	Competing interests	Describe of any financial or non-financial		Checklist	yes	

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Additional File 2. Web of Science Search Strategy Explanation

During scoping we found that our population search string did not find all eligible articles in the Web of Science Core Collection that were indexed without abstracts or without keywords, so we performed an additional search for these articles using an expanded search string (Figure 3.S1). The expanded search string contained all English common family names for birds (listed below). The justification for this strategy is detailed in our systematic map protocol. The results from the Web of Science Core Collection searches, before we applied any macros, are in

Additional Files 3A and 3B. We used the Microsoft Excel Macros in *Applying_No_A_or_K_Macro.xslm* (Additional file 3C) to: 1) extract form the expanded search string results only articles which lacked an abstract or lacked keywords (*No_Abstracts_or_Keywords* macro); 2) combine the results from the short and expanded searches (*Combine_Long_and_Short_Results* macro); and 3) remove duplicates with identical authors, titles, and journal names using Microsoft Excel's duplicate removal feature (*Remove_Duplicates* macro).

We used a pre-screening strategy to eliminate articles where our intervention search terms were only used in phrases irrelevant to our systematic map question. We used the *replace_terms* macro in the *Applying_Replace_Terms_Macro_CC.xlsm* workbook (Additional File 3D) to replace irrelevant uses of our intervention search terms with synonyms in capital letters (listed below). We then searched the revised records to find articles that contained one of the intervention search terms in any of the following categories: title, abstract, author keywords, Web of Science keywords, journal name, or Web of Science category. These articles were uploaded to Rayyan for further screening (Additional File 3E).

We searched the Web of Science Zoological Record citation index using the WOS search string (search record in Additional file B9) and applied the same strategy to replace irrelevant uses of search terms, with the macro edited to pre-screen the results of Zoological Record searches in *Applying_Replace_Terms_ZR* (Additional File 3G). We excluded from further screening any articles that were also found in the Web of Science Core Collection search, using the *Remove_dups_ZRCC* macro in the *Applying_Remove_dups_ZRCC.xlsm* workbook (Additional File 3H). We removed duplicates with the same title, source, and first author's last name. After removing duplicates, we uploaded the search results to Rayyan for further screening

(Additional File 3I). Additional files 3J – 3N provide records of the search and pre-screening processes for the updated search in Web of Science Core Collection, while Additional Files 3O - 3R provide the records for the updated search in Web of Science Core Collection.

In Additional Files 3S – 3V, we provide blank workbooks that can be used to apply these strategies to any Web of Science Core Collection or Zoological Record search.

Expanded Population Search String:

TS = (*bird* OR Avian OR Ave$ OR Ostrich* OR Rhea$ OR Kiwi$ OR Cassowar* OR Tinamous* OR Screamer$ OR Magpie$ OR Duck$ OR Megapode* OR Chachalaca$ OR Guineafowl OR Quail OR Pheasant$ OR Loon$ OR Penguin$ OR Petrel$ OR Albatross* OR Shearwater$ OR Grebe$ OR Flamingo$ OR Tropicbird$ OR Stork$ OR Ibis* OR Heron$ OR Hamerkop$ OR Shoebill$ OR Pelican$ OR Frigatebird$ OR Gannet$ OR Cormorant$ OR Anhinga$ OR Vulture$ OR Secretarybird$ OR Osprey$ OR Kite$ OR Bustard$ OR Mesite$ OR Seriema$ OR Kagu$ OR Sunbittern$ OR Flufftail$ OR Finfoot$ OR Rail$ OR Trumpeter$ OR Crane$ OR Limpkin$ OR Buttonquail$ OR Curlew$ OR Sheathbill$ OR Plover$ OR Oystercatcher$ OR Ibisbill$ OR Stilt$ OR Snipe$ OR Jacana$ OR Plains-wanderer$ OR Seedsnipe$ OR Sandpiper$ OR Courser$ OR Gull$ OR Skua$ OR Auk$ OR Sandgrouse OR Grouse OR Pigeons$ OR Hoatzin$ OR Turaco$ OR Cuckoo$ OR Owl$ OR Frogmouth$ OR Oilbird$ OR Potoo$ OR Nightjar$ OR Treeswift$ OR Swift$ OR Hummingbird$ OR Mousebird$ OR Trogon$ OR Roller$ OR Kingfisher$ OR Tody OR Todies OR Motmot$ OR Bee-eater$ OR Hoopoe$ OR Hornbill$ OR Jacamar$ OR Puffbird$ OR Barbet$ OR Toucan$ OR Honeyguide$ OR Woodpecker$ OR Caracara$ OR Parrot$ OR Cockatoo$ OR Wren$ OR Sapayoa$ OR Broadbill$ OR Pitta$ OR Ovenbird$ OR Antbird$ OR Antthrush* OR Antpitta$ OR Gnateater$ OR Tapaculo$ OR Crescentchest* OR Flycatcher$ OR Cotinga$ OR Manakin$ OR Tityra$ OR Lyrebird$ OR Scrubbird$ OR Bowerbird$ OR Treecreeper$ OR Honeyeater$ OR Bristlebird$ OR Pardalote$ OR Warbler$ OR Babbler$ OR Logrunner$ OR Satinbird$ OR Berrypecker$ OR Wattlebird$ OR Stitchbird$ OR Whipbird$ OR Wattle-eye$ OR Woodshrike$ OR Helmetshrike$ OR Bushshrike$ OR Boatbill$ OR Vanga$ OR Bristlehead$ OR Woodswallow$ OR Berryhunter$ OR Iora$ OR Cuckooshrike$ OR Whitehead$ OR Sittella$ OR Ploughbill$ OR Bellbird$ OR Whistler$ OR Shrike$ OR Vireo$ OR Figbird$ OR Drongo$ OR Fantail$ OR Monarch$ OR Crow OR Crows OR Mudnester$ OR Melampitta$ OR Ifrit$ OR Bird*-of-paradise OR Robin$ OR Rockfowl OR Rockjumper$ OR Waxwing$ OR Hypocolius OR Palmchat$ OR Oo OR Oos OR Hylocitrea$ OR Flycatcher$ OR Tit$ OR Nicator$ OR Reedling$ OR Lark$ OR Bulbul$ OR Swallow$ OR Wren-babbler$ OR Crombec$ OR Bushtit$ OR Grassbird$ OR Donacobius* OR Cisticola$ OR Fulvetta$ OR Laughingthrush* OR White-eye$ OR Dapple-throat$ OR Sugarbird$ OR Bluebird$ OR Goldcrest$ OR Elachura$ OR Hyliota$ OR Gnatcatcher$ OR Nuthatch* OR Wallcreeper$ OR Mockingbird$ OR Starling$ OR Oxpecker$ OR Thrush* OR Chat$ OR Dipper$ OR Leafbird$ OR Flowerpecker$ OR Sunbird$ OR Sparrow$ OR Weaver$ OR Waxbill$ OR Indigobird$ OR Accentor$ OR Wagtail$ OR Finch* OR Euphonia$ OR Longspur$ OR Tanager$ OR Spindalis* OR Wrenthrush* OR Oropendola$ OR Cardinal$ OR Emu$ OR Goose OR Geese OR Swan$ OR Guan$ OR Curassow$ OR Spoonbill$ OR Bittern$ OR Boobies OR Booby OR Shag$ OR Darter$ OR Hawk$ OR Eagle$ OR Crake$ OR Coot$ OR Tick-knee$ OR Avocet$ OR Pratincole$ OR Tern$ OR Skimmer$ OR Dove$ OR Falcon$ OR Calyptura$ OR Sharpbill$ OR Becard$ OR Longbill$ OR Butcherbird$ OR Greenlet$ OR Oriole$ OR Turnagra$ OR Jay$ OR Chickadee$ OR Martin$ OR Kinglet$ OR Thrasher$ OR Rhabdornis* OR Snowfinch* OR Widowbird$ OR Munia* OR Whydah$ OR Pipit$ OR Bunting$ OR Blackbird$ OR Grosbeak$) AND TS = (Light* OR Laser* OR Strobe$ OR Streetlight* OR Headlight$ OR Spotlight* OR Lamp$ OR Beacon$ OR Beam$ OR Flash* OR Flare$ OR Flaring OR Reflector$ OR Ceilometer$)

Terms to Find and Replace:

Find	Replace
in light of	CONSIDERING
in the light of	CONSIDERING
come to light	REVEAL
comes to light	REVEALS
in this light	FROM THIS PERSPECTIVE
lightweight	NOT HEAVY
shed light on	SHOW
shed some light on	SHOW
sheds light on	SHOWS
sheds some light on	SHOWS
light-level geolocator	LL GEOLOCATOR
light level geolocator	LL GEOLOCATOR
light-logging geolocator	LL GEOLOCATOR
light-logger	LL GEOLOCATOR
light-based geolocator	LL GEOLOCATOR
light rail	L RAIL
light-rail	L-RAIL

Additional File 8. Explanations of Eligibility Criteria

As we screened articles for study eligibility, we added details to the eligibility criteria published in the protocol to better define the scope of our map and promote consistency of evaluation by others (Table 1). As for our original criteria, we excluded specific interventions/exposures that did not involve an artificial light source, such as studies of reflected or filtered daylight. This necessarily excluded some studies of bird hazards (e.g. windows), deterrents (e.g. mylar, streamers, mirrors), and orientation (e.g. UV and polarized light filters).

For interventions that are so broadly applied as to make mapping their use prohibitive, we required that they compare bird behaviour under light of different wavelengths or intensities. Most laboratory studies use broad-spectrum white light to illuminate cages and mimic natural daylight with a light and a dark period, though the spectral qualities of the light are rarely reported. While these lights are artificial, including any laboratory study that used artificial light would require that we include nearly all laboratory studies in the map. Laboratory studies using only broad-spectrum (i.e. white) light of a single intensity were excluded. Similarly, we excluded artificial photoperiods because most laboratory studies subject birds to a photoperiod different from the local photoperiod. We included laboratory studies that compared, within the same study, bird responses to light of varying intensities, different spectral compositions, or different photoperiods, providing that they also studied an eligible outcome.

In making eligibility decisions about relevant outcomes, we included outcomes documenting movement through space including behaviours that directly precede movement through space, which we defined as movement from one specific place to another. We excluded outcomes that measured general locomotor activity (e.g. perch-hopping, time spent walking, overall activity levels), but not movement from one specific place to another. Examples of behaviours known to precede movement included overt reaction distance or alert response in the context of deterrents, and studies of orientation and disorientation in the context of aggregation.

We excluded outcomes that did not directly demonstrate the behaviours that illustrate or contribute to our secondary questions: aggregation, deterrence, disorientation, and habitat use or selection. For this reason, we excluded studies testing birds' ability to see specific wavelengths or using light as a visual cue in a trained response. We excluded outcomes involving temporal changes in daily or annual movements (e.g. timing of entering/exiting nest boxes or migration) or changes to circadian rhythms. We excluded laboratory or poultry studies in which changes to timing of feeding, sleeping, bathing, etc. were measured as part of a suite of variables showing changes in the birds' internal clock or overall activity levels. We agreed that these outcomes offered no direct evidence of the effect of light on bird aggregation, deterrence, or habitat use or selection. Temporal shifts potentially influence habitat selection -- birds may avoid artificial light because it disrupts their sleep or prefer artificially lit habitat to take advantage of extended day lengths and foraging times -- but we did not include these studies unless they demonstrated a change in habitat use, association or selection. For reference, Appendix X lists all excluded articles related to general locomotor activity or temporal changes in daily or annual movements that were excluded from the map.

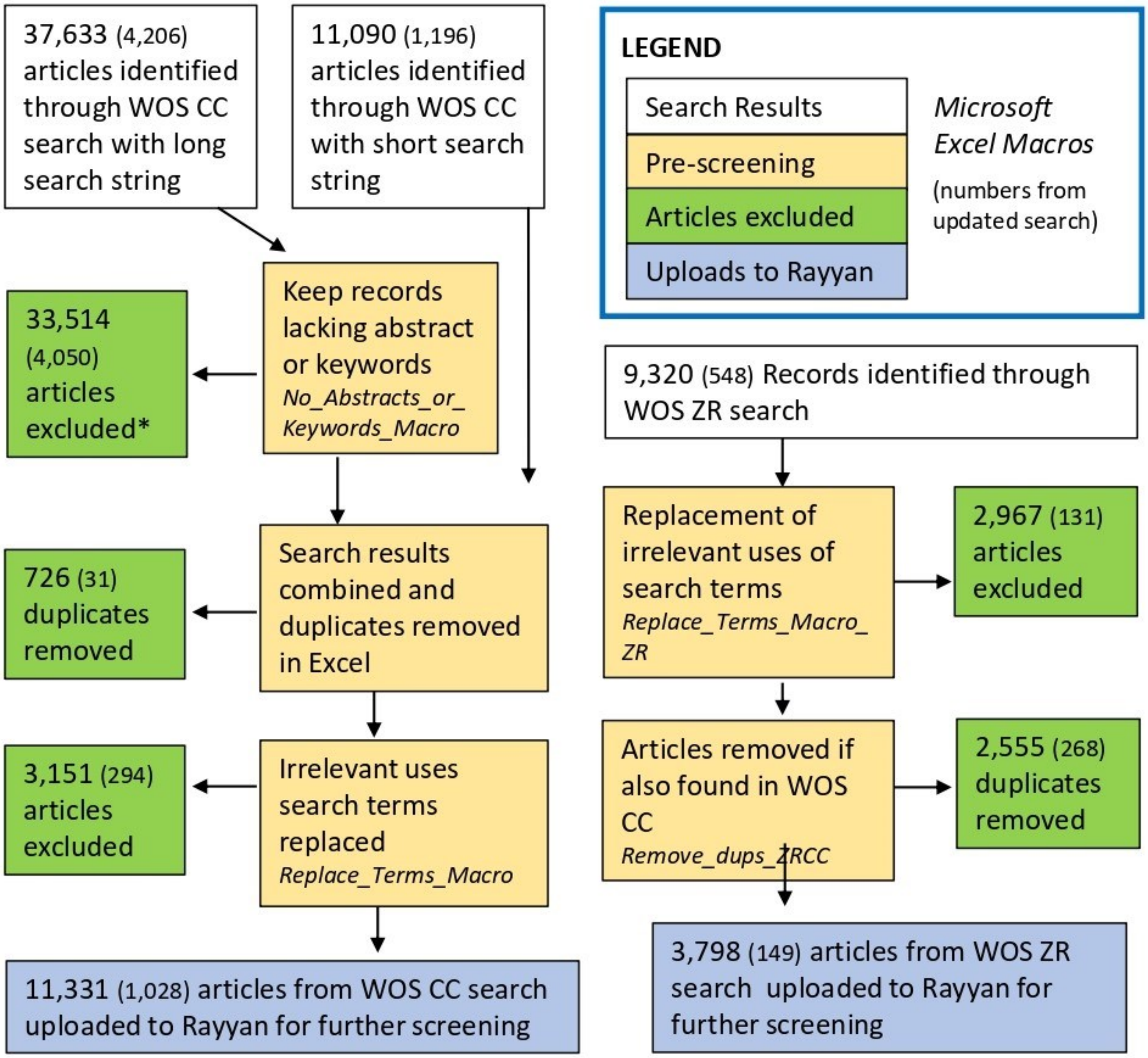
We included studies of foraging birds when they showed how artificial light affected foraging habitat selection or use. We included poultry or lab studies if the birds selected among foraging areas with different levels of illumination. We also included field studies that recorded how artificial light affected the abundance of birds in foraging sites such as feeders, including arrival or departure times, number of birds present, or amount of food consumed. We also included incidental reports of nocturnal foraging under artificial lights surrounded by dark habitat, while recognizing that observations without controls cannot conclusively demonstrate that birds were more likely to forage at night in sites that were artificially lit than in adjacent dark areas. We did not include studies of bird foraging behaviour that did not involve movement through space or changes to distribution (e.g. time spent foraging or changes foraging strategies).

We excluded studies measuring changes to timing of chick provisioning in artificially lit nest sites because these studies did not measure habitat use. While these studies indicated that adults birds with illuminated nests foraged later into the night or earlier in the morning than birds with dark nest sites, we cannot confidently infer that the adult birds foraged under artificial lights. They may have foraged in dark sites away from the nest. The parents may have increased their foraging duration to feed their nestlings whose metabolic activity increased under artificial light or because of changes in their circadian rhythm, outcomes which were not eligible for inclusion in the systematic map.

	Eligibility Criteria	Exclusion Criteria
Population	● Any bird species, including domesticated species	
Intervention/ Exposure	● Anthropogenic light sources, including, but not limited to, point sources of light, illuminated habitat, and skyglow ● Gas Flares	● Reflected daylight (e.g. mylar tape reflectors, windows) ● Filters on natural daylight
Comparator	● Same site under different lighting conditions ● Nearby site at the same time of day with similar habitat type, anthropogenic activity, migration density (if applicable) and weather as the treatment site ● Documentation of aggregation, mass landing, mortality, foraging, or other relevant outcomes near artificial light sources without comparator were included in the map and categorized as incidental reports	● ● Laboratory experiments that using only one intensity or spectral composition of light within the "light" or "dark" portions of the light cycle ● Laboratory experiments that use an artificial photoperiod but do not vary the photoperiod
Outcome	● Bird density or presence/absence, including (but not limited to) radar observations, visual counts and vocalization counts ● Bird mortality ● Resource consumption (such as crop damage or aquaculture predation) ● Behavioural outcomes directly involving movement through space, including (but not limited to) flight path, flight initiation, diving and flushing ● Behavioural response (flushing or immobilization) to spotlights used for capturing birds ● Behaviours known to precede movement: orientation, overt reaction distance, alert response (e.g. moving head laterally or vertical, crouching) ● Documentation of birds foraging under artificial lights ● Habitat use metrics at foraging sites such as feeders (e.g. arrival/departure times, feeder visit rates)	● Responses that are not conventionally associated with movement (e.g. hormonal responses) ● Behavioural responses that do not include or directly precede movement through space (e.g. preening, dust-bathing, sleep behaviour, vocalizing) ● General locomotor activity (e.g. perch-hopping or time spent walking) ● Temporal changes in daily or annual activity rhythms (e.g. entering/leaving nest box, migration) ● Changes to timing of activities in laboratory experiments (e.g. feeding, drinking) ● Total feed consumption in laboratory experiments ● Trained responses (e.g. trained to perform a task when a light is on) ● Ability to see specific wavelengths (e.g. mate choice or ability to distinguish objects under varying light conditions) ● Changes to timing in chick provisioning in field studies
Study Design	● BA, CI, BACI, RCT, time-series, post-hoc surveys, or description / anecdote (e.g. documentation of mass mortality event)	

Additional File 12. Supplemental tables and figures

Figure S3.1 Pre-screening process for Web of Science Searches. The macros used for these processes can be found in Additional File 3.



The names of the Microsoft Excel macros used for pre-screening processes are give in italics. The number of articles found or excluded during the updated search are give in parentheses.

*Any article excluded at this stance that had bird, avian, or aves in its abstracft or keywords was found by the search string and included in the WOS CC short search string search results. See Additional File 2 for details.

Table S3.1 Organizational Website Searches

Organization	Website	Number of Articles Found
Accipiter Radar	https://www.accipiterradar.com	0
Bird Avert	https://www.birdavert.com	0
Bird Control Group	https://www.birdcontrolgroup.com	0
Bird-X	https://bird-x.com	0
DeTect	https://detect-inc.com	0
Merlin Environmental	https://merlinenvironmental.co.uk/	0
Transport Canada	https://www.tc.gc.ca	0
USDA/Aphis	https://www.aphis.usda.gov/	2
Department for Environment, Food, and rural Affairs (UK)	https://www.gov.uk/government/organisations/department-for-environment-food-rural-affairs	0
United States Fish and Wildlife Service	https://www.fws.gov/	3
Bureau of Ocean Energy Management	https://www.boem.gov/	1
Bird Strike Association of Canada	https://canadianbirdstrike.ca	0
British Trust for Ornithology	https://www.bto.org	2
Bird-Life International	https://www.birdlife.org	1
FLAP	https://www.flap.org	2
International Dark Sky Association	https://www.darksky.org	2
IUCN SSC Human Wildlife Conflict Task Force	http://www.hwctf.org	0
Proceedings of the Vertebrate Pest Conference	https://digitalcommons.unl.edu/vpccollection/	4
Total		17

Table S3.2 Number of studies in each hemisphere

	E	W
N	129	290
S	53	18

Table S3.3 Number of studies applying treatment at each time of day

Time of Day Treatment Applied	Number of Studies
Day only	33
Multiple	58
UA – presumed multiple	21
Night only	127
Night and sunset or sunrise only	44
UA – presumed night	133
Sunset or dusk only	10
UA	64

Table S3.4 Migration status of study populations

Migration Status	Number of Studies
Yes	188
Yes (fledgling seabird)	29
No	218
Mixed	22
UA – presumed Mixed	1

*Table S3.5 Domestication status of study populations***.**

Domestication Status	Number of Studies
Captive Wild	81
Domesticated	32
Wild	377

Table S3.6 Orders with no studies in Systematic Map and the number of species in each order.

IOC Orders	Number of Species in Order
Pinafores	46
Trogoniformes	43
Otidiformes	26
Musophagiformes	23
Coliiformes	6
Phoenicopteriformes	6
Casuariiformes	4
Mesitornithiformes	3
Phaethontiformes	3
Eurypygiformes	2
Cariamiformes	2
Struthioniformes	2
Leptosomiformes	1
Opisthocomiformes	1

Table S3.7 Number of studies relevant to each secondary question that were conducted for each study purpose.

	Aggregation/ Mortality	Causes of Aggregation/Mortality		Deterrence	Habitat Selection
		Attraction	Orientation		
Basic behavioural research				2	5
Capture or count birds for wildlife research	6	3		34	
Deter birds	10	6		81	5
Document and/or reduce bird aggregations or mortality	168	15		84	1
Document birds foraging under artificial light at night	9			4	10
Document occurrence of a rare species	3			3	
Document unusual bird behaviours					
Improve welfare or production of captive birds				7	30
Monitor or describe bird migration	35	1		32	
Other	3			1	2
Study effects of AL on bird community					2
Study effects of AL on bird distribution or habitat selection	5			2	35
Study weight loss during nocturnal migration	2			2	
Test ability to orient under artificial light conditions	1		38		

Blank cells indicate a value of 0.

Table S3.8 Number of studies documenting each outcome that could demonstrate attraction in flying birds

Outcome	Number of Studies with Control	Number of studies without control
Discrete choice (instantaneous choice among lighting options)	1	0
Modeled flight behaviour based on observations of bird locations or distributions	2	0
Altitude	1	0
Change in flight direction relative to light source	4	1
Altitude	9	9
Capture of birds in flight	0	3
Studies measuring changing in flight direction, altitude, OR capture of birds in flight	11	12

Table S3.9. Number of studies testing each orientation mechanism

Orientation Mechanism	**Number of Studies**
Magnetoreception	30
Horizon glow	3
Clock-shift (same photoperiod shifted earlier or later)	3
Photoperiod change	2

Magnetoreception studies tested how artificial light influenced bird response to changes in the magnetic field. Horizon glow studies tested how the orientation of birds in open-air enclosures changed if horizon glow was present. Clock-shift experiments change the birds' perceived time-of-day to determine if they used the suns' position in the sky to orient. Photoperiod change experiments artificially altered day-length to determine if it changed the birds' preferred migratory direction.

Table S3.10. Lamp types for white lights used in magnetoreception studies

Study Name	**Lamp Type for White Light**
Wiltschko et al. 2014b	Fluorescent
Muheim et al. 2016	Halogen
Migalski 2011	Halogen
Rappl et al. 2000	Halogen, Incandescent
Wiltschko et al. 1993	Halogen, Incandescent
Wiltschko & Wiltschko 1995	Incandescent
Wiltschko & Wiltschko 1998	Incandescent
Munro et al. 1997	Incandescent
Wiltschko et al. 2007b	Incandescent
Wiltschko et al 2004a	Incandescent
Wiltschko et al. 2014a European Robins	UA
Muheim et al. 2002	Xenon

Table S3.11 Number of studies testing each wavelength of each deterrent type.

Includes all studies that could demonstrate deterrence, regardless of the purpose for which the study was conducted.

Color	**Flashing light**	**Laser**	**Line markers**	**Spotlight or beam**	**UV or near-UV light**
White	30	0	1	22	1
UA - presumed white	5	0	0	59	0
Red	27	21	0	11	1
Orange	1	0	0		0
Yellow	2	0	0	1	0
Green	5	10	3	1	1

Blue/green		7	0		0
Blue	7	1	0	1	0
Violet	1	1	0		3
UV	3	0	0		5
UA	10	14	0	47	0

Table S3.12 Number of studies conducted at different times of day testing each deterrent type.

Includes all studies that could demonstrate deterrence, regardless of the purpose for which the study was conducted.

Time of Day Treatment Applied	Flashing light	Laser	Line markers	Pyrotechnic	Spotlight or beam	UV or near-UV light	All
Day only	13	4	0	0	6	3	18
Multiple	4	9	3	0	5	0	23
Night only	9	6		0	55	0	72
Night and Sunset or Sunrise only	1	7	1	0	1	2	11
Sunset or Dusk only	0	4	0	0	1	0	5
UA - presumed multiple	9	0	0	0	3	0	12
UA - presumed night only	8	0	0	0	55	0	57
UA	13	16	0	1	1	2	32

Table S3.13 Preference tests using light sources typically used as deterrents.

Study ID	**Article Citation**	**Study Name**	**Control Design**
329	Werner and Clark 2006	Werner and Clark 2006	Preference Test - control UA
292	Kovach 1980	Kovach 1980 Experiment 1	Preference Test - no control
293	Kovach 1980	Kovach 1980 Experiment 2	Preference Test - no control
298	Kovach 1980	Kovach 1980 Stimulus brightness	Preference Test - no control
299	Kovach 1980	Kovach 1980 Stimulus colour	Preference Test - no control
300	Kovach 1980	Kovach 1980 colour preferences	Preference Test - no control
128	Goller et al. 2018	Goller et al. 2018	Preference Test - with control
254	Greenwood et al. 2004	Greenwood et al. 2004	Preference Test - with rotation or randomization
288	Widowski and Duncan 1996	Widowski and Duncan 1996	Preference Test - with rotation or randomization
326	Murdoch et al. 2018	Murdoch et al. 2018	Preference Test - with rotation or randomization

354	Blackwell et al. 2002	Blackwell et al. 2002 experiment 1	Preference Test - with rotation or randomization
355	Blackwell et al. 2002	Blackwell et al. 2002 experiment 2	Preference Test - with rotation or randomization
356	Blackwell et al. 2002	Blackwell et al. 2002 experiment 3 cowbirds	Preference Test - with rotation or randomization
357	Blackwell et al. 2002	Blackwell et al. 2002 experiment 3 starlings	Preference Test - with rotation or randomization
358	Blackwell et al. 2002	Blackwell et al. 2002 experiment 4 starlings	Preference Test - with rotation or randomization
359	Blackwell et al. 2002	Blackwell et al. 2002 experiment 4 doves	Preference Test - with rotation or randomization
360	Blackwell et al. 2002	Blackwell et al. 2002 experiment 5 geese	Preference Test - with rotation or randomization
361	Blackwell et al. 2002	Blackwell et al. 2002 experiment 5 mallards	Preference Test - with rotation or randomization

Table S3.14 Number of studies in the habitat selection evidence base with each control design and habitat selection study design.

Control Design	**Habitat Selection Study Design**	**Number of Studies**	
Preference Test - with rotation or randomization and control	NA	3	Total preference tests: 43
Preference Test - with rotation or randomization	NA	29	
Preference Test - with control	NA	1	
Preference Test - no control	NA	7	
Preference Test - control UA	NA	3	
Before/After	Relative Abundance	1	Total measuring relative abundance: 6
Control/Impact	Relative Abundance	1	
Gradient - spatial	Relative Abundance	4	
Gradient - spatial	Used vs. Available	1	Total measuring probability of selection or occupancy: 15
Gradient - spatial	Used vs. Random	4	
Before/After	Used vs. Random	1	
Gradient - spatial	Used vs. Unused	7	
Control/Impact	Used vs. Unused	2	
Gradient - spatial	Used vs. Unused; Relative Abundance	1	Total meausuring both: 1
Control/Impact	**A control/impact design with distance to light source as the response variable in a regression analysis	1	Total using other Control/Impact, Before/After, or Gradient designs: 19

Control/Impact	**Used vs. Available - light logger readings compared to average light level in site	2	
Control/Impact	NA	8	
Before/After	NA	7	
Before/After/Control/Impact - Rotating	NA	1	
Gradient - spatial	NA	2	
Analysis of the influence of species characteristics on the population's response to artificial light	**Analysis of how species traits influence their distributions relative to artificial light	2	
Qualitative observation of bird proximity to light sources	NA	1	
Behavioural Assay - no control	NA	1	

Table S3.15 Number of studies with and without controls in the Systematic Map and in the evidence base for each secondary question.

	All	Aggregation/Mortality	Attraction	Orientation	Deterrence	Habitat Selection
With Control	290	96	13	35	114	88
Without Control	200	122	12	3	116	0

Table S3.16 Number of studies with each control design

Control Design	Number of Studies
Analysis of the influence of species characteristics on the population's response to artificial light	2
Before/After	58
Before/After/Control/Impact	8
Before/After/Control/Impact - Rotating	2
Behavioural Assay - no control	51
Behavioural Assay - with control	67
Control/Impact	57
Gradient - spatial	34
Gradient - temporal	1
Incidental Report	3
No Control	156
Preference Test - control UA	4
Preference Test - no control	11

Preference Test - with control	2
Preference Test - with rotation or randomization	40
Preference Test - with rotation or randomization and control	3
Qualitative observation of bird proximity to light sources	10
UA	2

Additional File 16. How to use the systematic map database

We provide two versions of the database: a version in Microsoft Access and a version in Excel. The Access version has much greater capacity for searching and viewing metadata. Users without Microsoft Access on their computer can download the free version of Microsoft Access runtime from https://www.microsoft.com/en-ca/download/details.aspx?id=50040.

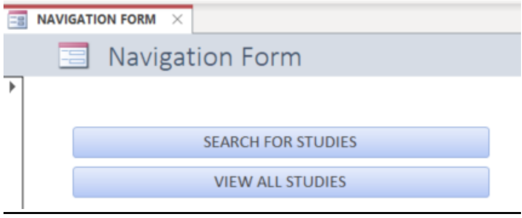
Instructions for the Access and Access Runtime versions:

Opening the Database

If you do not have Microsoft Access installed on your computer, you can download Access Runtime for free from https://www.microsoft.com/en-ca/download/details.aspx?id=50040. The Access version of the database is named *AF 13 Adams_et_al_2021_Systematic_Map.accdb*. The Access Runtime version of the database is named *AF 14 Adams_et_al_Systematic_Map_Runtime.accde*. Please not that Access and Access Runtime require Windows operating systems.

Navigation Form

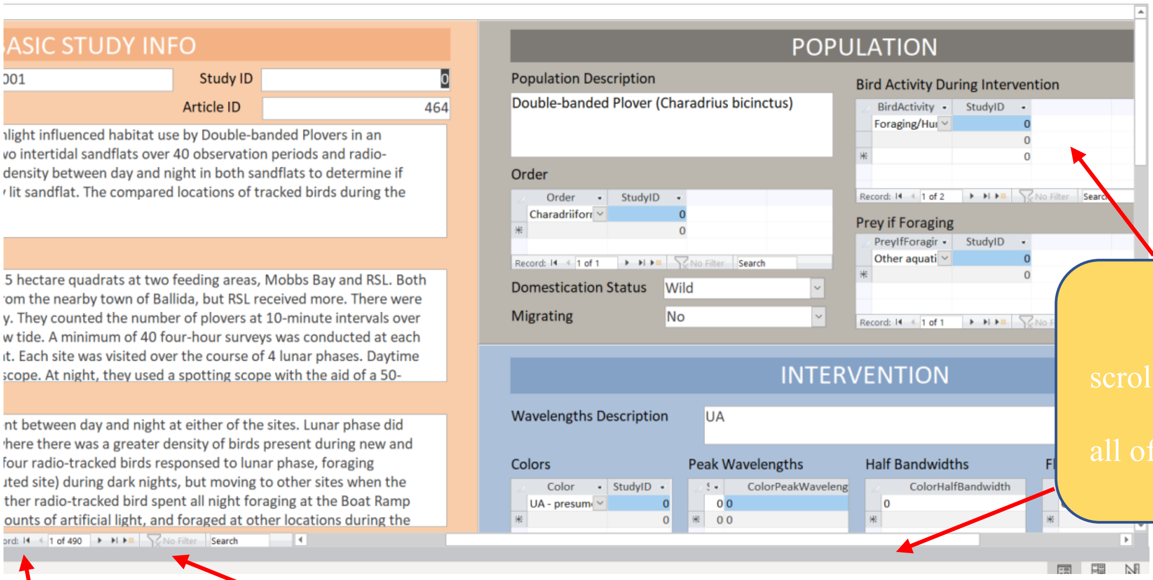
The database will open to the *NAVIGATION FORM*. You will see buttons called *SEARCH FOR STUDIES* and *VIEW ALL STUDIES*. Use these buttons to switch between the *View* and *Search* forms



Click the *VIEW ALL STUDIES* button to scroll through all studies, viewing all metadata. Click the *SEARCH FOR STUDIES* button to search for studies that meet particular criteria.

View Form

The View form allows you to scroll through all studies, as if you are reading a book. All meta-data are displayed for each study.



001

Study ID 0

Article ID 464

ılight influenced habitat use by Double-banded Plovers in an
vo intertidal sandflats over 40 observation periods and radio-
density between day and night in both sandflats to determine if
lit sandflat. The compared locations of tracked birds during the

5 hectare quadrats at two feeding areas, Mobbs Bay and RSL. Both
om the nearby town of Ballida, but RSL received more. There were
y. They counted the number of plovers at 10-minute intervals over
w tide. A minimum of 40 four-hour surveys was conducted at each
ıt. Each site was visited over the course of 4 lunar phases. Daytime
scope. At night, they used a spotting scope with the aid of a 50-

nt between day and night at either of the sites. Lunar phase did
here there was a greater density of birds present during new and
four radio-tracked birds responsed to lunar phase, foraging
ıted site) during dark nights, but moving to other sites when the
ther radio-tracked bird spent all night foraging at the Boat Ramp
ounts of artificial light, and foraged at other locations during the

ord: 1 of 490 No Filter Search

Population Description: Double-banded Plover (Charadrius bicinctus)

Order

Order	StudyID
Charadriiforı	0
	0

Record: 1 of 1 No Filter Search

Domestication Status: Wild

Migrating: No

Bird Activity During Intervention

BirdActivity	StudyID
Foraging/Hu	0
	0
	0

Record: 1 of 2 No Filter Searc

Prey if Foraging

PreyIfForagir	StudyID
Other aquati	0
	0

Record: 1 of 1 No F

Wavelengths Description: UA

Colors

Color	StudyID
UA - presum	0
	0

Peak Wavelengths

!	ColorPeakWaveleng
0	0
0	0

Half Bandwidths

ColorHalfBandwidth
0

Fl

Use the

scroll bars to view

all of the metadata

Use the

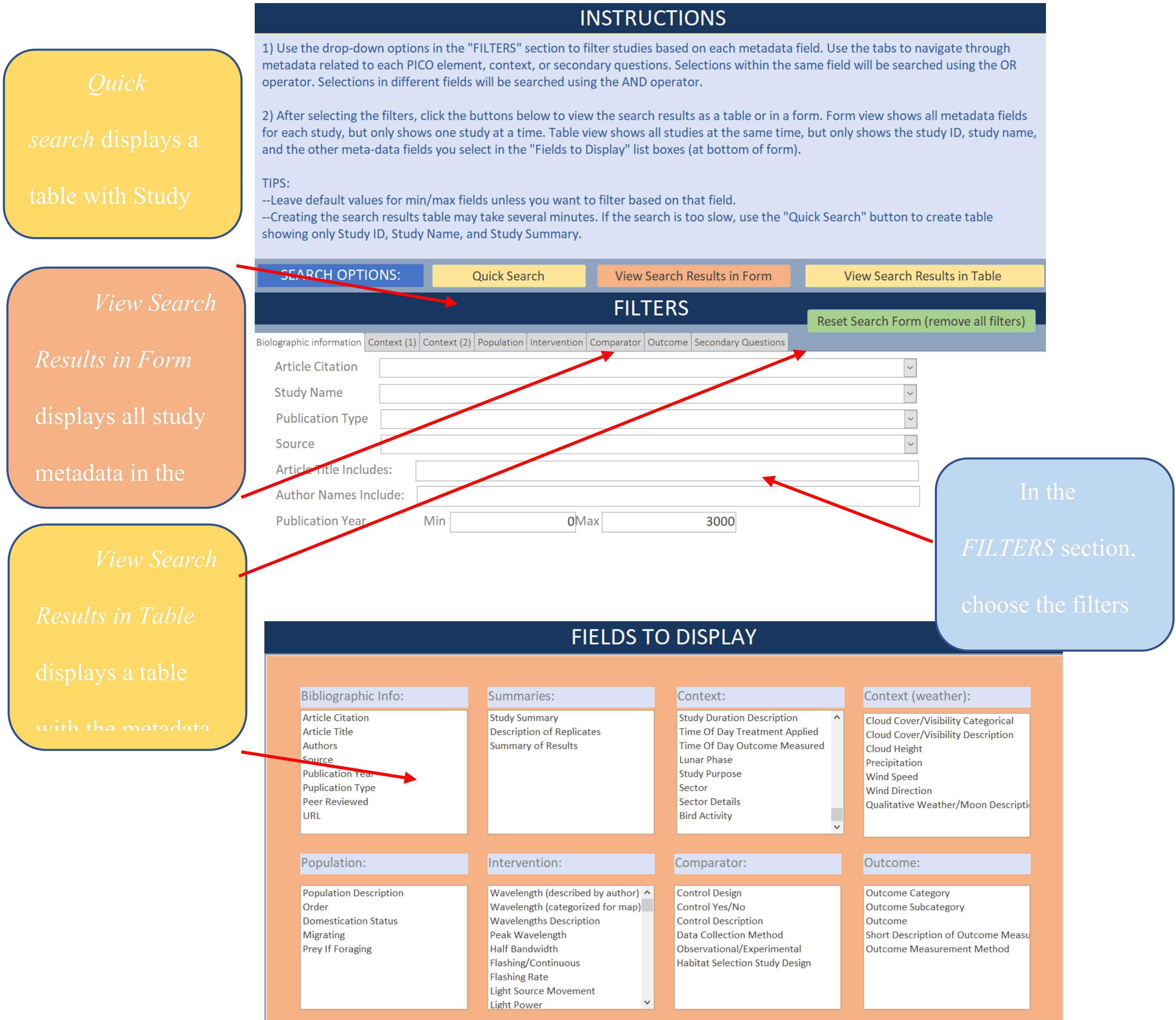
arrows to view the

You can use the search bar to search

for words within the metadata, but it is

Search Form

The search form allows you to search for studies that meet particular meta-data criteria.



Quick search displays a table with Study

View Search Results in Form displays all study metadata in the

View Search Results in Table displays a table with the metadata

In the *FILTERS* section, choose the filters

INSTRUCTIONS

1) Use the drop-down options in the "FILTERS" section to filter studies based on each metadata field. Use the tabs to navigate through metadata related to each PICO element, context, or secondary questions. Selections within the same field will be searched using the OR operator. Selections in different fields will be searched using the AND operator.

2) After selecting the filters, click the buttons below to view the search results as a table or in a form. Form view shows all metadata fields for each study, but only shows one study at a time. Table view shows all studies at the same time, but only shows the study ID, study name, and the other meta-data fields you select in the "Fields to Display" list boxes (at bottom of form).

TIPS:
--Leave default values for min/max fields unless you want to filter based on that field.
--Creating the search results table may take several minutes. If the search is too slow, use the "Quick Search" button to create table showing only Study ID, Study Name, and Study Summary.

Article Citation
Study Name
Publication Type
Source
Article Title Includes:
Author Names Include:
Publication Year Min 0 Max 3000

FIELDS TO DISPLAY

Bibliographic Info:
Article Citation
Article Title
Authors
Source
Publication Year
Puplication Type
Peer Reviewed
URL

Summaries:
Study Summary
Description of Replicates
Summary of Results

Context:
Study Duration Description
Time Of Day Treatment Applied
Time Of Day Outcome Measured
Lunar Phase
Study Purpose
Sector
Sector Details
Bird Activity

Context (weather):
Cloud Cover/Visibility Categorical
Cloud Cover/Visibility Description
Cloud Height
Precipitation
Wind Speed
Wind Direction
Qualitative Weather/Moon Descripti

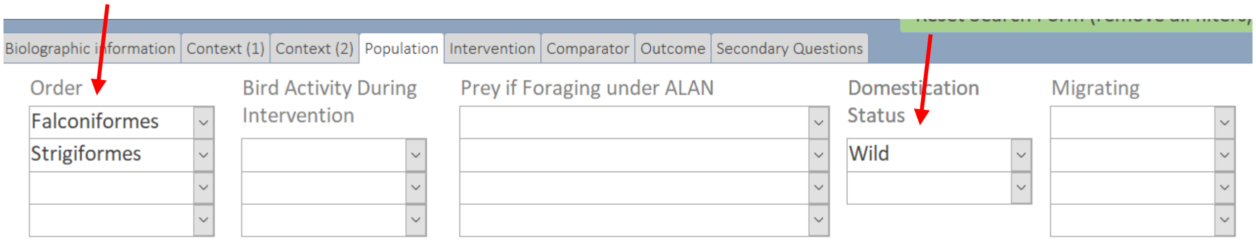
Population:
Population Description
Order
Domestication Status
Migrating
Prey If Foraging

Intervention:
Wavelength (described by author)
Wavelength (categorized for map)
Wavelengths Description
Peak Wavelength
Half Bandwidth
Flashing/Continuous
Flashing Rate
Light Source Movement
Light Power

Comparator:
Control Design
Control Yes/No
Control Description
Data Collection Method
Observational/Experimental
Habitat Selection Study Design

Outcome:
Outcome Category
Outcome Subcategory
Outcome
Short Description of Outcome Measu
Outcome Measurement Method

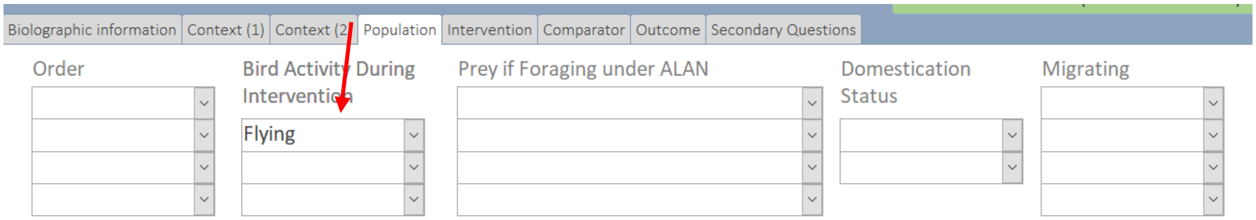
As explained in the *INSTRUCTIONS* section of the *SEARCH* form, selections within each field are separated by the OR operator, and the selections from different fields are connected using the AND operator. For example, the following set of filters would return all studies on **wild** birds that are in the orders ***Strigiformes* or *Falconiformes.*** It would not return studies of wild birds in other orders, nor would it return studies of domesticated populations of birds in *Strigformes* or *Falconiformes*.



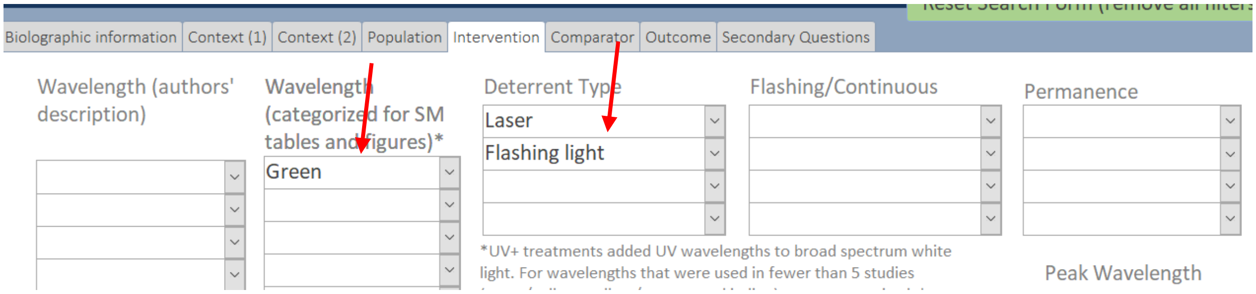
Order: Falconiformes, Strigiformes

Domestication Status: Wild

As another example, the following set of filters would return studies of **flying birds** that were exposed to **green lasers** or **green flashing light**



Bird Activity During Intervention: Flying



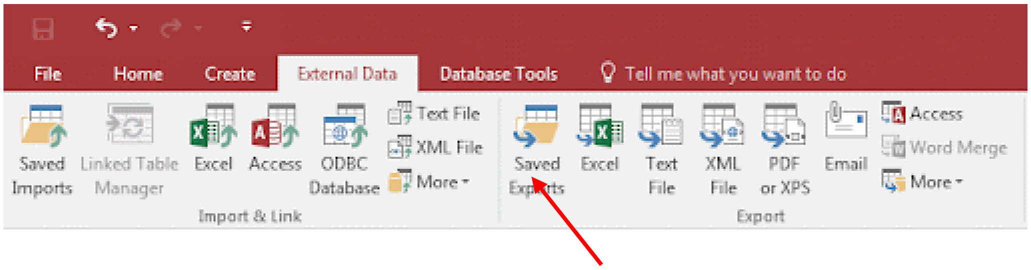
Wavelength (categorized for SM tables and figures)*: Green

Deterrent Type: Laser, Flashing light

*UV+ treatments added UV wavelengths to broad spectrum white light. For wavelengths that were used in fewer than 5 studies

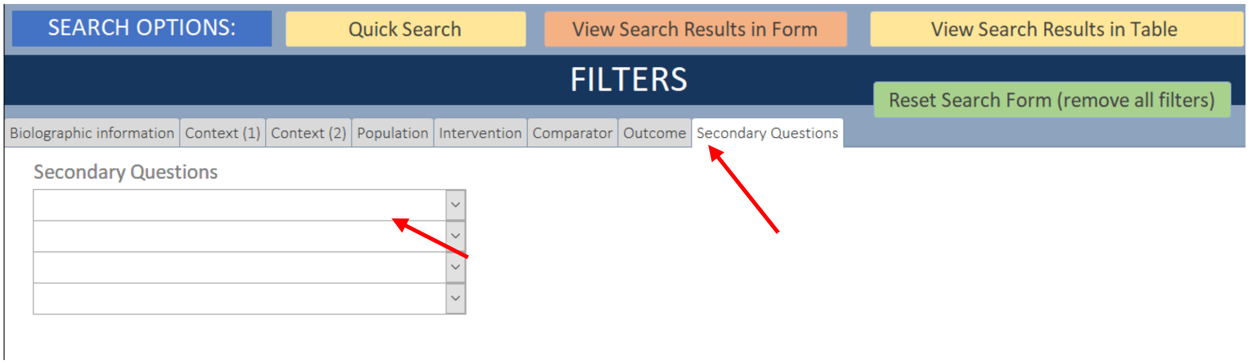
Exporting Data

To export a table as an excel of csv file, go to External Data → Excel.



Identifying evidence for each secondary question

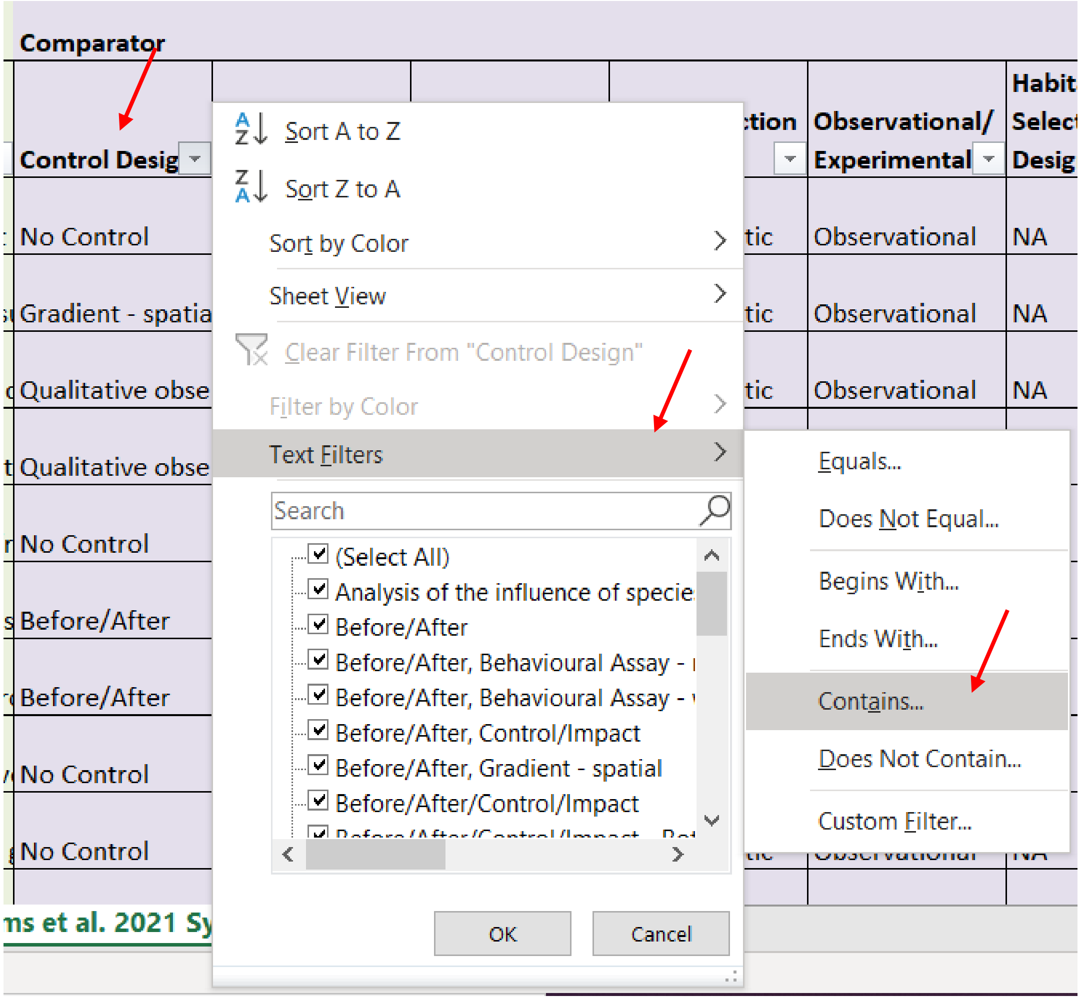
To view all of the evidence for each of our secondary questions, use the *FILTERS* section of the *SEARCH* form. Go to the *Secondary Questions* tab and select one or more of the secondary questions from the drop-down menu.



Instructions for the Excel version

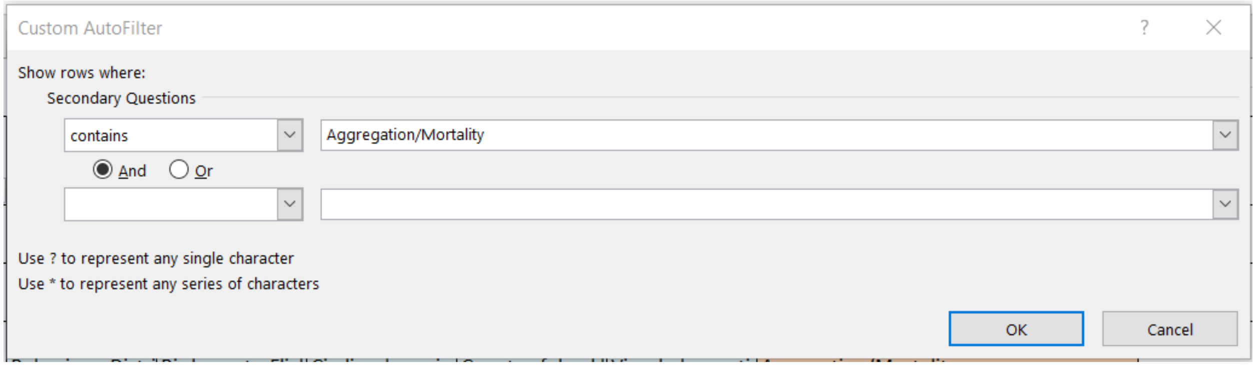
Searching for studies

The challenge with using the Filter function in the Excel version is that some studies have multiple codes for each metadata field. For example, light wavelength can be both blue and green for the same study. One way to search for studies that meet particular metadata criteria is to use the *Text Filters*.



Identifying Evidence for Each Secondary Question

The final column of the spreadsheet shows the secondary questions for which each study is relevant. Use text filters to find all studies relevant to a particular secondary question by searching for studies that contain the code for that secondary question. For example, to search for all studies relevant to our first secondary question, click on “Contains…” and apply the following filter:



Custom AutoFilter

Show rows where:

Secondary Questions

contains: Aggregation/Mortality

● And ○ Or

Use ? to represent any single character

Use * to represent any series of characters

Appendix C. Supplemental Tables and Figures for Chapter 4

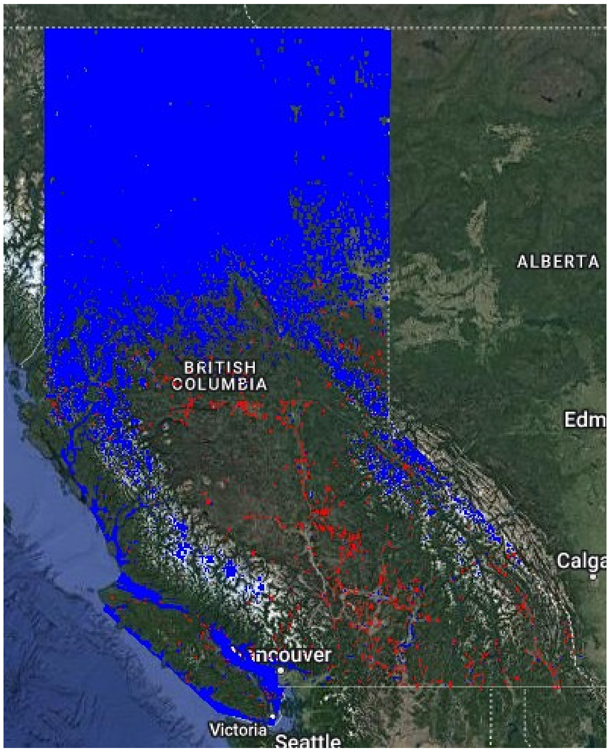


Figure S4.1 Comparison of artificial light estimates in NASA's Black Marble (BM) annual composite for 2015 to the Earth Observation Group's annual composite for 2015 version 1 (V1).

Blue areas show pixels assigned positive artificial light values by BM, but not by V1. Red areas show pixels assigned positive artificial light values by V1, but not by BM. Visual inspection showed that the red areas occurred along roadways and small communities, while blue areas more often occurred at high elevations or latitudes.

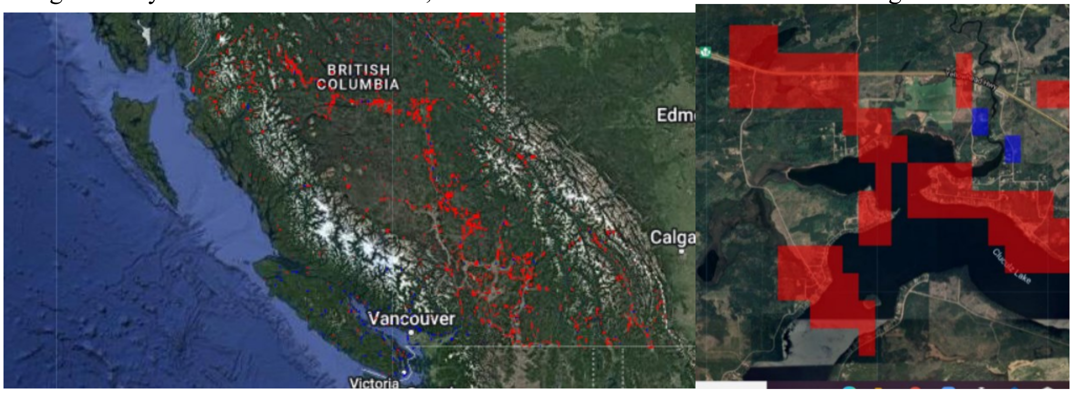


Figure S4.2 Comparison of the Earth Observation Group's Version 1 (V1) and Version 2 V(2) annual composites for 2015.

Red areas show pixels assigned positive artificial light values by V1, but not by V2. Blue areas show pixels assigned positive artificial light values by V2, but not by V1. Visual inspection showed that blue areas (missed by V1) likely involved skyglow in the pixels surrounding artificial light sources. The red pixels (missed by V2) occurred in areas with low levels of human development where V1 identified light sources that V2 missed. V1 is available for only

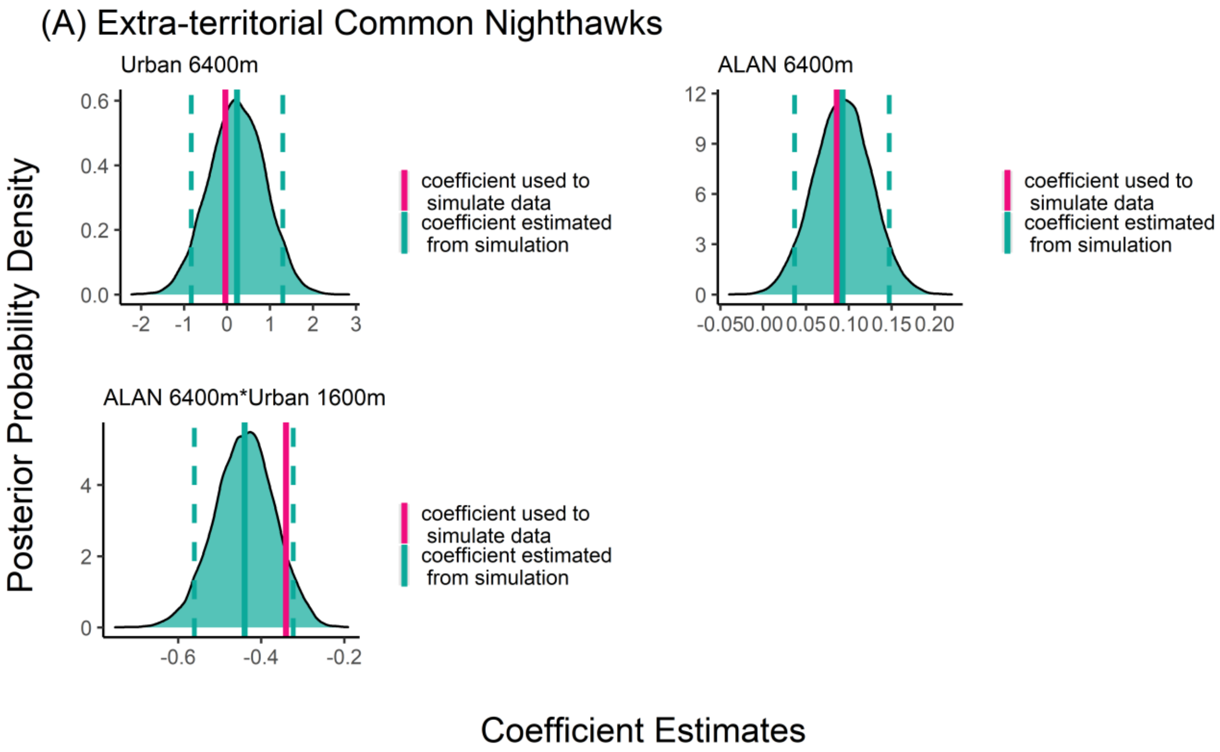
2015 and 2016, and uses a combination of automated and manual processes for distinguishing artificial light from aurora in the Northern aurora zone (Elvidge et al. 2017). V2 is available for all years between 2012 and 2020, but applies an additional manual filter before manual editing in the Northern aurora zone, filtering out many dim lights in our study area that were found in V1.

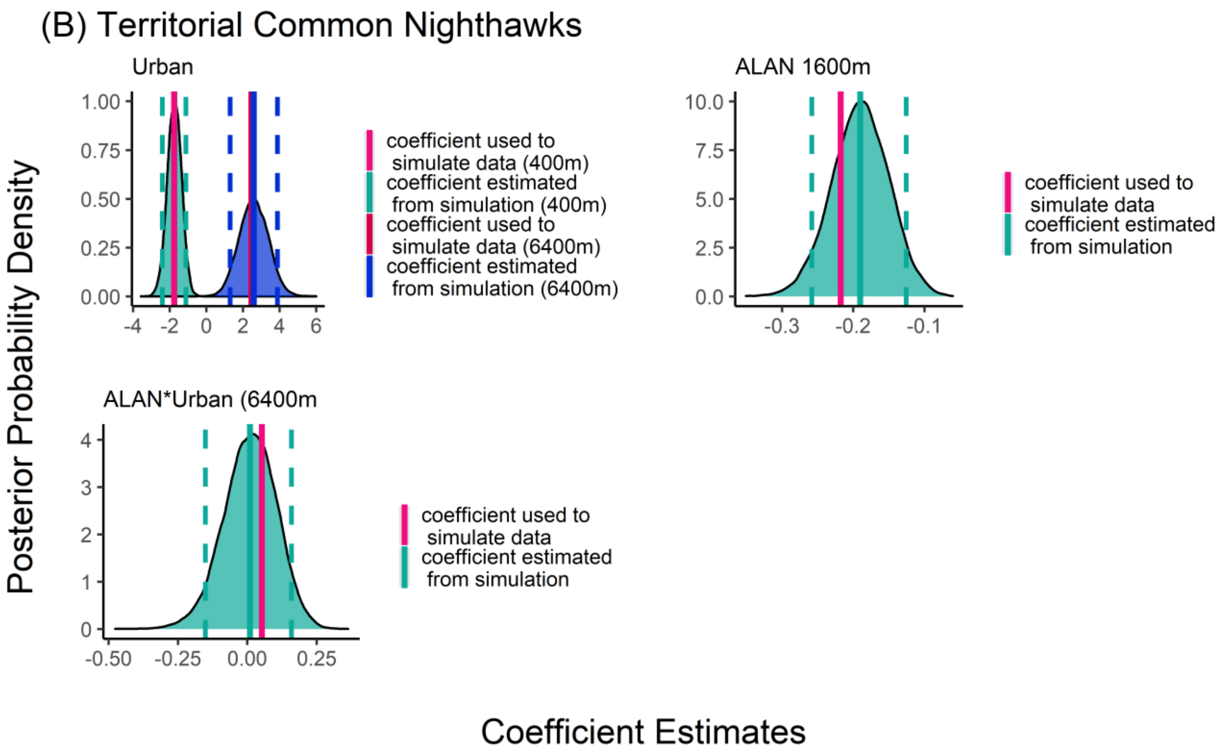
Table S4.1 Common Nighthawk associations with landscape features in previous studies

Species/Reference / Location	**Landscape feature**	**Method of measurement**
Common Nighthawk / **Ng 2008 /** Saskatchewan grassland	Percentage grassland cover (+) Distance to nearest water (-) NDVI (-) Roost on gravel roads	Generalised Landcover for the Canadian Prairies from the Prairie Farm Rehabilitation Administration
Common Nighthawk / Knight, Brigham, and Bayne 2021 / Alberta Boreal Forest	Time since harvest (-) Time since well pad abandonment (-) Time since fire (-) % Open pine forest (+) Mean wetland probability (quadratic)	ABMI Human footprint inventory (time since harvest and well-site) Alberta Agriculture and Forestry Historical Wildlife Perimiters Alberta Vegetation Inventory (Proportion Pine Forest) Boreal Wetland Probability
Common Nighthawk / Viel 2020 / Urban and agricultural areas in Wisconsin	% Agriculture (-) # of flat, graveled rooftops (+)	Aerial photos National Land Cover Dataset
Common Nighthawk / Newberry 1997 / Agricultural landscape in South Dakota	Developed landcover (+) (but only in the area where gravel rooftops were present) Agriculture (-) (but only in the area where there was no grassland left)	National Land Cover Dataset
Common Nighthawk / Newberry and Swanson 2018/ South Dakota, Nebraska, and Iowa	Agriculture(+/-) (negative overall but positive in one region) Grassland (+) Developed landcover (+) (but only in the area where gravel rooftops were present)	National Land Cover Dataset
Common Nighthawk / Farrell et al. 2019 / Ontario Boreal Forest	Open wetland (+) Age of clearcut (-)	Forest resource inventory
Common Nighthawk / Farrell et al. 2017 / Ontario boreal forest	Burned stands (+) Recent clearcuts (+) Open wetlands (+)	Fire maps from Ontario Ministry of Natural Resources and Fire Maps
Common Poorwill / **MacDonald, David, and McMaster 2003 /** Southwest Saskatchewan	Native prairie (+) Native rangeland (+) with sandy soil or shrubby vegetation	Saskatchewan's Southern Digital Landcover Classification

Table S4.2 DIC comparison for other model forms

	Model Form	**DIC**
Territorial Common Nighthawks	Negative binomial	7137.457
	Poisson	7975.703
	Zero-inflated negative binomial	*Does not converge*
	Zero-inflated Poisson	9092.844
Extra-territorial Common Nighthawks	Negative Binomial	10,189.92
	Poisson	11,001.56
	Zero-inflated Negative Binomial	*Does not converge*
	Zero-inflated Poisson	14,051.67
Common Poorwills	Negative binomial	2015.274
	Poisson	2258.389
	Zero-inflated Negative Binomial	2360.337
	Zero-inflated Poisson	2097.452





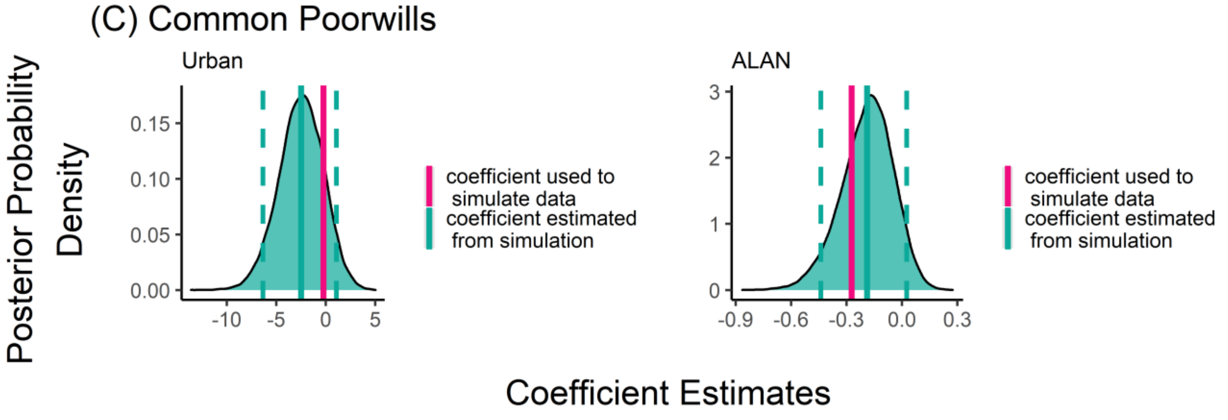


Figure S4.3 Coefficient estimates from model fit with simulation data

We simulated relative abundance data using the coefficient values and scales selected by our model. These blue posterior density plots show the coefficient estimates from models fit using these simulated relative abundance values, the mean estimates (solid lines), and 95% credible interval (dashed lines). The pink lines show the coefficient value used for the simulation. To estimate the coefficients from the simulated data, we used the same process that we used for the real data. We used the BLISS procedure to select the scale for each covariate, then we refit the model with each covariate at its selected scale. For all models, the BLISS model correctly selected the ALAN or urban scale that was used to simulate the data. For Common Poorwills, the BLISS model selected the wrongs scales for agriculture and water. This result may indicate that the BLISS model is less reliable at smaller sample sizes.

Table S4.3 Scale(s) selected for each landscape covariate and the proportion of the posterior distribution that selected these scales.

Modelling Step	**Predictor**	**Extra-territorial Common Nighthawks**		**Territorial Common Nighthawks**		**Common Poorwills**	
		Selected scale(s)	Prop. of posterior	Selected scale(s)	Prop. of posterior	Selected scale(s)	Prop. of posterior
1 (scale selection on all covariates)	**Agriculture**	6400	100%	1600	94%	1600	99%
	Grassland	1600	97%	1600	43%	1600	66%
	Shrub	6400	100%	6400	100%	6400(+), 400(-)	76%, 18%
	Sparse Tree	1600	100%	400	91%	1600	43%
	Water	1600	100%	1600	93%	1600	57%
	Urban	1600(-), 6400(+)	70%, 15%	400(-), 6400(+)	95%, 1%	6400(-), 1600(+)	45%, 37%
	ALAN	6400	97%	1600	100%	1600(-), 6400(+)	53%, 9%
	ALAN*Urban	6400	100%	6400	98%	6400(+), 400(-)	37%, 33%
2 (scale selection on ALAN and Urban only)	**Urban**	6400	52%	400(-), 6400(+)	89%, 7%	1600	42%
	ALAN	6400	96%	1600	100%	1600	53%
	ALAN*Urban	6400* 1600	98%*91%	6400*6400	92%*93%	400*6400	37%*38%

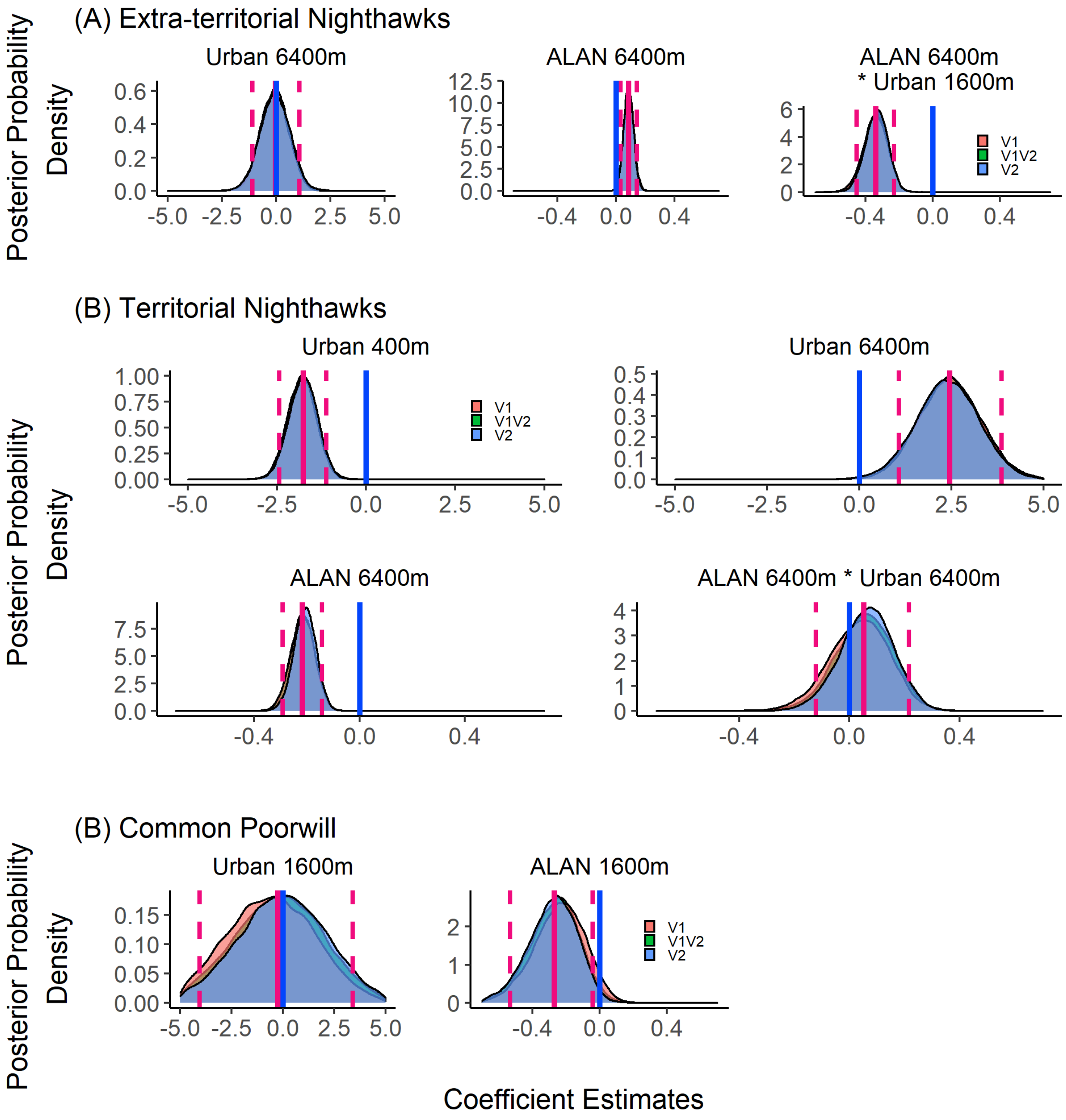
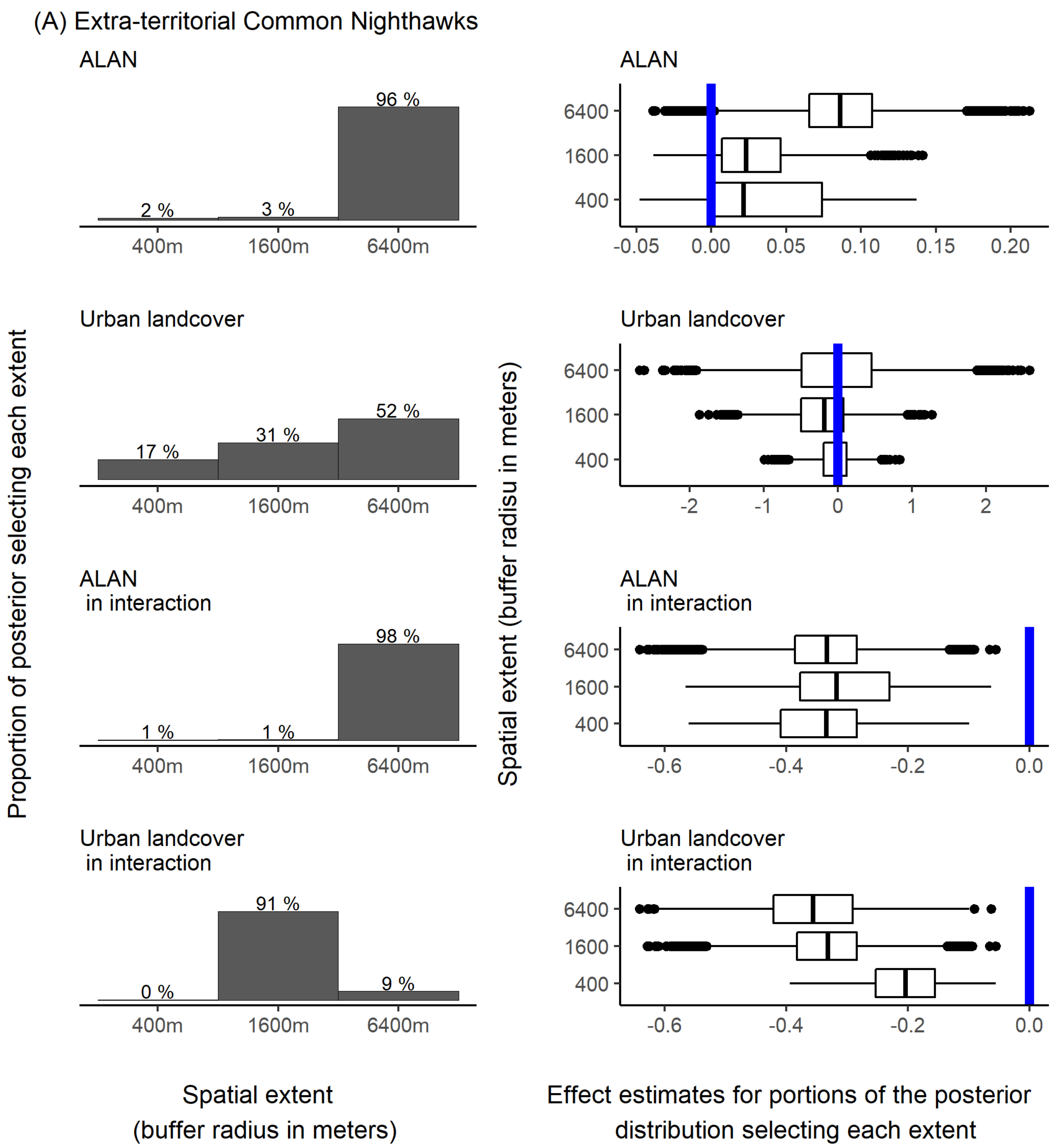
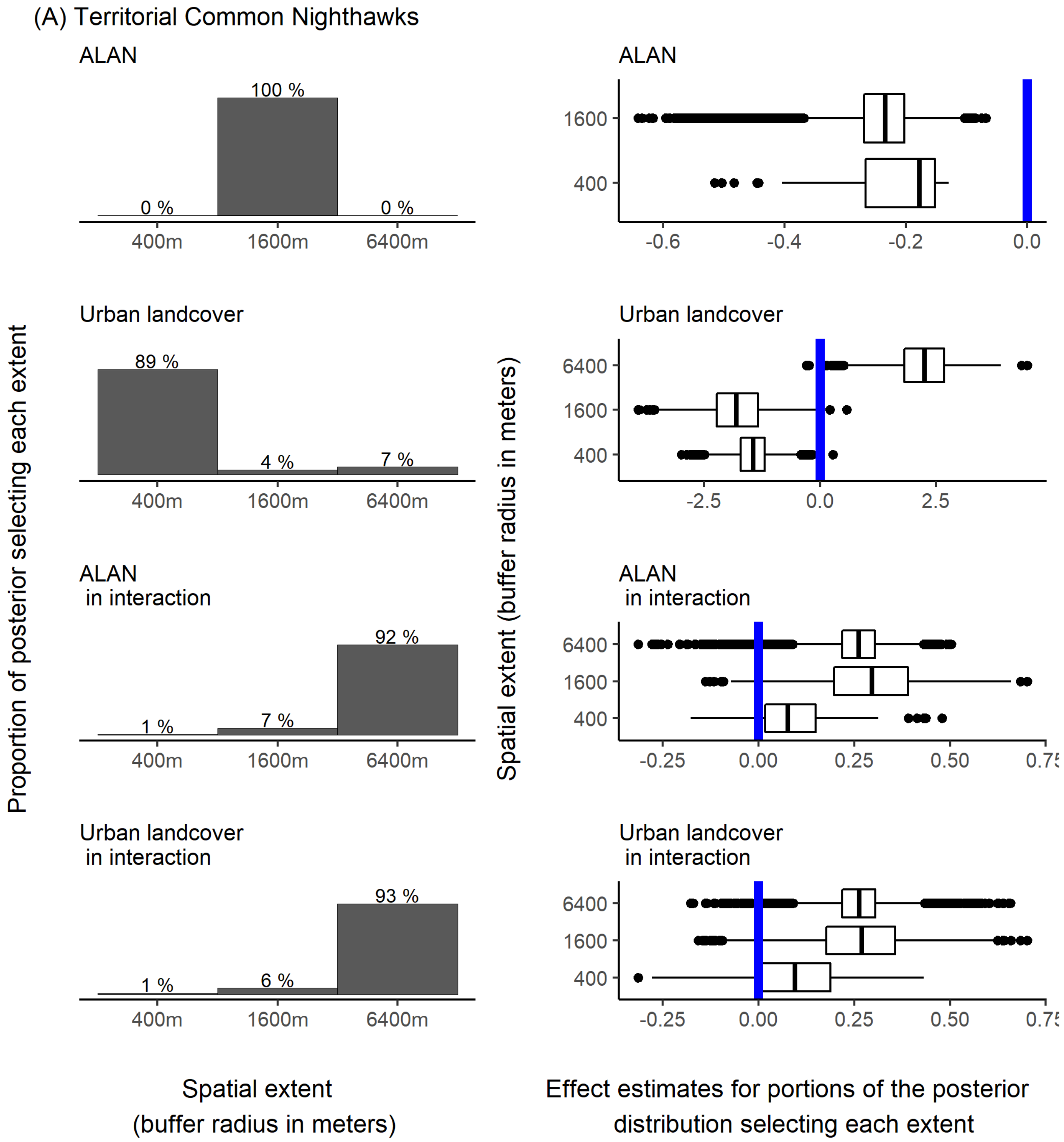


Figure S4.4 Posterior probability densities for ALAN and urban landcover covariates in the sensitivity analysis for the version of the annual composite used to estimate ALAN.

The solid pink lines show the mean coefficient estimate from our main model (using V1V2) and the dashed pink lines show the 95% CIs. V1 is the Earth Observation Group (EOG) Annual Composite V1 for 2016, V2 is the EOG Annual Composite V2 for the year in which the survey took place, and V1V2 is the average of these two composites.


(A) Extra-territorial Common Nighthawks
ALAN
96 %
2 %
3 %
400m
1600m
6400m
Urban landcover
52 %
31 %
17 %
400m
1600m
6400m
ALAN
in interaction
98 %
1 %
1 %
400m
1600m
6400m
Urban landcover
in interaction
91 %
0 %
9 %
400m
1600m
6400m
Proportion of posterior selecting each extent
Spatial extent
(buffer radius in meters)
ALAN
6400
1600
400
-0.05
0.00
0.05
0.10
0.15
0.20
Urban landcover
6400
1600
400
-2
-1
0
1
2
ALAN
in interaction
6400
1600
400
-0.6
-0.4
-0.2
0.0
Urban landcover
in interaction
6400
1600
400
-0.6
-0.4
-0.2
0.0
Spatial extent (buffer radisu in meters)
Effect estimates for portions of the posterior
distribution selecting each extent


(A) Territorial Common Nighthawks
ALAN
100 %
0 %
0 %
400m
1600m
6400m
ALAN
1600
400
-0.6
-0.4
-0.2
0.0
Urban landcover
89 %
4 %
7 %
400m
1600m
6400m
Urban landcover
6400
1600
400
-2.5
0.0
2.5
ALAN
in interaction
92 %
1 %
7 %
400m
1600m
6400m
ALAN
in interaction
6400
1600
400
-0.25
0.00
0.25
0.50
0.75
Urban landcover
in interaction
93 %
1 %
6 %
400m
1600m
6400m
Urban landcover
in interaction
6400
1600
400
-0.25
0.00
0.25
0.50
0.75
Proportion of posterior selecting each extent
Spatial extent (buffer radius in meters)
Spatial extent
(buffer radius in meters)
Effect estimates for portions of the posterior
distribution selecting each extent

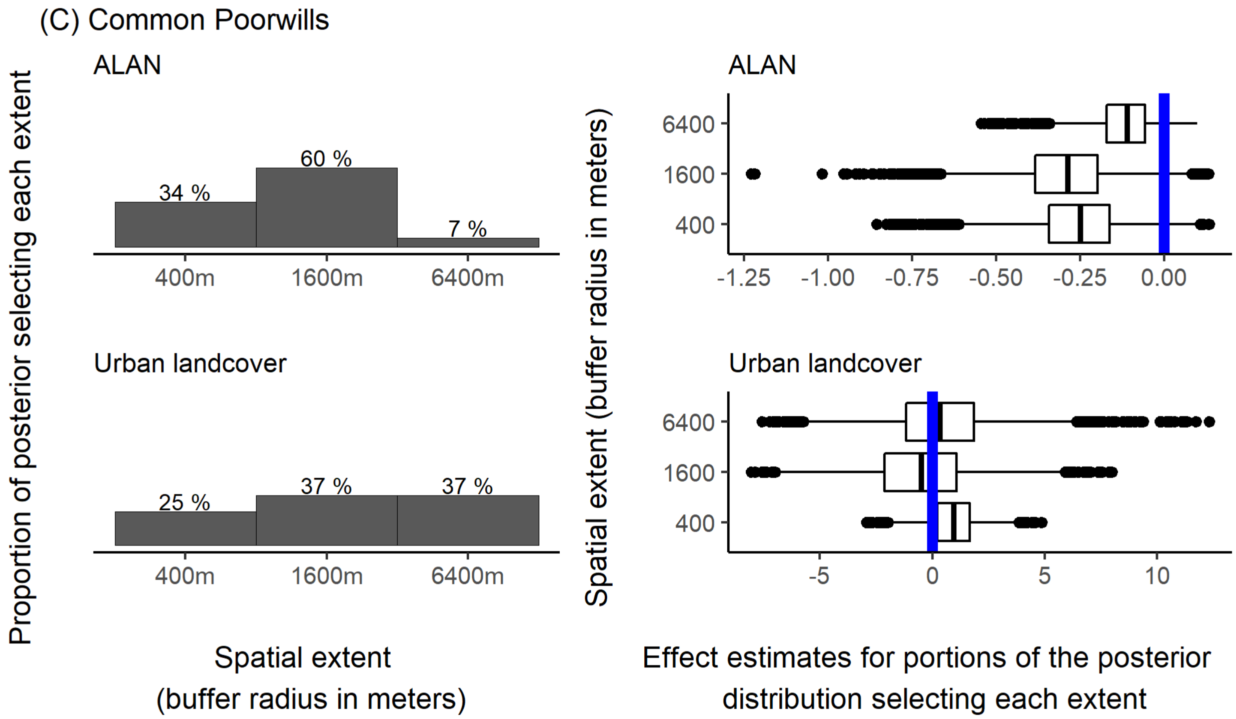


Figure S4.5 Results from BLISS scale selection

The left side of the figure shows the proportion of the posterior selecting each scale. The right side of the figure shows boxplots of the coefficient estimates from the portions of the posterior distributions that selected each scale.

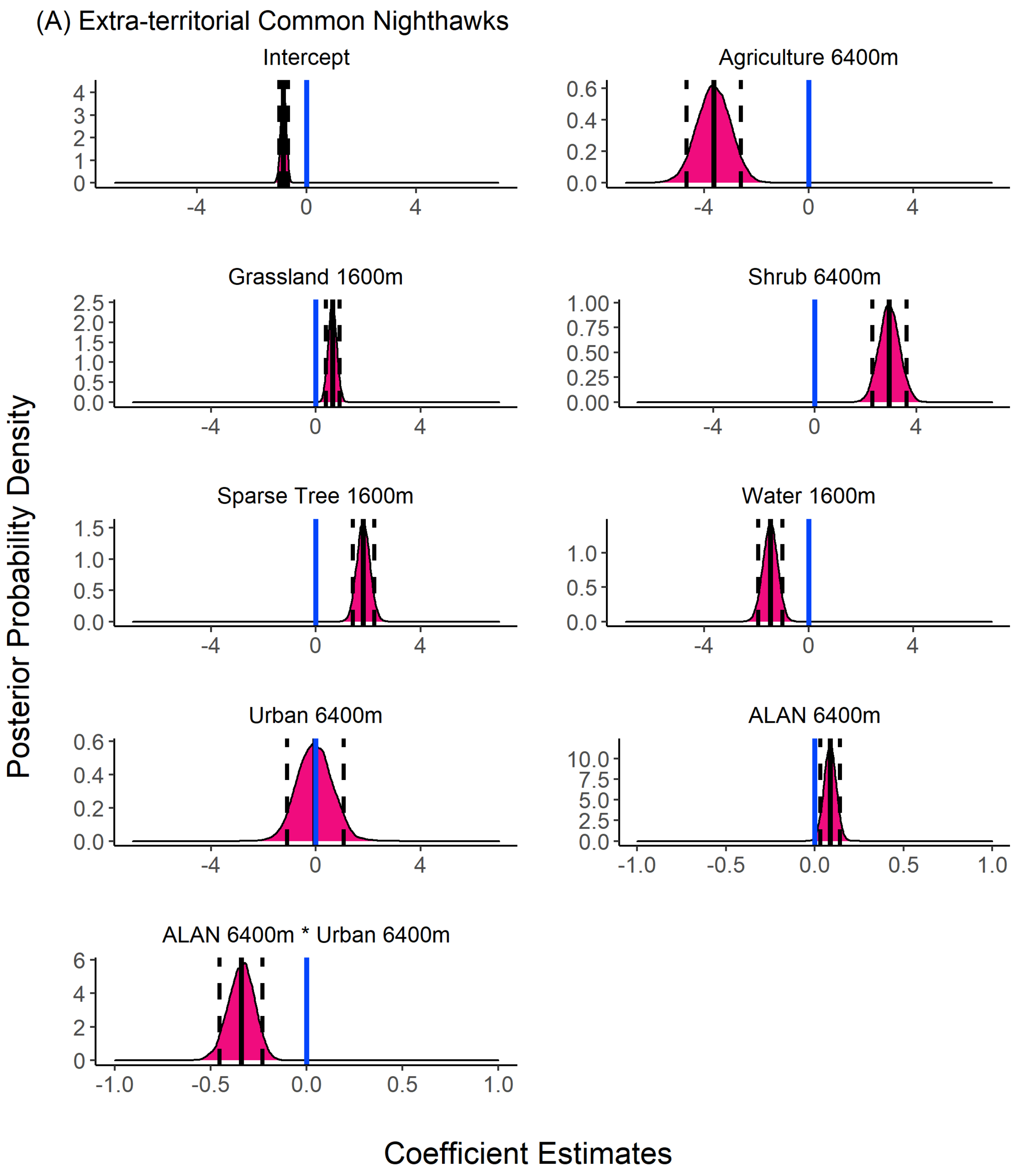


Figure S4.6 Posterior probability densities for landscapes covariates

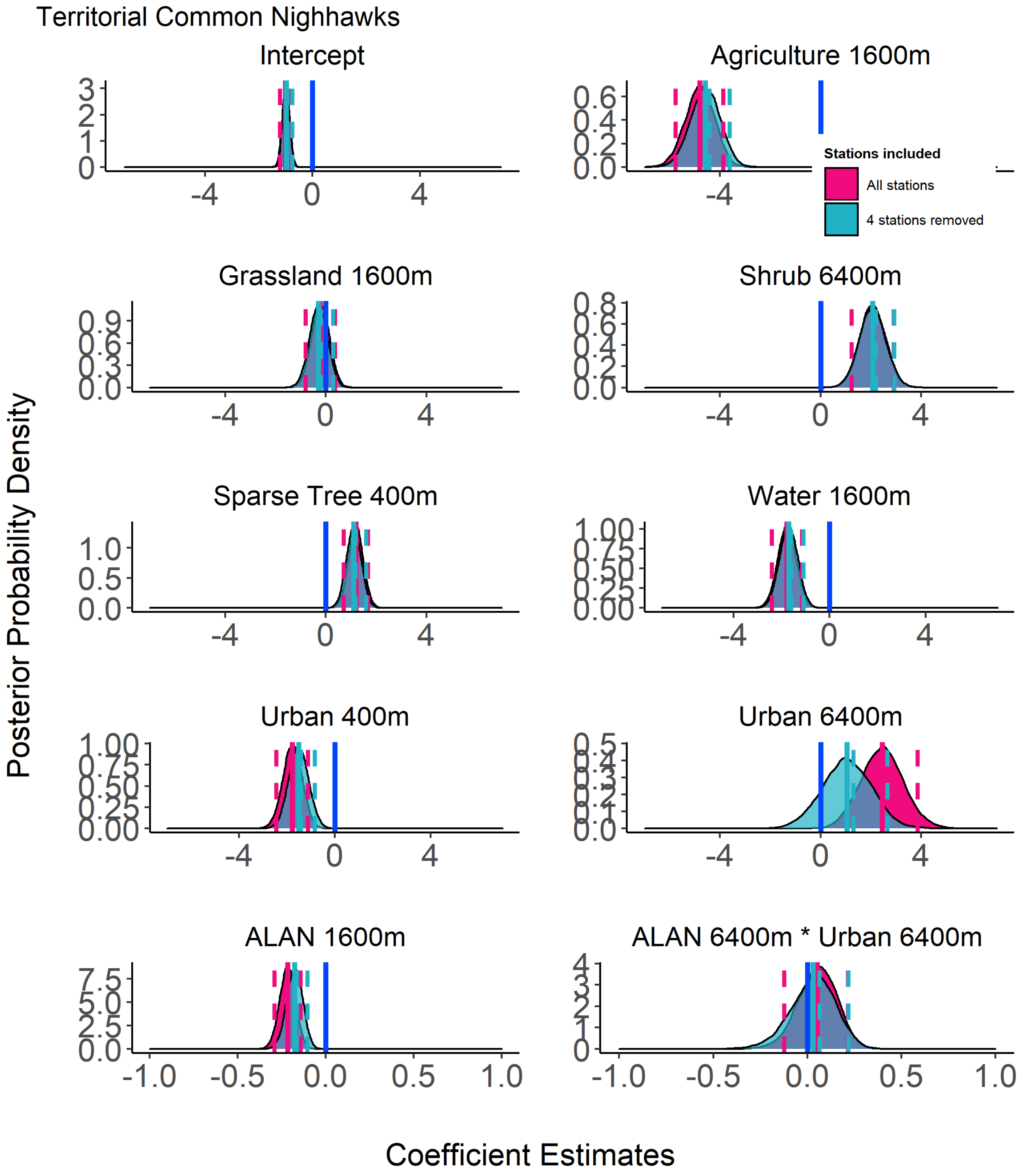


Figure S4.7 Posterior probability densities for landscapes covariates in the model excluding four influential survey stations near Victoria

Table S4.4 Estimates effect of increasing ALAN on relative abundance of nightjars at mean, median, and high levels of urban landcover

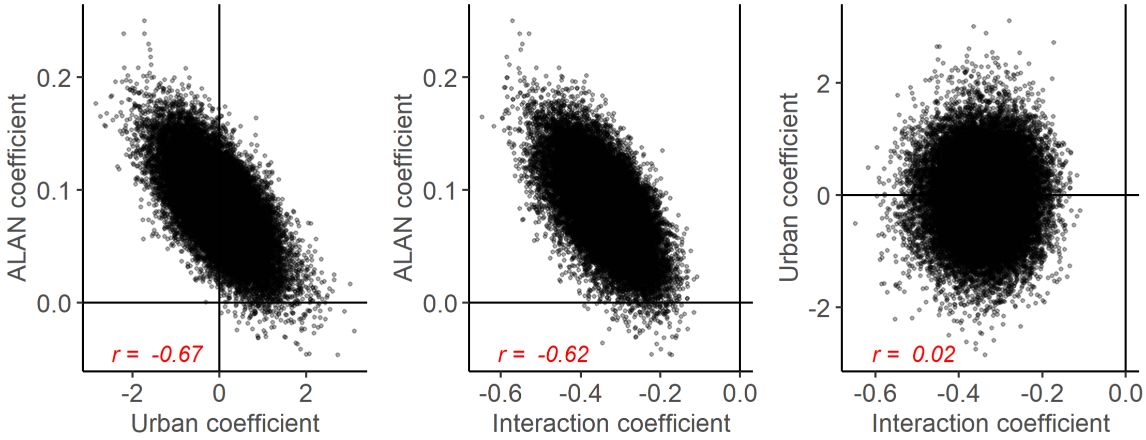
	Effect coefficient estimate (95% CI) for ALAN	**Effect coefficient estimate (95% CI) for ALAN interaction with urban landcover**	**Change in nightjar counts between 0 nWcm^{-2}sr^{-1} and 99th percentile ALAN value**		
			Median urban landcover	**Mean urban landcover**	**High urban landcover**
Extra-territorial Common Nighthawks	0.08 (0.02, 0.14)	-0.45 (-0.34, -0.23)	+35% (+3% , +72%) *3.98 nWcm^{-2}sr^{-1}*	+32% (-5%, +76%) *5.2 nWcm^{-2}sr^{-1}*	-43% (-70%, -5%) *10.3 nWcm^{-2}sr^{-1}*
Territorial Common Nighthawks	-0.21 (-0.29, -0.14)	0.05 (-0.12, 0.21)	-27% (-35%, -17%) *1.44 nWcm^{-2}sr^{-1}*	-55% (-69%, -39%) *3.76 nWcm^{-2}sr^{-1}*	-87% (-95%, -73%) *9.97 nWcm^{-2}sr^{-1}*
Common Poorwills	-0.27 (-0.04, -0.54)	*NA*	-20% (-39% , -1%) *0.81 nWcm^{-2}sr^{-1}*	-21% (-40%, 0%) *0.88 nWcm^{-2}sr^{-1}*	-32% (-97%, -2%) *6.07 nWcm^{-2}sr^{-1}*

Columns 1 and 2 show the coefficient estimates for ALAN and the interaction between urban landcover and ALAN in each model. The posterior distributions of the effect coefficients for other covariates are shown in Figure S5. Columns 3-5 show the expected change and the 95% CI for the change in the number of nightjars when ALAN increased from 0 to the 99th percentile. This 99th percentile ALAN value (shown in italics) was calculated for model and urban landcover level separately, using surveys with urban landcover less than or equal to the median, mean, and high (95th percentile) urban landcover values within the buffer size selected for each model.

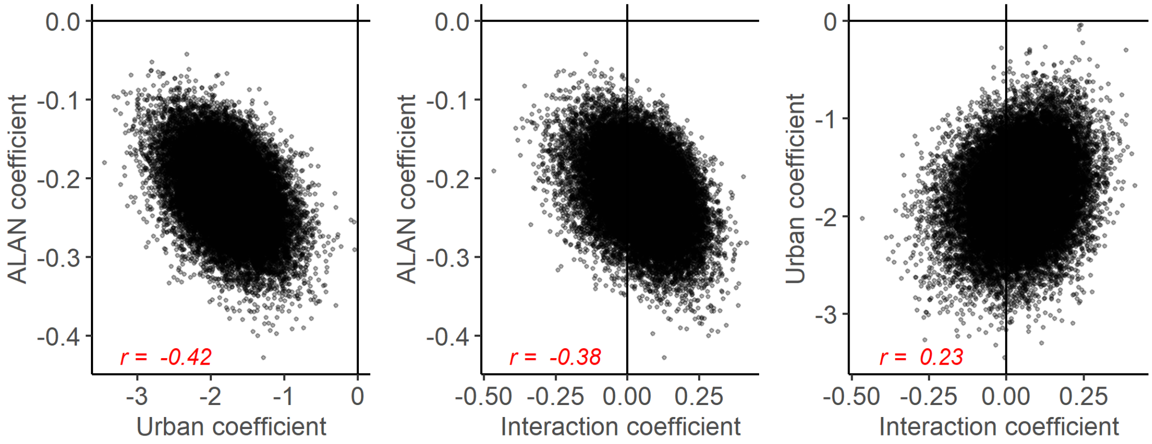
Table S4.5 Marginal effects of landscape-scale ALAN on nesting nighthawks

Scale	**Mean coefficient estimate (95% CI)**
6400 meters	-0.11 (-0.23, -0.01)
6400 meters, in model only including surveys at stations with no ALAN in 1600-meters	0.09 (-0.72, 0.526)

(A) Extra-territorial Common Nighthawks



(B) Territorial Common Nighthawks



(C) Common Poorwills

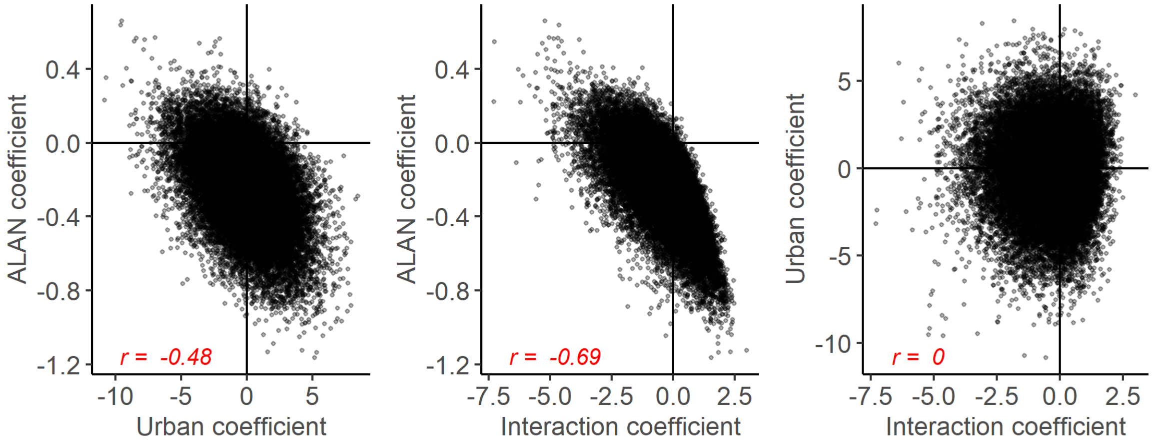


Figure S4.8 Cross-correlation among coefficient estimates for ALAN, urban, and their interaction term

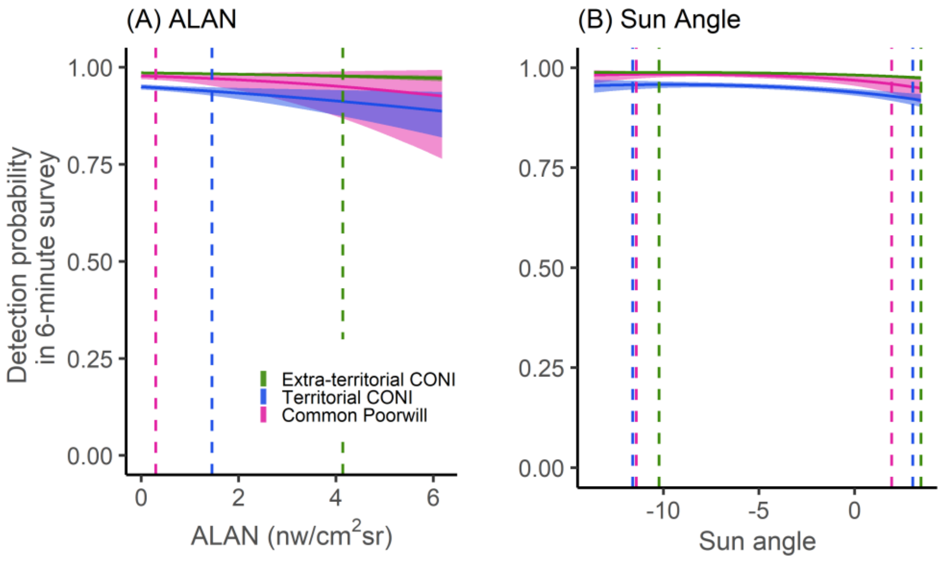
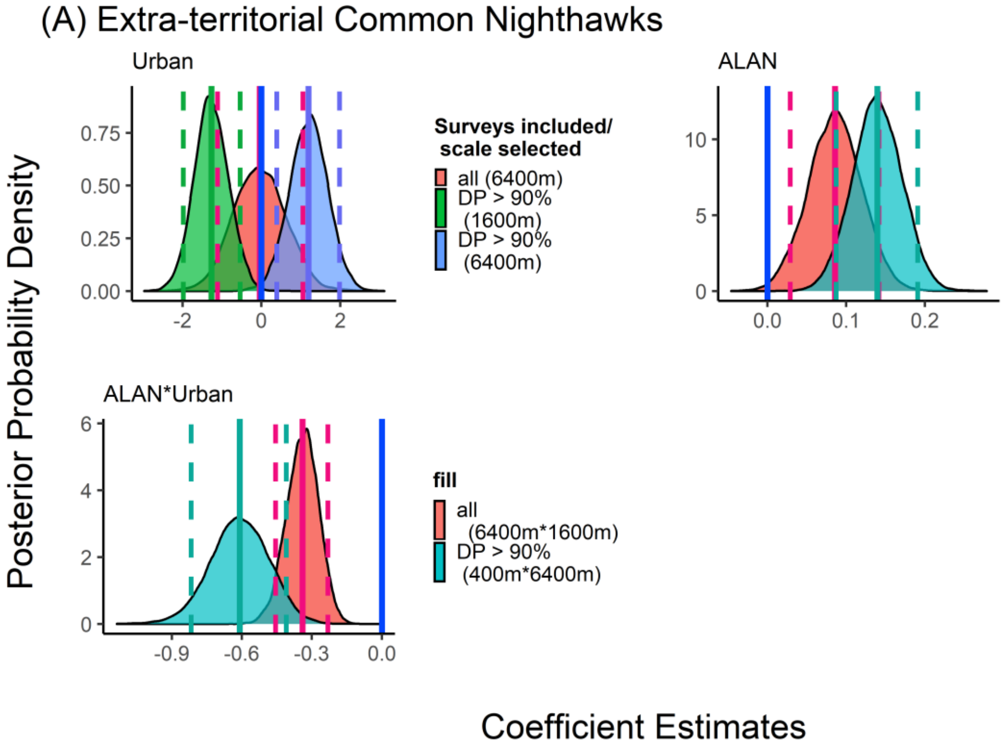
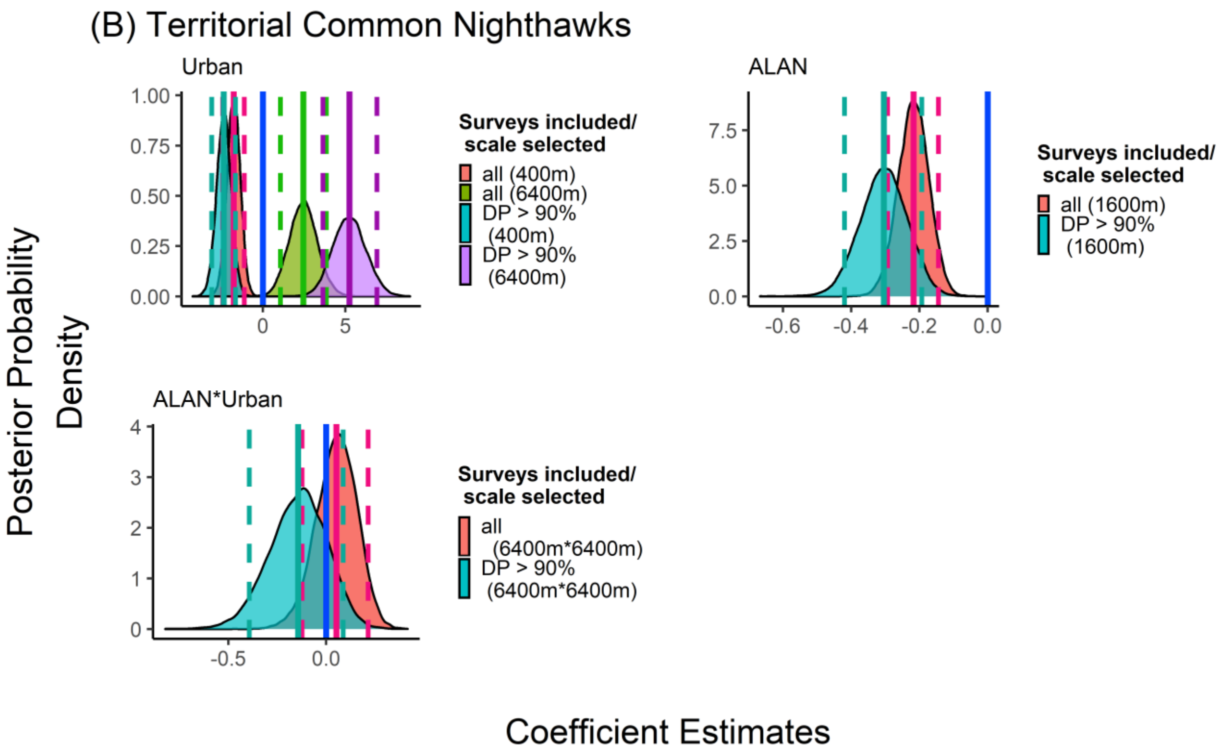


Figure S4.9. Effects of (A) ALAN and (B) sun angle on detection probability in a 6-minute survey.

We modeled the detection rate for each individual as a function of artificial light and the temporal covariates, and made predictions across ALAN and sun angle values, holding other temporal variables (ordinal day and moon presence/fraction) at their mean values. ALAN and sun angle values on the x-axis span the 5th to 95th percentiles of ALAN or sun angle values observed across all surveys. Dashed lines represent the 5th and 95th percentile ALAN or sun angle values observed in surveys where each nightjar species/behaviour occurred. The 5th percentile ALAN value for all species/behaviours was 0.





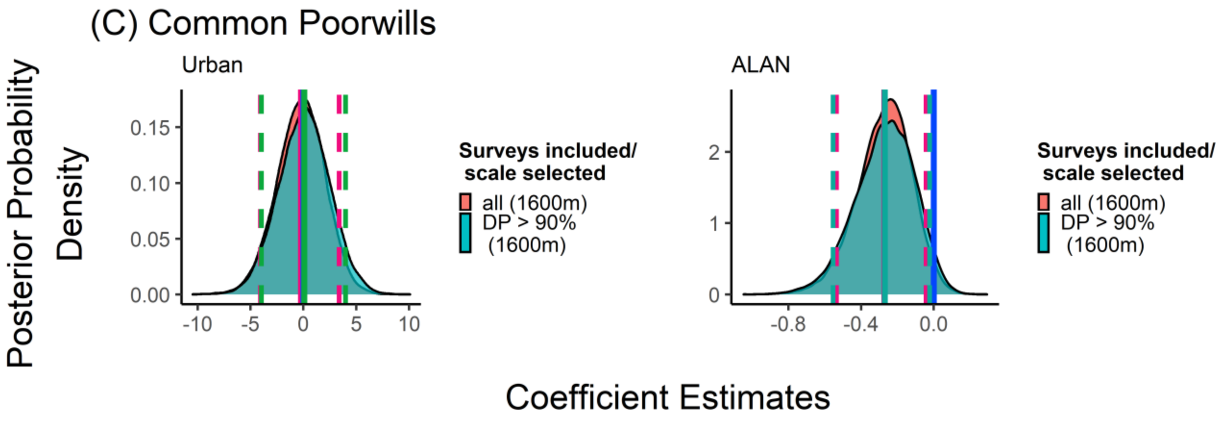


Figure S4.10 Posterior probability densities for ALAN and urban landcover coefficients in our sensitivity analysis for including/excluding surveys with less than 90% detection probability

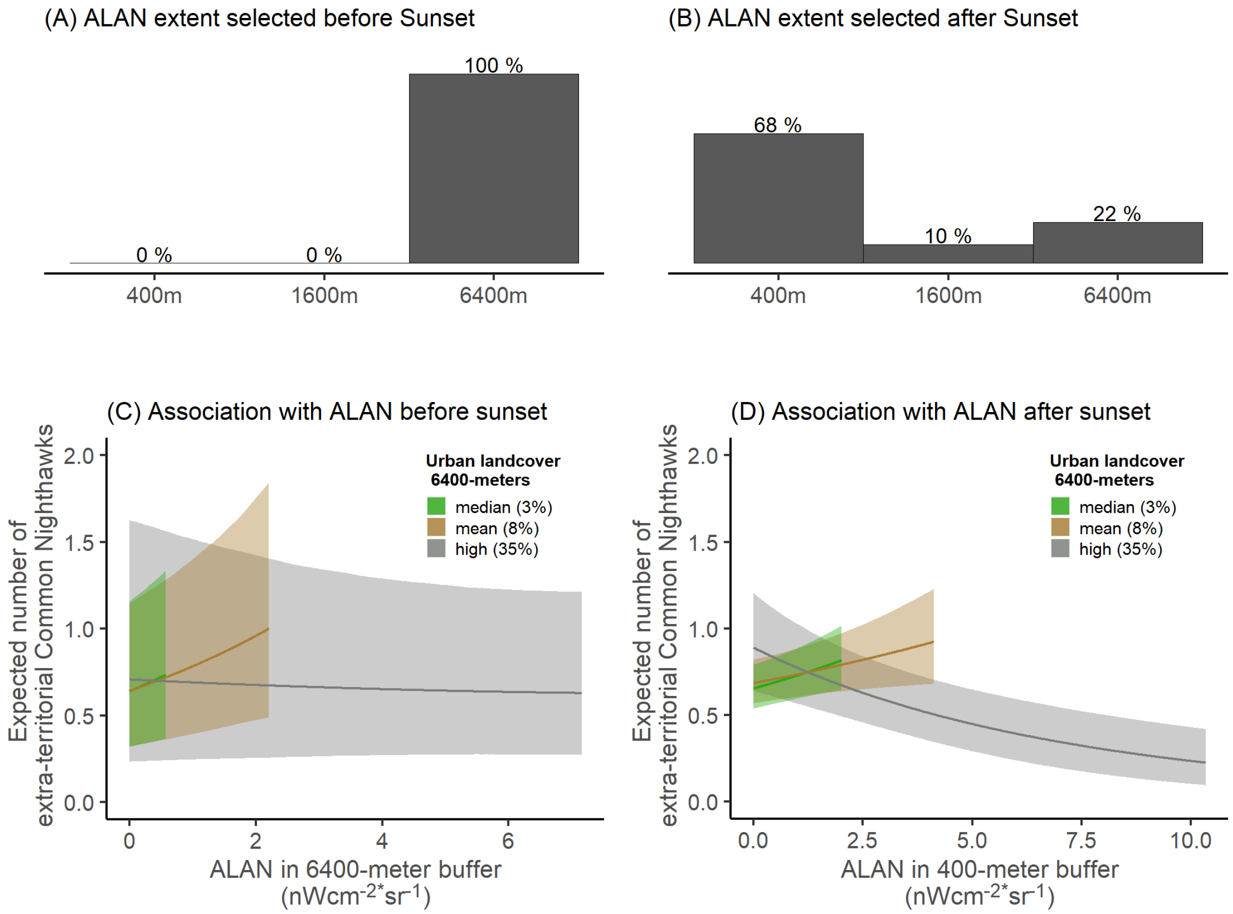


Figure S4.11 Comparison of the effects of ALAN on relative abundance of extra-territorial nighthawks before and after sunset

Panels A and B show the posterior distribution for the spatial scale selected by the BLISS model when including surveys (A) before and (B) after sunset . Panels C and D shows the predicted number of extra-territorial nighthawks across ALAN values (C) before and (D) after sunset. For each proportion urban land cover shown, we showed up to the 99th percentile of ALAN values in surveys with up to and including that proportion of urban land cover.

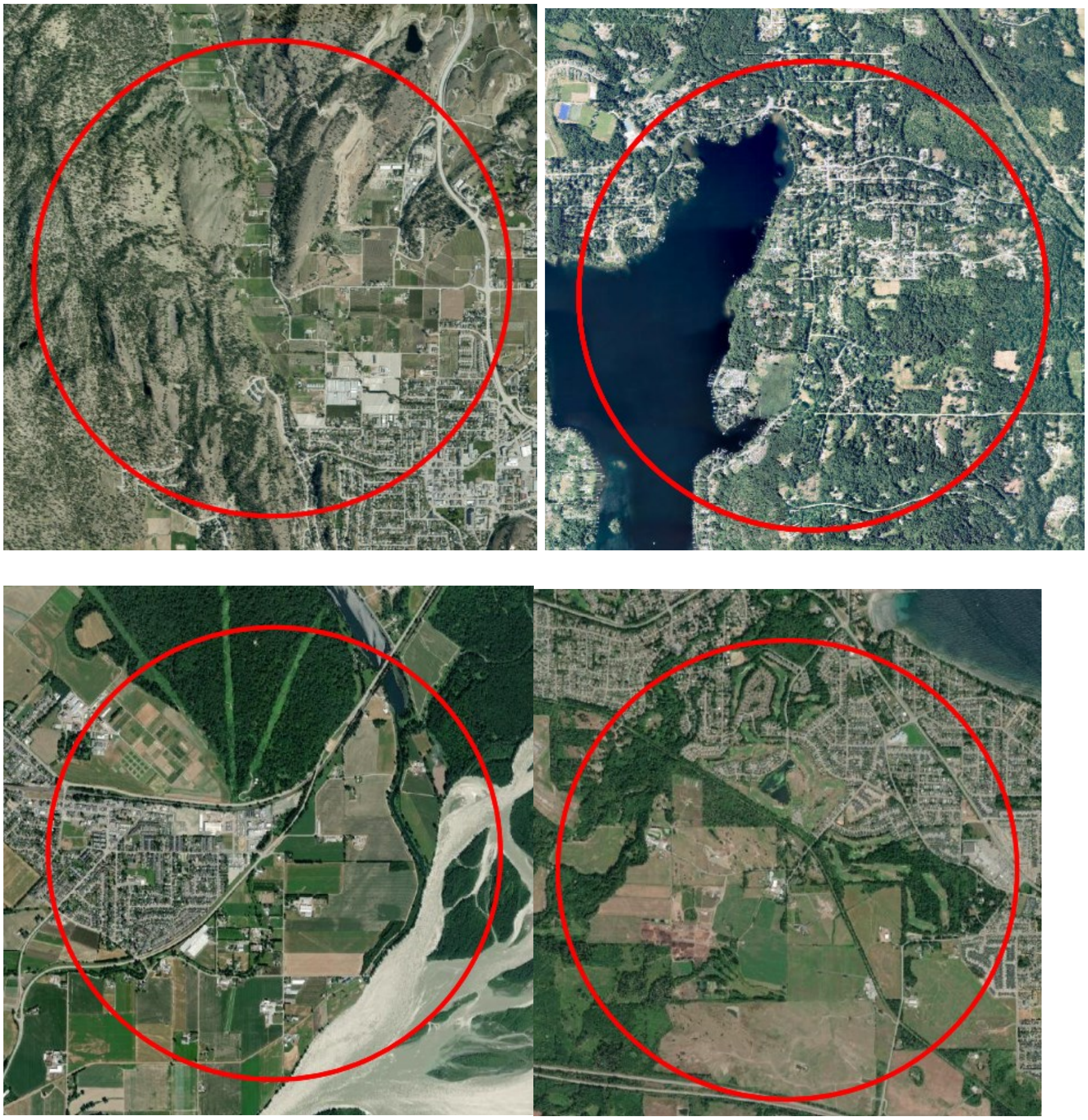


Figure S4.12. Examples of survey points with between 25% and 30% urban landcover within a 1600-meter buffer

Appendix D. Supplemental tables for Chapter 5

Table S5.1. Number of recordings in each sun angle increment in each region for temporal habitat use analyses

(A) Evening

	30° to 24°	**24° to 18°**	**18° to 12°**	**12° to 6°**	**6° to 0°**	**0° to -6°**	**-6° to -12°**	**<-12°**
Grassland	150	149	146	158	170	177	180	296
Boreal on dates with astronomical twilight	2	29	9	43	44	62	76	54
Boreal on dates without astronomical twilight	NS	NS	194	215	321	332	350	DNO

(B) Morning

	<-12°	**-12° to -6°**	**-6° to 0°**	**0° to 6°**	**6° to 12°**	**12° to 18°**	**18° to 24°**	**24° to 30°**
Grassland	277	179	177	171	165	162	172	172
Boreal on dates with astronomical twilight	53	73	72	57	49	54	NS	NS
Boreal on dates without astronomical twilight	DNO	351	341	324	331	301	NS	NS

We randomly selected 6 recordings in each 6° sun angle increment from each location. In this table, we combined the sun angle bins -12° to -18° and <-18° in the Grasslands region. "NS" indicates that the sun angle increment was not sampled in that region, and "DNA" indicates that those sun angles did not occur in that region. Panel (A) shows the evening sun angles from earliest to latest (highest to lowest) and (B) shows the morning sun angles from earliest to latest (lowest to highest).

Table S5.2 Comparisons of vocal activity during each twilight period at stations with and without artificial light

(A) Grassland region

	Estimate	**SE**	**z-ratio**	**p-value (Sidak)**	**p-value (Bonferroni)**
Evening civil	-0.424	0.574	-0.739	0.4597	0.9195
Evening nautical	-0.687	0.638	-1.076	0.2819	0.5638
Astronomical	-0.946	1.110	-0.852	0.3942	0.7884
Morning nautical	-0.368	0.583	-0.632	0.5277	1.0000
Morning civil	0.388	0.623	0.622	0.5338	1.0000

(B) Boreal region on dates with astronomical twilight

	Estimate	SE	z-ratio	p-value (Sidak)	p-value (Bonferroni)
Evening civil	0.694	0.845	0.822	0.4113	0.8225
Evening nautical	-1.039	1.049	-0.990	0.3222	0.6444
Astronomical	-0.388	1.387	-0.280	0.7796	1.0000
Morning nautical	0.718	0.775	0.926	0.3542	0.7085
Morning civil	-0.433	1.381	-0.313	0.7540	1.0000

C) Boreal region on dates without astronomical twilight

	Estimate	SE	z-ratio	p-value (Sidak)	p-value (Bonferroni)
Evening civil	0.975	0.420	2.322	0.0202	0.0404
Evening nautical	0.631	0.454	1.390	0.1645	0.329
Morning nautical	0.652	0.426	1.531	0.1258	0.2516
Morning civil	1.010	0.544	1.855	0.0636	0.1271

(D) Boreal region on dates without astronomical twilight, with occupancy predictions included in model

	Estimate	SE	z-ratio	p-value (Sidak)	p-value (Bonferroni)
Evening civil	0.555	0.433	1.284	0.1991	0.3982
Evening nautical	0.202	0.477	0.423	0.6722	1.0000
Morning nautical	0.568	0.447	1.270	0.2039	0.4078
Morning civil	0.764	0.447	1.236	0.2166	0.4333

We used a binomial GLMMs with a random effect for station and used post-hoc comparisons for light and dark stations during each twilight period. The estimate represents the estimate difference in the odds ratio between light and dark stations, and the p-value was calculated using a Sidak and Bonferroni correction for multiple comparisons.

Table S5.3 Likelihood ratio test model comparisons for binomial generalised linear models of vocal activity across twilight periods that included twilight, light, and their interaction

	Null model	**Full model**	**Chi-squared value**	**p-value**
Grasslands	twilight	Light + twilight	0.588	0.4432
	Light + twilight	Light + twilight + light*twilight	3.0345	0.5521
Boreal with astronomical twilight	twilight	Light + twilight	0.1774	0.0674
	Light + twilight	Light + twilight + light*twilight	1.2602	0.7386
Boreal without astronomical twilight	twilight	Light + twilight	4.6515	0.03103
	Light + twilight	Light + twilight + light*twilight	1.2602	0.7386
	Twilight + occupancy predictions	Light + twilight + occupancy predictions	1.8404	0.1749
	Light + twilight + occupancy predictions	Light + twilight + light*twilight + occupancy predictions	1.1187	0.7726

Table S5.4 Coefficient estimates and correlation for spatial habitat use model in the Boreal region that included latitude in interaction with artificial light

	Territorial	**Extra-territorial**
Artificial light coefficient	-0.31(-0.98, 0.10)	0.12(-0.11, 0.36)
Latitude*Artificial light coefficient	0.62(-0.47,2.33)	-0.18(-0.78, 0.30)
Pearson's correlation coefficient	-0.87	0.86
p-value for Pearson's correlation coefficient	< 0.0001	<0.0001

Results from a quasi-binomial generalised linear model of intensity of habitat use including main effects for artificial light and latitude and an interaction term. Latitude was scaled to mean 0 and standard deviation 1. The rows for coefficients show the mean and 95% confidence intervals from 10,000 bootstrap iterations. The Pearson's correlation coefficient and associated p-value show the correlation across bootstrap samples between coefficient estimates for artificial light and its interaction term with latitude.

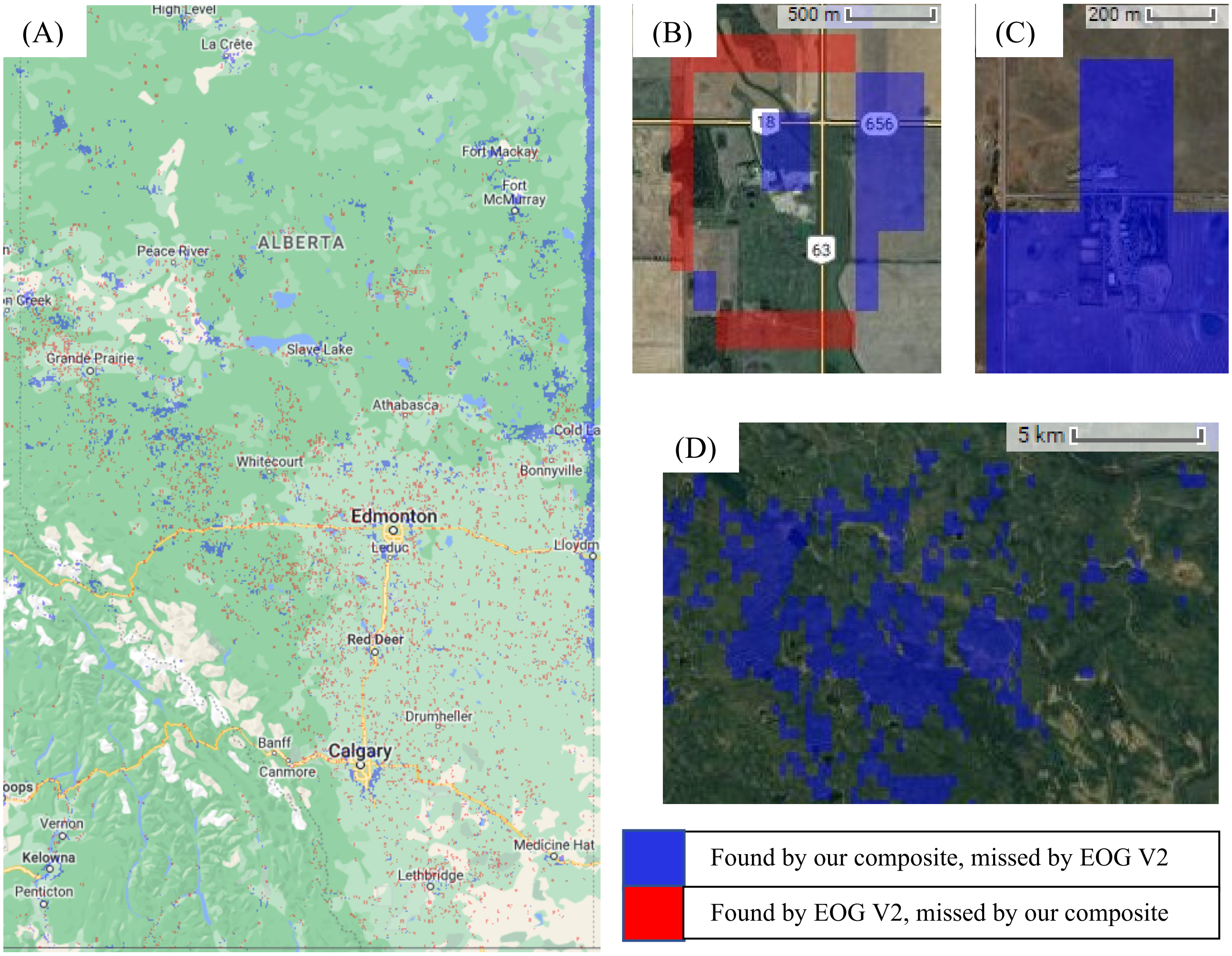


Figure S5.1 Comparison of my artificial light estimates to the Earth Observations Group's annual composite in 2015

A) A comparison of our annual composite to the Earth Observation Group's annual composite VNL V2 in 2015 for the province of Alberta.
B) Many of the differences between these composites occurred on the edges of illuminated areas, where the two composites likely assigned the same light sources to different, adjacent pixels.
C) In other cases, our correction detected isolated light sources that were missed by EOG V2.
D) In the northern region, our composite produced positive radiance estimates where there was likely no artificial light. These detections likely represent residual aurora that was not removed by our aurora correction procedure. To ensure that these cases did not influence the outcome of our analyses, we examined every ARU station where positive radiance was detected to confirm that there was a plausible light source using Esri WorldImagery. Only one ARU station, occurring in the Boreal region, had a positive radiance value where no light source was apparent.

Sources for Esri World Imagery (basemap for B – D): Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community
Sources for Esri NatGeo World Map (basemap for C): Sources: National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC